Eur J Wildl Res
DOI 10.1007/s10344-013-0791-y

ORIGINAL PAPER

Predator–prey relationships in a middle Asian Montane steppe: Persian leopard versus urial wild sheep in Northeastern Iran

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Received: 22 April 2013 / Revised: 10 October 2013 / Accepted: 16 December 2013

Abstract Management controversies arise when both of the prey and predator in an ecosystem are species of conservation concern. We investigated trophic interactions between the endangered Persian leopard (*Panthera pardus saxicolor*) and a declining mountain ungulate, urial wild sheep (*Ovis vignei*), on a high-altitude steppe of Iran. During two consecutive photo-trapping seasons of 1,300 nights in total, a minimum population of four adult leopards (one female and three males) was documented. Scat analysis indicated that urial wild sheep was the staple of the leopard diet with 48.44 % of total biomass consumed. Remains of domestic livestock in leopard scats were negligible yet alarming (14.53 % biomass consumed), followed by wild pigs (8.13 %) and wild goat (1.26 %). Financial costs of leopard depredation to livestock breeders during our study period were comparatively lower than livestock–leopard conflict hotspots across Iran. Using distance sampling, urial density was 15.8 individuals km^{-2} (±SE 6.2), and a total biomass of 47,621.5 kg for wild ungulates in the study area was estimated. We estimated that the annual removal rate of urial by leopards during our study period was 9.4 % of the total urial population. We suggest that continuous monitoring of the leopard and prey populations to assess predation impact should be considered, particularly in areas where a single species comprises a remarkable proportion of the leopard diet. In the meantime, assessing probable conflicts with local communities is recommended as a parallel management action to ensure long-term human–leopard coexistence. Our findings will aid wildlife managers in prey-depleted arid environments of western Asia to identify susceptible wild prey populations to predation by large carnivores; hence, significantly contribute in development and implementation of effective conservation measures to mitigate management conflicts.

Keywords Persian leopard · *Panthera pardus saxicolor* · Feeding ecology · Distance sampling · Camera trap · Predation impact · Urial wild sheep · Iran

Introduction

Facilitated by their highly adaptable hunting behaviour (Bothma and Le Riche 1984; Bertram 1999), leopards *Panthera pardus* have the broadest diet of larger felids (Goyal et al. 2000; Mills and Harvey 2001; Sunquist and Sunquist 2002). Though medium-sized herbivores within a weight range of 10–40 kg are preferred (Hayward et al. 2006), the leopard diet appears to track relative densities of wild ungulates, with the most abundant species as the main prey (Sunquist and Sunquist 2002). Despite the wealth of information available on the predatory behaviour of leopards (e.g. Schaller 1972; Bothma and Le Riche 1984; Johnsingh 1992; Johnson et al. 1993; Karanth and Sunquist 1995; Miquelle et al. 1996; Bailey 1993; Henschel et al. 2005); surprisingly, little is known about their feeding habits and prey selection in high-altitude ecosystems (Rödel et al. 2004; Odden and Wegge 2009). Large mammalian communities found in these fragile environments are prone to management controversy when both the prey and predators are species of conservation concern (Rominger et al. 2004; Lovari et al. 2009). Additionally, low productivity and human-induced changes

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Communicated by C. Gortázar

Electronic supplementary material The online version of this article (doi:10.1007/s10344-013-0791-y) contains supplementary material, which is available to authorized users.

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can indirectly promote single-prey food webs and, locally, unsustainable predation (Festa-Bianchet et al. 2006; DeCesare et al. 2010). Effective management of predator–prey systems requires robust estimates of their demographic status and predation patterns, such as prey composition and predation impact. But obtaining such data for mountain ungulates and secretive carnivores that occur at low densities is difficult (Lovari et al. 2009; Wingard et al. 2011).

