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Wolves can suppress goodwill for leopards: Patterns of human-predator coexistence in northeastern Iran

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ABSTRACT

Mammalian carnivores often cause problems for people by preying on domestic stock. Exploring the factors that affect people's attitudes to predators, in particular the circumstances when some degree of loss is tolerated, is needed for developing predator management plans. When more than one species of predator is involved, there may be unexpected interactive effects in shaping people's tolerance. We addressed this hypothesis in a west Asian multi-predator montane landscape with high density of both wild ungulates and livestock harboring two large predators, Persian leopard and grey wolf. A semi-structured questionnaire survey of herders residing around Tandoureh, Salouk and Sarigol National Parks, northeastern Iran was carried out. The perceived role of leopards in depredation was negligible compared with that of wolves which were reported to be more frequent stock raiders and responsible for an average of 5.7 times more annual losses per herd by than were leopards. Non-predatory causes of mortality, particularly diseases, were clearly the major threat to livestock. Interviewed herders showed different attitudes toward each predator. Regardless of any recent occurrence of stock raiding by wolves, they were predominantly considered negatively. Although people showed mainly positive attitudes toward leopards, respondents who reported more wolf attacks tended to have more negative attitudes toward leopards. Hence, in multiple predator ecosystems, peoples' attitudes toward each species may be affected by the perceived activity of other predators. Often neglected in conservation programs, this phenomenon is clearly important in sustaining people tolerance particularly if endangered large predators are involved.

1. Introduction

The arid montane landscapes of west and central Asia host a low density of wild ungulates, mostly confined to protected areas (Baskin and Danell, 2003). They are also densely occupied by increasing numbers of pastoral herds of small stock (Mallon and Zhigang, 2009). It is estimated that west and central Asia harbor more small-bodied livestock than North and South America combined (Thornton, 2010). As a result, competition over limited resources between wild and domestic ungulates is inevitable (Namgail et al., 2007) and conflict with large carnivores is widespread (Dar et al., 2009; Kabir et al., 2013; Suryawanshi et al., 2013).

A number of large carnivores share the montane areas of west and central Asia with humans, with the leopard *Panthera pardus* and the grey wolf *Canis lupus*, generally causing the greatest level of conflict. They are subject to different patterns of tolerance and attitudes by human communities across their very large geographic ranges (Kansky et al., 2014). The co-existence of leopards with humans is often characterised by moderate to severe levels of conflict (Dar et al., 2009; Kabir et al., 2013; Shehzad et al., 2015). The conflict is unsurprisingly often linked to the extent to which they kill domestic stock (Babrgir et al., 2017; Shehzad et al., 2015) or domesticated carnivores, particularly dogs (Farhadinia et al., 2015; Ghoddousi et al., 2016). The grey wolf is also generally considered as a nuisance due to its consumption of livestock (Kikvidze and Tevzadze, 2015; Suryawanshi et al., 2013), even in areas with abundant multiple wild prey species (Hosseini-Zavarei et al., 2013).

People's attitude toward predators are not shaped solely by perceived economic loss, however, and may be influenced by a wide range of socioeconomic factors (Babrgir et al., 2017; Dar et al., 2009; Hosseini-Zavarei et al., 2013). Age, gender, and education (Suryawanshi et al., 2014), risk to human life (Behdarvand and Kaboli, 2015) and beliefs about predator behaviour (Kikvidze and Tevzadze, 2015) can play a role.

Spatiotemporal accessibility of domestic ungulates is known to be the driving factor for large felid depredation (Jumabay-Uulu et al.,

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2014; Miller et al., 2015; Zanin et al., 2015). Thus, even in areas with high wild prey availability but with easily accessible stock resources, large felids regularly depredate on livestock (Suryawanshi et al., 2013; Ghoddousi et al., 2016). Furthermore, wild prey depletion is an additive determinant of livestock depredation by large cats in montane landscapes (Babrgir et al., 2017; Dar et al., 2009; Sharma et al., 2015; Shehzad et al., 2015). Considering these drivers of conflict, we might expect low levels of leopard depredation on livestock, and less hostility toward leopards by the local communities where there is a stable prey base, good law enforcement and where livestock are excluded.

In this paper, we explored patterns of coexistence between humans and large carnivores across a sample of well-protected semi-arid montane reserves in northeastern Iran. We investigated perceived carnivore-caused mortality using the herders' records rather than actual loss, because the perceived rather than actual level of depredation often drives powerful negative attitudes to predators (Mishra, 1997).

We investigated temporal, spatial, and socio-economic factors affecting perceived conflict with large carnivores across some key leopard reserves in northeastern Iran. We documented perceived spatiotemporal variation in livestock loss due to wild predators and other causes, by season and by locality. We expected that losses to predators would be considerably exceeded by those to other causes, and we expected that diligent husbandry would reduce depredation. Furthermore, we hypothesized that people's attitudes toward larger carnivores are mainly driven by socio-economic factors. We anticipated that our research would clarify the dynamics of human-carnivore coexistence in a poorly studied ecosystem, as well as assist to design mitigation activities to reduce conflict and inform policy for the conservation of the endangered Persian leopard *P. p. saxicolor*.