The endangered Persian leopard *Panthera pardus saxicolor* ranges over remote mountains and rugged foothills of West and Central Asia (Gavashelishvili and Lukarevskiy 2008). Experts estimate that its current population size does not exceed 1,300 individuals, of which around two thirds occur in Iran (Kiabi et al. 2002; Khorozyan 2008). However, human-caused mortality has become a major concern in recent years and paired with habitat fragmentation and prey loss, threatens Persian leopard populations across almost their entire range (Kiabi et al. 2002; Ziaie 2008; Breitenmoser et al. 2010). Yet, the lack of scientific-based estimates of leopard population size and records of interactions with their main prey make it difficult to develop a country-wide assessment of their status and conservation needs.

The present paper aims to explore predator–prey relationships in one of the main strongholds of the Persian leopard in northeastern Iran; Sarigol National Park (SNP). The vulnerable urial wild sheep (*Ovis vignei*; hereafter urial) is thought to be one of the leopard main prey in this region (Kiabi et al. 2002), where this ungulate is threatened by poaching, habitat loss, and competition with livestock (Ziaie 2008; Valdez 2008). These small and isolated ungulate populations are susceptible to predation by large carnivores, which sometimes shape their main cause of mortality (Rominger et al. 2004; Festa-Bianchet et al. 2006; Lovari et al. 2009; Wegge et al. 2012). On such human-disturbed landscapes, depletion of the wild prey base and availability of domestic ungulates is likely to fuel livestock depredation, leading to human–leopard conflicts (Edgaonkar 2008; Martins et al. 2011). Thus, it is vital to assess both the extent of leopard–urial interactions and relative importance of domestic stock in the leopard diet for future management implications. Our objectives in this study were to: (1) explore population status of the leopard and its ungulate prey in a well-protected reserve; (2) determine the dietary composition of the leopard and extent of livestock depredation; and (3) illustrate prey removal rates by the leopard where a single dominant prey, urial, exist. Results of this study can help us to recognize whether more than four decades of official protection of both the prey and predator species by the Iran Department of the Environment (DoE) has been effective at securing prey base for the leopards. Furthermore, since parts of the leopard's range in Iran are subject to ungulate trophy hunting, knowledge of its predation patterns is vital for a better management of this endangered system.

Study area

With an area of 70.4 km^2, SNP is located some 20 km east of the city of Esfarayen, North Khorasan Province (36° 55′ to 37° 02′ N and 57° 41–47′ E). As part of larger Sarigol Protected Area, this site has received protection measures since 1973, and promoted to National Park status in 2002. SNP is mainly composed of hilly terrain developing into high rolling mountains, ranging from 1,400 to 2,940 m, with four main valleys laid in a south-north direction. A mean annual temperature of 14 °C and mean annual precipitation of 273 mm give the region a temperate semi-arid climate (Darvishsefat 2006). The vegetation is generally dominated by *Astragalus* spp. and *Artemisia sieberi*, forming a bush-steppe habitat in most of the area, with pockets of juniper *Juniperus* spp., barberry *Berberis* spp., and willow *Salix alba* (Bijani 1997). Potential ungulate prey in the leopard diet includes urial, Persian wild goat *Capra aegagrus*, and Eurasian wild pig *Sus scrofa.* SNP also supports diverse range of carnivores, including gray wolf *Canis lupus*, striped hyena *Hyaena hyaena*, wild cat *Felis silvestris*, and Pallas' cat *Otocolobus manul* (Bijani 1997). Livestock grazing is not permitted in SNP. Nonetheless, a number of nomadic pastoralists graze the neighboring protected area (i.e., outside SNP) during summer (May–August) each year, and local residents in surrounding villages keep domestic animals, mainly sheep *Ovis aries* and goat *Capra aegagrus hircus.*

Materials and methods

Ungulate density and biomass

Ungulate surveys were conducted across SNP in order to estimate ungulate abundance using a distance sampling method as described by Buckland et al. (2001). As the encounter rate with wild goats and wild pigs was extremely low (see Results), we designed and analyzed our distance sampling survey for urials only. During the urial's rutting season in autumn 2007, a time when they are the most active, four transects varying in length between 3 and 10 km were laid in the study area to cover various parts of the park. The total transect length of 24 km was monitored four times by teams of at least two experienced people between 06.00 and 11.00. During a given transect, the time, location, sex/age structure (using 12×42 binoculars) of all urial sightings were recorded. Furthermore, distance to the group (visually estimated), and angle to the transect line were recorded, so as to compute the perpendicular distance for each observation. Through the fitting of a detection function to the distance data, an estimate of density is possible (Buckland et al. 2001).