2. Materials and methods

2.1. Study area

The Kopet Dagh and Aladagh Mountains in northeastern Iran host a number of montane reserves, including Tandoureh National Park and Protected Area, Salouk National Park and Protected Area and Sarigol National Park and Protected Area, lying at the eastern extreme of the Irano-Anatolian Biodiversity Hotspot (E57°15′ to E59°15′, N36° 20′ to N37°20′; Fig. 1 & Table 1). They total almost 930 km^2 of very rugged mountainous landscapes of steep cliffs and deep valleys at altitudes of 1000 to over 3000 m a.s.l.. Mean annual precipitation and temperature are 200 to 300 mm and around 15 °C, respectively, leading to a temperate semi-arid climate (Darvishsefat, 2006).

The vegetation is generally dominated by scrub species, particularly *Astragalus* spp. and *Artemisia sieberi*, forming a bush-steppe habitat in most areas, with pockets of juniper *Juniperus* spp. and barberry *Berberis* spp. (Darvishsefat, 2006). Potential ungulate prey for leopards include urial *Ovis vignei*, Wild goat *Capra aegagrus*, and Eurasian wild pig *Sus scrofa*. These areas also support a diverse carnivore community, including leopard, grey wolf, striped *hyaena Hyaena hyaena*, Eurasian *lynx Lynx lynx*, wild cat *Felis lybica*, and Pallas' cat *Otocolobus manul* (Ziaie, 2008).

Table 1
Details of interviewed herders around multiple reserves in northeastern Iran.

	Sarigol	Salouk	Tandoureh	Total
No. villages	9	6	12	26
No. herds	18	22	60	100
No. interviewed herders	12	16	44	72
Percentage of sampling	66.7	72.7	73.3	72.0
Total livestock number of interviewed herds	5500	10,290	18,229	34,019
Mean herd size (SE)	458.3 (39.3)	643.1 (63.7)	414.3 (47.8)	472.5 (34.8)

Our three study sites encompass areas of National Park and non-National Park (hereafter NP and non-NP). NPs experience greater law enforcement, and livestock grazing is completely banned. Non-NPs designated in Iran as Wildlife Refuge or Protected Area, have lower levels of protection, and enjoy less intense anti-poaching efforts. Furthermore, nomadic pastoralists are permitted to graze their herds in non-NPs during summer (May–August). Herds are comprised largely of sheep *Ovis aries* (%84 ± 2) with goats *Capra hircus*. Livestock grazes in seasonal pastures in wilderness areas for most of the year, but they are herded closer to villages during winter, where the main food stock is often the stubble of crops.

2.2. Sampling design

From August 2013 to September 2014, we conducted a semi-structured questionnaire survey with selective open-ended questions, to obtain data on people's attitudes, perceptions and interaction with large carnivores (i.e. Persian leopard and grey wolf). Closed-format questions reportedly result in less uncertainty than open-ended ones, for both the respondent and the researcher (White et al., 2005).

We focused on villages located on the borders of the three study sites and/or their associated herds of livestock spending part of each year within the reserve's pastures (n = 29). Inside each village, several households usually merge their herds of domestic stock to create a single large herd, always accompanied by at least one shepherd and several dogs. We targeted these aggregated herds from each village and interviewed the shepherd assigned to each.

We interviewed shepherds from 91 herds (from a total of 100 herds; Table 1), representing 302 households living around three reserves, i.e. Tandoureh, Salouk and Sarigol. Each herder was interviewed between 1 and 3 times. However, we used responses only from those respondents who were interviewed more than once during the survey year. This provided data on seasonal patterns of loss. Accordingly, 72 herders' data were entered into the analysis, representing 79.1% of our initial

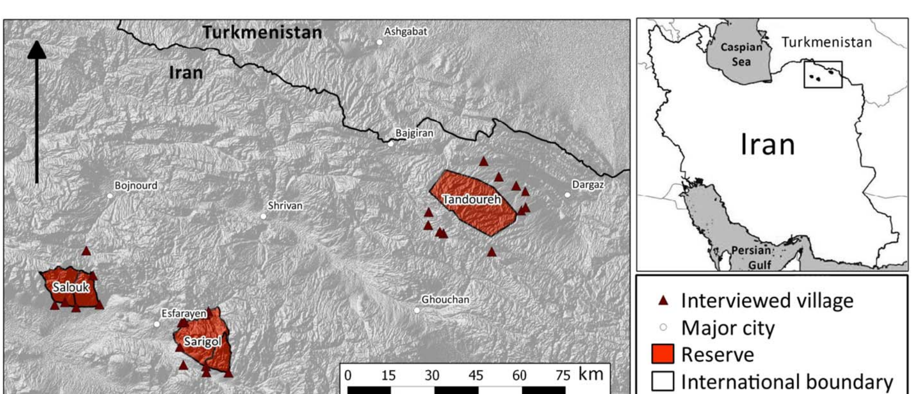

Fig. 1. Location of investigated villages (triangles) around three study sites in northeastern Iran.

target population. Each herder was interviewed on average 2.3 (SE 0.1) times, representing 269 households (3.7 ± 0.3 households per each herd). Except for the villages of Noushirvan (Sarigol), Haji Ghelichkhan and Doroungar (Tandoureh), we interviewed herders living in all surrounding villages around three reserves, totaling 26 (Fig. 1 & Table 1).