Data were analyzed using the software DISTANCE (version 5.0, release 2; Thomas et al. 2006) after truncation and grouping, as recommended in Buckland et al. (2001). In order to fit alternative models (key function+adjustment terms) for the detection function curve, various models were tested (for detailed description see Buckland et al. 2001). The estimator used to compute density estimated was chosen based on the least Akaike Information Criterion value (AIC; Burnham and Anderson 1998). Accordingly, the most parsimonious model was used to derive an estimate of urial population size based on our 70.4-km^2 study area. The precision of the resulting estimate was assessed by the 95 % confidence intervals.

To get reliable information about the urial population structure in order to calculate the biomass, we improved the accuracy of urial detection at sex/age level using images taken by digital zoom camera EOS 300 Canon equipped with a lens 70–300 mm. For better identification of age/classes based on size and shape of horn (Ziaie 2008), urial images were analyzed using the zoom function on computer and thus the proportion of individual within each sex/age class category was calculated. Since our estimation of the urial abundance was in accordance with the Iran DoE's annual total count (see Results), we used the DoE data of wild goat and pig numbers to calculate the species biomass in the study area using each species average live weight from literature.

Leopard demography

We carried out a reconnaissance survey for a period of 18 months (March 2005–October 2006) to identify optimal camera trap locations within the study area. The main trails and animal travel routes were searched regularly to define three types of camera trap locations based on presence of leopard scats and scrapes (excellent points), pugmarks (good points), and signs of other carnivores (weak points). A total of 25 potential camera trap sites were identified, which were then monitored opportunistically using camera traps to test if the sites were appropriate for maximizing leopard photo-captures, to examine the points' security against thieves, and to check battery life.

In winter seasons of 2006/2007 and 2007/2008, we carried out our leopard population survey in a total of 16 and 12 selected sites, consecutively (mostly excellent points). One DeerCam camera (DC-200 model, Park Falls, WI) was used at each station so to capture only one flank of the leopard in each photograph. We placed cameras approximately 2–4 m apart across the trails or sign sites, generally faced in a northly direction to avoid false trigger by the sun. We programmed the cameras with a 15–30-s delay, and each independent photograph/event was defined following O'Brien et al. (2003). Spatial configuration of camera traps approached an approximate systematic coverage of the study area. The average distance between camera locations was 1.5 km to ensure that there were no major gaps in the sampled area (Balme et al. 2009a). Using leopard rosette pattern as a unique identifier, we created photo-capture histories and unidentifiable individuals were excluded from the analyses.

Diet composition and prey selection

During April 2005 to March 2007, we collected leopard scats primarily along the four main valleys of different habitat types in SNP to ensure that the sampling area can be considered representative for the park. To minimize the chance of misidentification with those of sympatric large carnivores' (i.e. wolf, hyena), we followed a conservative sampling criteria and only unambiguous scats with characteristic shape (cat-like segmentation and pointed ends) and ≥25 mm in diameter defecated at leopard scrapes (Sunquist and Sunquist 2002) were collected. We omitted from our analyses scats of which the identity of the predator was uncertain, particularly from southern lowland areas where wolves had been occasionally photo-captured.

All scats were individually stored in plastic bags and later analyzed using techniques standardized by Mukherjee et al. (1994). In brief, samples were washed in running water through a fine-mesh sieve to remove surface oil and to separate the hair from other undigested organic matter. Afterward, all remains were air-dried for further analyses. To create slides for mammalian species identification, hairs were selected randomly from each sample (20 hairs/sample), placed parallel on the slide, and mounted with cover slip using DPX mount. Five slides were made per scat sample and examined at 400X using a Leica microscope. Hairs were identified using a reference collection compiled by Sepasi and Falahatkar (2006). Rodents were also detected based on their bones and skulls, while feather and scale were useful to record birds and reptiles respectively.

For statistical quantification, we determined frequency of occurrence (FO: percentage of total scats in which a food item was found) and percentage of occurrence (PO: number of times a specific food item was found as a percentage of all food items found) (Ackerman et al. 1984). Using FO may exaggerate the importance of smaller-sized prey in a predator's diet, since the consumption of small prey generally produces more indigestible matter in scats, but represents less biomass consumed (Ackerman et al. 1984). To correct for this bias, relative frequencies of prey were converted to a relative estimate of biomass consumed (Corbett 1989; Hayward et al. 2006; Edgaonkar 2008). Biomass calculation models are ecologically the most relevant and have already been used in various studies for the estimation of prey consumption by leopards (e.g. Karanth and Sunquist 1995; Henschel et al. 2005; Wegge et al. 2009; Martins et al. 2011). Thus, we used the model developed by Ackerman et al. (1984) for cougars *Puma concolor*, based on the assumption that these large felids have body size and digestive system similar to leopards

(Karanth and Sunquist 1995). The regression equation used is: $Y=0.035X+1.980$, where Y is the biomass consumed per scat and X is the total live prey weight. The correction factor is not applied for small prey species with <2 kg body weight, because each occurrence is assumed to represent a whole individual (Ackerman et al. 1984).

We obtained the average body masses of each food item from the literature (urial: Valdez et al. 1977; domestic sheep: Moghadam 1993; wild pig: Goshtasb 2001; *Hystrix indica*: Sever and Mendelssohn 1991) and unpublished body measurements carried out by Iranian experts in reserves adjacent to our study area. For wild pigs, we used mean annual census data to estimate the biomass per square kilometre using 3/4 of adult female body mass following Schaller (1972) to account for sub-adults and young which are preferentially selected by leopards (Hayward et al. 2006).

Predation pattern

We investigated predation pattern of leopards in the study area by estimating annual removal rate of each ungulate species. Assuming that predation is randomly distributed among sex/age groups, this was defined as percentage of biomass of each ungulate species consumed divided by the ungulate total biomass available to leopards in SNP. To this aim, we used: the minimum population size of leopards derived from the two sampling years, the ungulate abundance, the leopard diet composition, and the predator consumption rate (Wegge et al. 2009). The leopard age/sex structure was considered stable through the sampling years, thus the consumption rate was calculated based on the food requirements of three males and one single female (see Results). First, we used information on the food consumption rate of Asian leopards from Odden and Wegge (2009), equivalent to: males=4.3 and single females=3.3 kg/day. An alternative approach is to calculate the average daily meat requirements of different sexes based on live weight of leopards (see Stander et al. 1997). Nevertheless, using average weights of 67.4 kg (n=18) for males and 35.0 kg (n=1) for the female Iranian leopards (Farhadinia 2010) these approaches both produce identical estimates. Meanwhile, we considered 70 % consumption of >20 kg-prey in our model of biomass consumption and total biomass of ungulate prey (determined as population size of each species multiplied by the mean live weight; Table 1), as suggested by Stander et al. (1997). For calculating total biomass of each ungulate prey annually killed by leopards, the relative biomass of each prey consumed (specified in the scat analyses) was multiplied to annual food consumption of all the leopards. This was divided to the total biomass of each species to obtain annual prey removal by leopards. Annual economic loss of livestock due to leopard depredation was estimated as the mean domestic sheep biomass consumed, considering each kg of meat equal to USD 6.3 (1 USD=9,350 Iran Rials) in 2007.