2.3. Interview surveys

The questionnaire was tested by piloting in a different area with similar herding practices to highlight potential ambiguities (White et al., 2005). All team members received training based on guidelines for in-person interview-based surveys developed from similar studies (e.g. Zimmermann et al., 2005; Majić and Bath, 2010; Hosseini-Zavarei et al., 2013).

Only one person associated with each herd was interviewed (normally the only person accompanying the herd in the pasture). Before interviews, respondents were asked for consent following an explanation of the research objectives and assurance that all personal information would remain strictly confidential. We conducted unstructured interviews in a friendly environment in order to gain the trust of interviewees and to make the interviews less biased. We evaluated respondents' ability to identify carnivores by showing them photographs of different species known from the area (leopard, wolf, striped hyena and Eurasian lynx). Each interview was limited to 20–30 min; animals grazing away from the shepherd made him anxious because unattended herds can be susceptible to attacks.

The questionnaire collected the following information: (1) socio-economic variables (respondents' age, education, as well as the types, numbers, and insurance status of livestock, number of dogs as well as shepherds), (2) details on herders' encounters with leopards in the wild within past five years; (3) experiences of livestock loss due to predation or non-predation causes during the past 3–6 months; and (4) herders' attitudes toward leopards and wolves. There was no active compensation program running during our survey period. Responses were not therefore biased upwards for this reason. Also, we randomly cross-checked responses with other families owning the same herd to verify loss claims.

We asked interviewees about the prevailing market value (at the time of the interview) of each type of livestock (sheep and goat) and then calculated weighted arithmetic mean market price for each herd, based on the proportion of sheep and goat in his herd as well as their associated price. We collected details on recent experiences of carnivore predation on livestock, including season, time, location, number of detected predators (in case the carnivore has been sighted) and number of killed domestic animals. The numbers for losses are as perceived by the respondents, as are the causes of loss. So when phrases like ‘wolf losses’ are used in the results this is shorthand for perceived losses as reported by the respondents.

We also collected detailed information about non-predatory causes of loss, such as number and timing of mortalities as well as their causes. We accepted disease as the cause of mortality where diagnosis was made by a local vet; otherwise we recorded putative cases as unknown. In order to obtain fine-scale data on losses, we tried to approach the herders in different seasons to ask them for their recent mortalities. Finally, we asked herders to rate their attitude toward leopards and wolves on a Likert scale from ‘strongly like = 0’ to ‘strongly dislike = 4’.

2.4. Statistical analysis

Collinearity between predictor variables was assumed to occur when r was > 0.7 using Pearson product moment correlation analysis. Accordingly, number of households owning each herd was excluded, because it was correlated with herd size.

We used three proxies for efficiency of herding practices: herd size, the number of dogs with the herd and each herd's reported loss due to diseases. To illuminate underlying factors affecting losses to predators, we fitted generalized linear mixed models (GLMM) with a Poisson error distribution. The numeric response variables included number of livestock reported to be depredated by wolf or leopard. Since all herds are generally accompanied by one herder, this was not a useful predictor and was excluded. We used reserve identity as a fixed blocking factor and village identity as a random effect. For models which included a season effect, each respondent contributed a response for multiple seasons; therefore the respondent ID was also included as a random effect, nested in village.

We also built a GLMM predicting the numbers reported lost to each predator (wolf and leopard) to explore spatiotemporal variation in livestock loss. Season (4 levels) and reserve (3 categories) were entered as categorical fixed predictors, with similar random effects as previous models. Again, a GLMM with Poisson error distribution was developed. The ‘lme4’ library (Bates et al., 2016) was used to fit all these models with the default Laplace Approximation for estimating maximum likelihood.

Herding characteristics (herder age, current price and number of dogs) as well as frequency of livestock loss to wolf, leopard and diseases were then considered as variables affecting the respective people's attitude toward each predator (as measured on a Likert scale).

Each herd was composed of both domestic sheep and goat which have different market prices, and sometimes respondents were uncertain of the exact species lost. We assumed that stock losses were proportional to their relative abundance in the stock population, and we calculated a weighted arithmetic mean for each respondent, based on proportion of sheep and goat in his herd to which we applied the respective associated price.

To construct models predicting Likert scale ordinal responses, we fitted a cumulative link mixed model with the clmm function in R package ‘ordinal’ (Christensen, 2015). All numeric predictor variables were standardised to z scores.

An information theoretic or ‘IT’ approach was used for model selection. This enables examination of several competing models or hypotheses simultaneously to identify the best set of models (Grueber et al., 2011) via information criteria such as Akaike's information criterion (Burnham and Anderson, 2002), after correction for small sample size (AICc). Convergence problems for models predicting people attitudes toward leopards using ‘clmm’ led us to use the closely related ‘clmm2’ function in package ordinal. We permitted our GLMM models to have a maximum of four and three parameters for each model fitting to people's attitude toward wolf and leopards, respectively in order to enable proper model convergence. The categorical blocking effect reserve identity was included in all models as a design feature.