Table 1 Total ungulates biomass (in kilogramme), categorized by age and sex class in Sarigol National Park (70.4 km^2), northeastern Iran

	Total count (percentage)	Average live body weight (kg)[a]	Biomass (kg)
Total urial population	1,111		44,219
Adult ram (>4 years)	144 (13.0)	57.5	8,280
Young ram (1 <≤4 years)	89 (8.0)	49	4,361
Ewe	767 (69.0)	39	29,913
Lamb	111 (10.0)	15	1,665
Total wild goat population	25	36.0	900
Total wild pig population	35	71.5[b]	2502.5
Total biomass			47,621.5

[a] Weights of urial and wild goat have been calculated based on available literature (Valdez et al. 1977) and various unpublished weight measurements of different age/sex groups

[b] Mean body mass was obtained from 41 adult wild pigs of both sexes in Golestan National Park, northeastern Iran (x=95.3 kg, Goshtasb 2001) multiplied by 3/4 following Schaller (1972) to account for sub-adults and young

Results

Ungulate density and biomass

Histograms of perpendicular sighting distances indicates that a large proportion of urials were detected within close distance of the transect line, and that detection fell rapidly with distance. It also exhibited a slight shoulder after the first distance interval, illustrating evasive movement of urials prior to detection. Most of the tested models had very similar AIC values. Therefore, we selected model 'half-normal' with adjustment function cosines comparing to other models, because it is known to perform well with data showing a markedly fall in detection (Buckland et al. 2001). Detection probability was 7.1 with ESW of 255.4 m. The estimated density of urials was calculated (±SE) as 15.78±6.20 (CI 95 % 7.36–33.82) individuals/km^2. The population size was estimated to be 1,111.0 (±SE 436.7) (CI 95 % 519.0–2381.0).

The detection probability remained high (above 80 %) up to a distance of 150 m from the transect line, suggesting that there was movement of urials away from the line. Furthermore, the 0 distance fitting was not particularly good and the detection probability plot peaked in 100–150 m. Together with minimum numbers of wild pig and wild goat derived from DoE's total counts, a total biomass of 47,621.5 kg for wild ungulates in the national park was estimated (Table 1).

Leopard demography

Despite, we initially designed this camera-trapping survey to estimate abundance of SNP leopards via a conventional capture–recapture framework (Karanth and Nichols 1998) because of extremely low recaptures and our prolonged trapping period we suspected that some of underlying assumptions of the capture–recapture theory might be flawed. We therefore calculated the total number of identified leopards in both trapping seasons as minimum population size of leopards in SNP.

During two consecutive trapping seasons of 90 days for each winter season, 35 images of leopards were obtained in 32 independent captures (16.4 % of total photo-captures) in 1,300 trap nights (Table 2). In both years, we used only right flank captures of the leopard as we had more captures (21 right vs. 11 left flank photographs in total). During the first capture season (winter 2006/2007), 21 images of leopards in 18 captures corresponding to one adult male, one adult female and one individual of non-identified gender (assumed to be an adult male due to his large and thick body features; Balme et al. 2012) were obtained (13 right vs. 4 left captures) whereas one of the left-flank captures was excluded from analysis due to its low quality. In the second capture season (winter 2007/2008), 14 images in 14 captures corresponding to one adult female and three adult males were obtained (eight right vs. six left captures). Three males captured by their right flank, while there was an adult female captured on her left flank. Therefore, we included this female leopard in the analysis, resulting in four identified individuals (i.e., three male: one female). One male and one female leopard were photo-captured in both years.

Diet composition, prey selection and predation pattern

A total of 157 scats were gathered over course of the survey period. Twenty-eight of these samples did not meet our sampling criteria and were discarded from the laboratory procedure. Thus we analyzed a total 129 leopard scats (Table 3), which is considered to be more than necessary scat number for proper diet analysis (Trites and Joy 2005). The scats contained 161 different food items, yielding an average of 1.25 prey items per scat for the entire survey period. The majority of prey items were identified to species level, whilst birds and rodents were identified to the taxon level. Only 3 % of prey items could not be identified. The leopard scats contained 12 different species (assuming that all bird and rodent remains belonged to single species), and diet was dominated by medium-sized ungulates (Table 3). Eighty-eight percent of leopard scats contained single prey species and 12 % contained two prey species. No scat had remains of more than two prey species.