We used package ‘MuMIn’ (Bartoń, 2009), to calculate the model weights. The proponents of this methodology recommend that these weights are best interpreted as the probability for a model that it is the best model for the observed data, given the set of candidate models (Bolker, 2008). We chose not to interpret model-averaged coefficients for predictor variables in order to determine predictor importance, as their interpretation may be problematical when there is multicollinearity among predictor variables, which is unavoidable in observational studies (see Cade, 2015). We conducted all analyses in *R* (R Development Core Team, 2013).

3. Results

3.1. Interviewee characteristics

Respondents were on average 43.6 (SE 1.3, range 21 to 70, median 43) years old and relied primarily on stock breeding as well as farming. Our survey covered herders with a total of 34,019 of domestic ungulates grazing within the study area. Average herd size was 472.5 animals (SE 34.6). Herd size differed among reserves ($F_{2, 69}$ = 3.874, p = 0.025), being largest in Salouk (643.1 ± SE 54.3). Each herd was

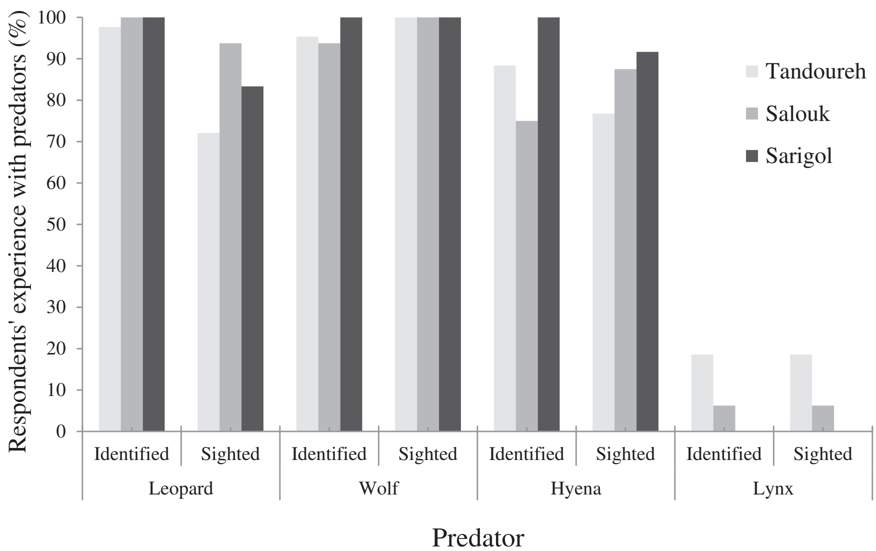

Fig. 2. Percentage of interviewees who were able to identify the species based on indicated image (labeled as "identified") and those who saw the animal in the wild (denoted as "sighted").

accompanied by a shepherd as well as an average of 3.6 (SE 0.3) herding dogs, and there was no evidence that number of dogs per herd varied among sites ($F_{2,\,68} = 0.796$, $p = 0.45$).

Only 16.9% of interviewed herders had complete or partial insurance coverage for their livestock. The reasons given for this by interviewees were: ignorance i.e. they lacked awareness of the key authorities involved, lack of financial resources to buy it, and dissatisfaction with insurance process. This last reason is particularly relevant for livestock loss due predators, because compensation is conditional on recovering the tagged ear of the killed animal, which is problematic in cases of predation when the carcasses is not located.

3.2. Knowledge, attitude and perception

Almost all respondents were able to identify wolves and leopards based on photographs; lynx were relatively unfamiliar (Fig. 2). Furthermore, most herders had reported seeing individuals of leopard, hyena and wolf over their lifetime; the latter was seen by all interviewees, while about 80% had seen hyena and leopard (Fig. 2).Only the responses of those who recognized leopard and wolf were used in the analyses regarding this species. Twenty two percent of interviewees (n = 16) reported leopard attacks on humans for the preceding five years, while only four respondents were attacked themselves by leopards. All attacks happened when herders tried to push away leopards from their stock. In contrast, only five herders reported wolf attacks on humans.

62.5% of interviewed herders (n = 45) reported an encounter with leopards during the past five years, resulting in 68 sightings within or around the three reserves. All herders had made recent (i.e. within 5 years) sighting of wolves. Eighteen percent (n = 13) of respondents reported leopard attack on humans, either themselves or other herders in their area. In contrast, only four herders reported wolf attacks on humans. Almost all herders (98.4%) perceived the grey wolf to be the main predator of their domestic stock. A Wilcoxon Signed-Ranks Test indicated that herders' attitude toward the predators was significantly different, i.e. attitude toward the wolves was strongly negative compared to the leopards where attitudes tended to be positive (Z = 124.5, $p \le 0.001$; Fig. 3).