Excluding non-food items and non-nutritive plant materials, 59 % of total food items were medium-sized mammals. A highly significant difference was seen among medium-sized preys ($x^2=141.00$, $df=3$, $p<0.001$). 79.7 % of medium-sized mammals comprised wild ungulates (Table 3), while the rest represented domestic ungulates ($x^2=64.45$, $df=1$, $p<0.001$). As the dominant ungulate in SNP, urial wild sheep scored the highest FO in the entire survey period (Table 3). Leopard hair was identified in two scats in negligible volumes, presumably due to hair ingestion while grooming.

In terms of relative biomass consumed, urial was the single most important prey species for leopards in the study area, making up 49.2 % of the total biomass consumed. Domestic animals comprised 14.8 % of biomass consumed, followed by wild pig (8.3 %). The most important prey taxa for leopards in SNP were wild ungulates, making up 58.8 % of the biomass consumed. Another important prey was Pika (*Ochotona rufescens*) with constituting almost 24.0 % of the total biomass consumed by leopards; however, this prey item was mainly detected during 2005.

Applying data from Odden and Wegge (2009), the SNP leopard population of three males and one single female have a combined daily food consumption of 16.2 kg of meat for all four individuals during the study period. Consequently, the removal rate of urials by leopards by the quantification method described above was revealed to be approximately 9.4 %. This prediction is slightly higher for wild goat (12.0 %), but appears more intensive on the wild pig population in SNP (27.9 %). Furthermore, our data shows annual livestock depredation rate of 872.8 kg by leopards in SNP (c. 36

Table 2 Results from camera trapping of leopards conducted in the winters of 2006/2007 and 2007/2008 in Sarigol National Park

	Winter 2006/2007	Winter 2007/2008
No. of trap stations	16	12
No. of trap nights	770	530
No. of wildlife images	110	103
No. independent wildlife captures	88	87
No. of leopard photographs	21	14
No. independent leopard captures	18	14
No. leopard photos/100 trap nights	2.3	2.6
No. of different leopards (male/female/unknown sex)	3 (1/1/1)	4 (3/1)

Table 3 Frequency of prey items of the leopard based on scat analysis in Sarigol National Park, 2005–2006

Food item	Total			Assumed weight of prey (kg)	Ingested biomass per scat (kg/scat)	Corrected No of prey without multiple preys	Corrected FO	% biomass consumed
	N	FO (%)	PO (%)					
Large-sized food items								
Domestic horse	1	1	1					
Medium-sized food items								
Urial wild sheep	64	50	40	34	3.2	59	0.46	49.23
Wild goat	2	2	1	36	3.2	1.5	0.01	1.28
Wild pig	9	7	6	71.5	4.5	7	0.05	8.26
Livestock	20	16	12	35	3.2	17.5	0.14	14.76
Small-sized food items								
Common fox	4	3	2	5	2.1	3.5	0.03	1.90
Hare	1	1	1	2.5	2.0	0.5	0.00	0.26
Afghan pika	38	29	24	0.5	2.6	35	0.27	24.04
Indian porcupine	1	1	1	18	2.0	0.5	0.00	0.26
Rodents	9	7	6					
Birds	6	5	4					
Reptiles	1	1	1					
Unknown	5	4	3					
Non-food items								
Stone	6							
Plant material	24							
No. of food items	161							
No. of scats	129							
No. of food items/scat	1.25							

individuals by considering 70 % consumption of 35-kg domestic livestock; Table 3). This equals a total loss of USD c. 5,500 to local stock breeders in 2007.

Discussion

Prey density and composition

Average density derived from distance sampling method was disappointing in terms of presenting a useful tool for monitoring population trends precisely across years. As an indicator of precision, coefficient of variation (CV) showed high values in this study (39.4 %) which is a result of low numbers of detections. Burnham et al. (1980) suggested that sample sizes of ≥40 sighted objects would be adequate for line transect surveys. In contrast, estimation based on less than 60–80 detections are not considered robust by some other authors (Karanth and Nichols 2002). Most of critical assumptions of distance sampling could be met when applying it to mountainous areas (Perez et al. 2002; Wingard et al. 2011), except the 0 distance fitting, suggesting more concentration of observers on two sides of the transect line. Additionally, reliability of wild pig and wild goat abundance data used in our calculations might be controversial as we relied on absolute counts derived from Iran DoE's annual counts with unknown variances and uncertainties associated with them. Yet, we found these censuses in consistent with our independent urial abundance estimation and field observations. Further research is needed to assess reliability of data derived from the annual ungulate censuses on different landscapes and calibrate them accordingly.

Leopard demography

Our study area is quite small and barely encompasses the home range of several identified leopards, according to available home range size estimates (Stander et al. 1997; Marker and Dickman 2005), particularly if we refer to large home range of the Persian leopard in Iran (H. Jowkar et al. unpublished report). However, Iranian leopard populations are normally small even within national parks (Ghoddousi et al. 2010). Male leopards were captured more frequently than females which can be due to the greater distances they cover daily compared to females (Bailey 1993) and more likely usage of roads to patrol their areas (Balme et al. 2009a), along which most (84 %) camera-trap stations were situated. Our study period in both years overlapped with the Persian leopard mating season, as inferred from the animal's behaviour in the photos such as forming mate pair, increased urinating and sniffing by both sexes (Farhadinia et al. 2009), which coincides with higher activities of males. On the other hand, due to coincidence of depletion of prey base outside SNP and winter aggregation of most urials inside SNP where it encompasses lower altitudes with less snow, more male leopards are expected to share a proportion of their home range inside the small national park. Additionally, prior to our camera-trap survey an adult male leopard was poached in August 2006 inside the national park. The possible home-range vacancy produced as a result of this poaching could play a major role in the highly skewed sex ratio of photographed leopards toward males (Balme et al. 2009b). Hence, we believe that the minimum population size of leopards derived from our survey is close to actual population of the predator in SNP during the study period.

Feeding ecology, predation pattern, and livestock depredation

The present study reveals that urial, followed by livestock, were the most frequently prey taken by leopards in our study site, as expected given they fit within the leopard's preferred weight range whereas Suidae are normally avoided (Hayward et al. 2006). Afghan pika was also frequently consumed, reflecting heavy dependence of leopards on locally abundant small prey in difficult times when ungulate populations are scarce (Bothma and Le Riche 1984; Henschel et al. 2005; Hayward et al. 2006). We showed that the leopard in SNP selectively prey on medium-sized ungulates. Though the leopard's reliance on urials seems to be mainly affected by availability of this prey species (Sunquist and Sunquist 2002), scarcer wild goats and wild pigs were not avoided. The latter ungulates occurred to a much lesser extent in the leopard diet in our study area, but patterns of predation on them were remarkably higher than that on the regularly-taken urial. Thus, one might assume that limiting the impact of the leopard predation would have been more beneficial for the more vulnerable ungulate populations. Wegge et al. (2009) have shown that for prey species with annual removal levels of less than 15 %, ungulates can still maintain an increasing growth rate, given that habitat quality is also improved. Similar to the findings of Wegge et al. (2012) on predation pattern of snow leopards *P. uncia*, an estimated annual loss of 17.7 % of total prey population attributed to Persian leopards in SNP will be close to the balancing recruitment rate of wild ungulates. While overall predation rate seems to be in part reasonable for the current prey population size in SNP, but it can produce a variety of different demographic effects, as a consequence of different selection of prey age classes, and of the seasonal variation in their predation pressure (Gervasi et al. 2012). Despite high percentage of ewes in SNP urial population, we found only 10.0 % of this population were lambs. This can be due to predation by large predators (Lovari et al. 2009; Wegge et al. 2012). Earlier works on multi-prey ecosystems have found that the predator staple prey might regulate the predation impact on smaller prey populations (e.g. Jedrzejewski et al. 2000). Wegge et al. (2009) found the same pattern in Nepal, albeit environmental factors and habitat quality is suggested to contribute in level of susceptibly in lower density prey populations. Although knowledge of urial fecundity and population trend (two main components explaining impact of predation) in our study area is lacking, given the current pattern of predation, we believe that, at least, in short term, it is unlikely that the SNP urial population will be limited by leopard predation.