3.3. Spatiotemporal patterns of livestock loss

The questionnaires produced information about all three large carnivores taking livestock, although the striped hyena was reportedly seen only once killing a sheep, in Tandoureh. 29 herders (40.3% of total

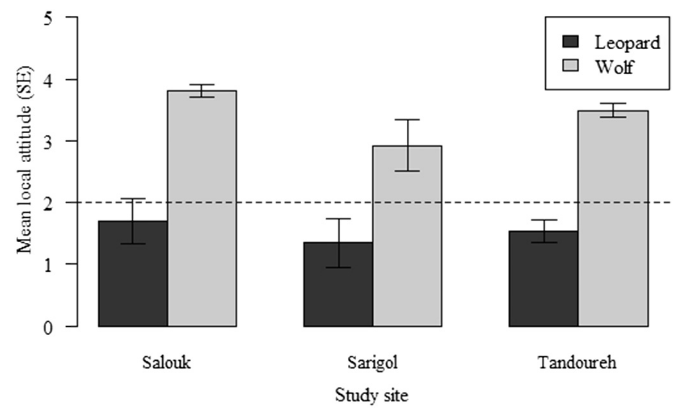

Fig. 3. Comparative mean attitude of herders toward large carnivores killing livestock around multiple study sites in northeastern Iran. The score ranges from 0 (most positive) to 4 (most negative), with 2.0 neutral (dotted line). Error bars represent standard error for each mean.

interviewees) experienced stock loss perceived to be due to leopards during the previous year, whereas most of the interviewees (93.1%) reported experiencing wolf attacks during the previous year. Herders reported that they lost fewer animals per herd to leopards (mean 0.9 ± SE 0.2) compared to wolves (mean 5.1 ± SE 0.6; ranging 1 to 10), (Paired *t*-test = −6.15, df = 71, $p < 0.001$), yielding a ratio of 1:5.7 annual livestock loss to leopards and wolves, respectively (Fig. 4). Stock loss due to leopards and wolves were reported to be 0.4 (SE 0.1) and 1.5 (SE 0.2) animals, respectively between August 2013 to September 2014.

There was evidence that perceived leopard predation on livestock differed between reserves and seasons. It was reported to be least prevalent in Tandoureh (GLMM, Z = −2.186, $p = 0.028$). More than half of leopard attacks occurred during spring in all surveyed reserves. In contrast, there was no evidence that the rate of reported wolf attacks varied among reserves (Table 2). There was evidence that losses to wolves varied with season, peaking in summer (GLMM, Z = 3.358, $p \le 0.001$) and lowest in winter (Z = −4.263, $p \le 0.001$). There was no evidence that the seasonal patterns for either predator differed among reserves (the interaction between seasons and reserves on livestock loss was non-significant for both predators).

During the one year period targeted by the questionnaire survey, a total of 2172 domestic sheep and goat were reported to have died to non-predation causes. On average, each herder reported losing 26.8 ± SE 6.6 (Sarigol), 27.7 ± SE 4.2 (Tandoureh) to 39.6 ± SE

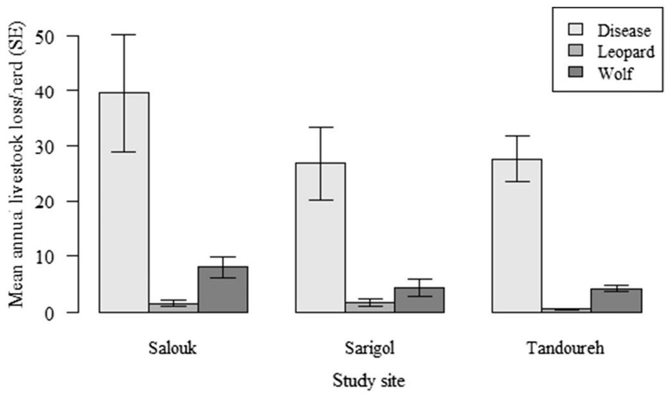

Fig. 4. Mean annual livestock loss per each herd mediated by three main sources of mortality, i.e. diseases or depredation by wolves or leopards. Error bars represent standard error for each mean.

Table 2
Results of GLMM of effect of season and reserve on predatory events committed by the a) leopards and b) wolves in northeastern Iran. The reference level for season and reserve is respectively autumn and Salouk, so these estimate values are the difference with the reference levels. No significant interaction between seasons and reserves on livestock loss due to each predator was seen.

a) Leopard					
Random effects: groups	Name	Variance	SD		
Respondent: village	(Intercept)	1.577	1.2559		
Village	(Intercept)	0.214	0.4626		
Fixed effects:	Estimate	Std. error	z value	Pr(> |z|)	
(Intercept)	− 2.5072	0.6432	− 3.898	9.69E-05	***
ReserveSarigol	− 0.1294	0.7286	− 0.178	0.859069	
ReserveTandoureh	− 1.4024	0.6417	− 2.186	0.028845	*
SeasonSpring	1.4553	0.4196	3.468	0.000524	***
SeasonSummer	0.452	0.4833	0.935	0.349713	
SeasonWinter	0.2513	0.5038	0.499	0.617882	
b) Wolf					
Random effects: groups	Name	Variance	SD		
Respondent: village	(Intercept)	0.4118	0.6417		
Village	(Intercept)	0.1888	0.4345		
Fixed effects:	Estimate	Std. error	z value	Pr(> |z|)	
(Intercept)	0.2984	0.2945	1.013	0.310888	
ReserveSarigol	− 0.5428	0.4077	− 1.331	0.18304	
ReserveTandoureh	− 0.3397	0.3496	− 0.972	0.331207	
SeasonSpring	− 0.1488	0.1478	− 1.007	0.313862	
SeasonSummer	0.4334	0.1291	3.358	0.000786	***
SeasonWinter	− 0.7591	0.1781	− 4.263	2.02E-05	***

* = $p \le 0.05$, ** = $p \le 0.01$, *** = $p \le 0.001$.