Studies in Africa have suggested that in ecosystems with fluctuating resource availability, livestock form an important secondary prey to large predators, although they appear to balance the trade-off between stock raiding and the risks associated with it (Valeix et al. 2012). FO of livestock remains in the diet of SNP leopards was not much different from the <15 % range in other investigated populations across the Asian range (Sathyakumar 1992; Johnson et al. 1993; Ramakrishnan et al. 1999; Maheshwari 2006; Edgaonkar 2008; Aryal and Kreigenhofer 2009; Ramesh et al. 2009). Martins et al. (2011) concluded that a proportional biomass contribution of 23.7 % for domestic goats in leopard diet was an indicator of human–leopard conflict in Cape, South Africa. This is almost twice as high as in our study area (14.53 % biomass consumed), but lower than in the Alborz area of northern Iran (>30 %; Sharbafi et al. in prep) where there is an intensive human–leopard conflict (Farhadinia et al. 2007). We therefore conclude that during our study period frequency of livestock depredation by leopards was not remarkable in SNP. Our opportunistic inquiries with local people and nomadic pastoralists in the study area also supported this, since no local efforts to eradicate leopards due to conflict have occurred during the past decade. With respect to livestock availability to the leopards (year round in surrounding villages and nomads during summers in the adjacent protected area), communities' annual loss to leopards does not appear to be sufficiently severe to elicit a serious conflict situation.

Management Implications

Continuous monitoring to obtain detailed knowledge of prey–predator dynamics is critical in wildlife management, particularly for small and isolated populations (Enk et al. 2001; Lovari et al. 2009). Thus, establishing reliable estimates of population abundance and density of leopards (e.g. via capture–recapture framework) across the entire Sarigol Complex must be an ongoing focus of research. In addition, given the leopard population relies mainly on a single prey species (urial) in SNP, continued monitoring of the ungulate population dynamics is necessary. Therefore, besides the annual total count conducted by the Iran DoE (twice a year), reproductive parameters must be recorded (at least during the census programs) because the predators can affect the prey population growth through removing the kid cohort (Lovari et al. 2009).

Different kinds of data we obtained indicate that there is no remarkable leopard–human conflict due to depredation on livestock, at least in close proximity to our study area. However, cautious recording and monitoring of occasional cases of livestock attack by predators, particularly leopards, is highly recommended and may be helpful when introducing necessary schemes in case of an emerging problem. Finally, we strongly recommend to the Iran DoE to manage trophy hunting permissions for mountainous ungulates in such a single prey ecosystem as detected in SNP, because the adult/old rams targeted are also regularly taken prey for the leopards.

The knowledge of leopard-prey interactions on mountainous landscapes remains limited in many areas, and further research is needed to understand the complex demographic and dynamic consequences of predation on small and endangered prey populations (Festa-Bianchet et al. 2006). The majority of previous studies report the impact of leopard predation on local prey populations in the presence of higher hierarchical sympatric carnivores (e.g. African lions *Panthera leo*: Funston et al. 2013; tiger *Panthera tigris*: Karanth and Sunquist 1995; Wegge et al. 2009). Our study in SNP provides a baseline to support future more rigorous research on feeding ecology of leopards, not only in this region, but also in landscapes where leopards are the dominant predator.

Acknowledgements We are grateful to North Khorasan Provincial Office of Department of the Environment (DoE) for supporting field surveys. We are also indebted to the Conservation Leadership Programme, particularly for providing field equipments. Special thanks go to Esfarayen Office of the Environment and SNP's game guards for their companionship and commitment. AR Braczkowski, F Zimmermann, and two anonymous reviewers provided helpful comments on previous versions of this manuscript. Thanks to Amy Hinks for linguistic editing. Finally, we are grateful to A Mahdavi, M Taghdisi, M Azadi, K Baradarani, and A Hosseinizadeh for their occasional involvement in field surveys.

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