Table 3
Details of different causes of non-predatory mortality, particularly diseases among local stock between August 2013 to September 2014 in northeastern Iran.

Mortality cause	Tandoureh	Sarigol	Salouk	Total	Percentage
Foot-and-mouth disease (FMD)	125	49	158	332	15.3
Theileriosis	20	0	51	71	3.3
Enterotoxaemia	8	5	0	13	0.6
Peste des petits ruminants (PPR)	49	22	0	71	3.3
Still-birth[a]	440	170	282	892	41.1
Black disease	0	46	0	46	2.1
Unknown	569	36	127	732	33.7
Lost	14	0	1	15	0.7
Total	1225	328	619	2172	

[a] Still-birth, a common problem among local stock, can be mediated by various causes. But our interviewees were not aware of causes, calling all cases of mortalities between birth up-to first month a generally as "still-birth".

Table 4
Results of GLMM of herding practice effects on predation events attributed to a) leopards and b) wolves in northeastern Iran.

a) Leopard					
Random effects: groups	Name	Variance	SD		
Village	(Intercept)	0.7717	0.8785		
Fixed effects:	Estimate	Std. error	z value	Pr(> |z|)	
(Intercept)	0.17138	0.46712	0.367	0.7137	
ReserveSarigol	− 0.20205	0.63082	− 0.320	0.7487	
ReserveTandoureh	− 1.35735	0.61882	− 2.193	0.0283	*
Z_Herdsize	− 0.45266	0.25181	− 1.798	0.0722	
Z_Dog	− 0.30324	0.21402	− 1.417	0.1565	
Z_DiseaseLoss	0.05663	0.18424	0.307	0.7585	
b) Wolf					
Random effects: groups	Name	Variance	SD		
Village	(Intercept)	0.3441	0.5866		
Fixed effects:	Estimate	Std. error	z value	Pr(> |z|)	
(Intercept)	1.72583	0.27881	6.190	6.02e-10	***
ReserveSarigol	− 0.44578	0.38154	− 1.168	0.243	
ReserveTandoureh	− 0.23151	0.34065	− 0.680	0.497	
Z_Herdsize	− 0.02966	0.08717	− 0.340	0.734	
Z_Dog	0.09318	0.08234	1.132	0.258	
Z_DiseaseLoss	0.07479	0.04860	1.539	0.124	

* = $p \le 0.05$, ** = $p \le 0.01$, *** = $p \le 0.001$.

10.7 (Salouk) domestic sheep and goat as a result of non-predatory factors per annum (Fig. 4). The respondents were not aware of type of disease for 33.7% of losses, but they allegedly assigned five different diseases to have resulted in death of livestock, based on local vet diagnosis (Fig. 4 and Table 3). Thieves, loss, and catastrophes comprised a negligible part of the local non-predatory economic loss (< 2%).

Reported losses due to non-predatory causes differed between seasons, peaking in winter (GLMM, Z = 22.613, $p \le 0.001$) and spring (GLMM, Z = 17.524, $p \le 0.001$). However, studied reserves showed no significant spatial difference in total annual loss. Non-predatory causes of mortality accounted for many more losses than all predation combined (predatory causes: 6.0 ± SE 0.7 vs. non-predatory causes 30.2 ± SE 3.6, t = − 6.54, df = 75.96, $p < 0.001$, Fig. 4).

3.4. Factors affecting perceived loss and attitudes

There was no evidence that herding practices (either herd sizes or the number of dogs used) affected reported livestock loss numbers to either leopards or wolves (Table 4). Livestock loss was identified as a possible influence on attitudes. The seven top models ($\Delta AIC_c < 2$) for predicting attitude to leopards contained livestock loss due to wolves (WolfLoss) as a predictor. The five models with this predictor had clearly the highest weight of those compared (cumulative AICc weight: 0.61). Higher perceived loss to wolves was associated with more negative views toward leopards with the largest relative importance within top models (Fig. 5 & Table 5). The maximum likelihood parameter estimate for this predictor in the best performing model was positive and with a confidence interval excluding zero (Fig. 5 & Table 6). None of the other factors examined had a larger influence on attitudes toward leopards. There was little evidence that any of the predictors explored were associated with respondents' attitude toward wolves, including perceived losses to wolves (Table 5).

4. Discussion

The livestock herders we surveyed appear to have had a sophisticated understanding of the causes of livestock mortality. They believed their economic loss due to predation by large carnivores was low in absolute terms, and much lower than losses to non-predatory causes. Further, herders made fine-scale distinctions between the impacts of different carnivores, regarding the wolf as the main nuisance animal to

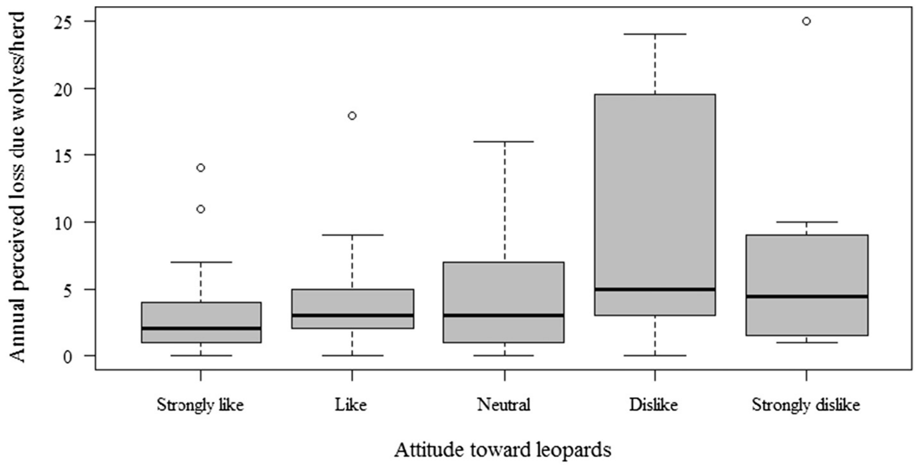

Fig. 5. Median effect of livestock loss caused by the wolves on the respondents' attitudes toward the leopards in northeastern Iran. Each box represents inter-quartile range whereas whiskers delineate scores outside the inter-quartile range.

livestock, regardless of peoples' recent experiences. In contrast, the leopard was reported to be responsible for a small proportion of herders' recent losses (0.4%) between August 2013 to September 2014, well below typical values reported for wild felids regionally (Babrgir et al., 2017; Dar et al., 2009; Kabir et al., 2013) or globally (up to 3% of annual domestic stocks; Nowell and Jackson, 1996). Despite this high level of understanding and a general pattern of more positive attitudes to leopards, we showed that perceived losses to wolves have a negative effect on attitudes to leopards.

Table 5
Results of GLMM of factors affecting attitudes toward leopard and wolf in northeastern Iran.

Model number	Model	K	AICc	AICc delta	AICc weight	Cum. AICc weight
Leopard						
1	Attitude ~ Reserve + WolfLoss	2	224.70	0.00	0.19	0.19
2	Attitude ~ Reserve + WolfLoss + Price	3	224.80	0.10	0.18	0.37
3	Attitude ~ Reserve + Age + LeopardLoss	3	225.95	1.25	0.1	0.48
4	Attitude ~ Reserve + Age + WolfLoss	3	226.26	1.56	0.09	0.56
5	Attitude ~ Reserve + LeopardLoss + Price	3	226.30	1.61	0.09	0.65
6	Attitude ~ Reserve + Herdsize + WolfLoss	3	226.64	1.94	0.07	0.72
7	Attitude ~ Reserve + LeopardLoss + WolfLoss	3	226.64	1.94	0.07	0.8
8	Attitude ~ Reserve + LeopardLoss	2	227.10	2.40	0.06	0.85
9	Attitude ~ Reserve + Price	2	228.23	3.53	0.03	0.89
10	Attitude ~ Reserve	1	228.45	3.75	0.03	0.92
11	Attitude ~ Reserve + Herdsize + LeopardLoss	3	229.06	4.36	0.02	0.94
12	Attitude ~ Reserve + Age + Price	3	229.44	4.74	0.02	0.95
13	Attitude ~ Reserve + Age	2	229.64	4.94	0.02	0.97
14	Attitude ~ Reserve + Herdsize + Price	3	230.23	5.53	0.01	0.98
15	Attitude ~ Reserve + Herdsize	2	230.44	5.74	0.01	0.99
16	Attitude ~ Reserve + Age + Herdsize	3	231.64	6.94	0.01	1
Wolf						
1	Attitude ~ Reserve	1	149.8	0	0.19	0.19
2	Attitude ~ Reserve + Price	2	150.9	1.06	0.11	0.3
3	Attitude ~ Reserve + Price + DiseaseLoss	3	151.4	1.57	0.09	0.39
4	Attitude ~ Reserve + DiseaseLoss	2	151.5	1.69	0.08	0.47
5	Attitude ~ Reserve + WolfLoss	2	151.8	1.98	0.07	0.54
6	Attitude ~ Reserve + Herdsize	2	152.2	2.39	0.06	0.6
7	Attitude ~ Reserve + Age	2	152.3	2.48	0.05	0.65
8	Attitude ~ Reserve + Price + WolfLoss	3	153.1	3.25	0.04	0.69
9	Attitude ~ Reserve + Age + Price	3	153.4	3.58	0.03	0.72
10	Attitude ~ Reserve + Price + Herdsize	3	153.4	3.6	0.03	0.75
11	Attitude ~ Reserve + DiseaseLoss + WolfLoss	3	153.5	3.65	0.03	0.78
12	Attitude ~ Reserve + Price + DiseaseLoss + WolfLoss	4	153.6	3.73	0.03	0.81
13	Attitude ~ Reserve + Age + DiseaseLoss + Price	4	154	4.16	0.02	0.83
14	Attitude ~ Reserve + Herdsize + DiseaseLoss	3	154.1	4.24	0.02	0.85
15	Attitude ~ Reserve + Age + DiseaseLoss	3	154.1	4.26	0.02	0.87
16	Attitude ~ Reserve + Price + Herdsize + DiseaseLoss	4	154.1	4.28	0.02	0.89
17	Attitude ~ Reserve + Herdsize + WolfLoss	3	154.3	4.48	0.02	0.91
18	Attitude ~ Reserve + Age + WolfLoss	3	154.4	4.57	0.02	0.93
19	Attitude ~ Reserve + Age + Herdsize	3	154.8	4.98	0.02	0.95
20	Attitude ~ Reserve + Herdsize + Price + WolfLoss	4	155.7	5.88	0.01	0.96
21	Attitude ~ Reserve + Age + Price + WolfLoss	4	155.7	5.88	0.01	0.97
22	Attitude ~ Reserve + Age + Herdsize + Price	4	156.1	6.24	0.01	0.98
23	Attitude ~ Reserve + Herdsize + WolfLoss + DiseaseLoss	4	156.1	6.32	0.01	0.99
24	Attitude ~ Reserve + Age + WolfLoss + DiseaseLoss	4	156.2	6.33	0.01	1
25	Attitude ~ Reserve + Age + Herdsize + DiseaseLoss	4	156.7	6.91	0.01	1
26	Attitude ~ Reserve + Age + Herdsize + WolfLoss	4	157	7.18	0.01	1

Table 6
Maximum likelihood estimates corresponding to the best performing AICc model: Attitude toward Leopards ~ Reserve + WolfLoss.

Parameter	Estimates from best performing model Attitude toward Leopards ~ Reserve + WolfLoss	
	Coefficient estimate	Standard error
WolfLoss	0.54	0.22

4.1. Attitudes and perception

Attitudes toward wolves were generally negative, regardless of occurrence and intensity of livestock loss mediated by the predator. Stockholders were questioned only about successful wolf attacks on livestock. However, many herders noted that wolves were frequent visitors but were apparently deterred by guard dogs and shepherds. We were unable to quantify unsuccessful predation events - stockholders rarely remembered the details of these. Besides economic costs, predation on livestock poses a hidden impact incurred through the cost of guarding practices (Barua et al., 2013) which can lead to more negative attitudes.

The lower economic impact of leopards compared with wolves probably promotes more positive attitudes. The fact that leopards are responsible for many more attacks on humans does not seem to outweigh this which appears unexpected. Conflict with wolves was the main determinant of people's attitude toward the leopards. People experiencing more loss to wolves tended to have more negative attitudes toward leopards.

The primary reason that people are relatively tolerant of leopards compared with wolves is economic; both perceived losses and the costs of guarding are influential. Leopard attacks clearly followed a seasonal pattern, coinciding with the main grazing season in highlands. However, guarding is necessary throughout year, as a response to year-round predation risk in lowlands by wolves. This may contaminate attitudes toward predators which have negligible economic impact.

Neither herd size nor number of accompanying dogs was associated with livestock loss. In contrast, higher level of livestock depredation in warm seasons when local herds graze in remote mountainous areas support the idea that increased availability at this time triggers predation by the leopards. As has been observed in previous surveys in prey-rich landscapes (Farhadinia et al., 2014; Ghoddousi et al., 2016), limited spatiotemporal accessibility of domestic ungulates with basic herding practices can result in infrequent depredation by the leopards.

5. Conclusions

In a mosaic landscape hosting a guild of large carnivores, an understanding of how attitudes to different species interact in human communities may help conservation planning, especially for conservation-dependent species such as the Persian leopard. Our research calls for measures to reduce conflict not only with the threatened species, i.e. Persian leopard, but also with the more resilient carnivore, i.e. wolf.

Disease is perceived as the main economic threat to livestock-based livelihoods in this part of the world (Dar et al., 2009; Hosseini-Zavarei et al., 2013) and focusing on interventions to reduce its real and perceived burden would likely benefit both people and carnivores. Most importantly, the provision of veterinary services to control disease in livestock may increase people's tolerance toward the large carnivores, particularly if these veterinary initiatives are explicitly deployed as part of a conservation program (Nawaz et al., 2016). Compensation payment methods, in terms of conservation impacts, have ambiguous effect in reducing human–carnivore conflict (Dickman et al., 2011). An effective insurance program must compensate for losses to wolves, not only leopards, to encourage more peaceful human–leopard coexistence. Finally, maintenance of the current exclusive grazing pattern for wild and domestic ungulates is necessary, boosted by anti-poaching attempts to secure the leopard populations within the current network of national parks.

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