Predator, prey and humans in a mountainous area: loss of biological diversity leads to trouble

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Abstract  Large carnivore-human coexistence is a challenging issue in wildlife conservation worldwide. An adequate and diverse prey spectrum favours carnivore persistence. Prey depletion and habitat loss elicit conflict with humans and require sound conservation measures. We evaluated the conflict between common leopards and humans in a densely populated Himalayan forest area of Pakistan. In two decades, the local forests decreased at an average rate of 65.5 ha/year (6.6%), with a concomitant increase in areas covered by human settlements (81.5%) and agricultural lands (15.4%). Ranging movements of a GPS/GSM-radiotagged male leopard over 16 months encompassed an area inhabited by c. 124,000 people. Livestock dominated the leopard’s diet (absolute frequency of occurrence: 80%), while wild ungulates were rarely eaten (absolute occurrence: 22%). Domestic goats were the most frequent diet item (61%), followed by domestic dogs (12%) and Bos spp. (6%). Wild prey included canids, small carnivores, rhesus monkeys, small mammals and gallinaceous birds. Socioeconomic implications of human-leopard coexistence were investigated: 18.5% of the households interviewed (N = 1016) suffered livestock depredation by leopards, with an overall loss of 123 USD/km²/year, in an area of 328 km². In the first c. 15 years of this century, about 2 attacks to humans/year were recorded, half of which were lethal, whereas c. 6 leopards/year were killed in retaliation. The common leopard is ‘critically endangered’ in Pakistan mainly because of habitat loss and concurrent prey depletion.

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To increase the long-term survival of leopards and mitigate human-carnivore conflicts, priority should be given to restoration of a diverse natural prey assembly and protection of forest habitats, together with improved livestock management practices and livestock compensation. The latter will require a sustainable financial mechanism.

**Keywords**  Human-carnivore coexistence · Human-wildlife conflict · Food habits · *Panthera pardus*

**Introduction**

The loss of biodiversity triggers a number of negative ecological consequences (e.g., Cardinale et al. 2012; Hooper et al. 2012). Additionally, it can alter processes which provide ecosystem services to humans, in turn affecting human well-being (e.g., Diaz et al. 2006; Cardinale et al. 2012). In some cases, the loss of even one or a few key taxa can lead to significant ecological effects (e.g., Paine 1969; Mills et al. 1993), especially if it involves species interacting with other components of ecological communities. At the same time, human-wildlife conflict is a major determinant, as well as a consequence, of biodiversity loss, through habitat destruction, poaching, intensive hunting and livestock depredation. Despite these effects, biodiversity loss as a catalyst of human-wildlife conflict has been studied relatively little.

Top predators and meso/large wild herbivores play a key role in ecosystems, as they are involved in both top-down and bottom-up processes, involving—as they do—organisms belonging to several trophic levels (e.g., McLaren and Peterson 1994; Sinclair et al. 2003; Hebblewhite et al. 2005; Festa-Bianchet et al. 2006; Lovari et al. 2009; Ripple et al. 2014). Large terrestrial carnivores are usually dependent on large vertebrate prey to meet their food requirements (Carbone et al. 2007; but see e.g., Schaller et al. 1985; Bojarska and Selva 2012, for Ursidae). In turn, habitat conservation and the availability of a diverse spectrum of large, wild prey is expected to favour the persistence of large carnivores.

Coexistence of humans and large carnivores is one of the most challenging, sometimes controversial, issues in wildlife conservation worldwide (e.g., Treves and Karanth 2003; Inskip and Zimmermann 2009; Chapron et al. 2014; Treves et al. 2016). In areas where wild prey are scarce or unavailable, livestock depredation would be predicted to increase (e.g., Meriggi and Lovari 1996; Bagchi and Mishra 2006; Khorozyan et al. 2015; but see e.g., Sharma et al. 2015; Suryawanshi et al. 2013; Nelson et al. 2016). In turn, a potential for conflict with humans will develop, resulting in lethal outcomes for carnivores (because of retaliatory killing), livestock and sometimes humans (Dinerstein et al. 2003; Treves and Karanth 2003; Packer et al. 2005). Removal, over-hunting and poaching of wild herbivores together with habitat loss, are often interlinked determinants of prey depletion. Additional poor management practices are likely to increase human-carnivore conflict, e.g., inadequate protection measures for livestock, or absent or slow financial compensation for livestock losses. Conflict leads to serious consequences especially when a threatened taxon is involved. In turn, multi-disciplinary studies are required to assess ultimate determinants of local conflicts and to identify suitable solutions to mitigate them.

We used a multidisciplinary approach, involving behavioural ecology, socioeconomics and remote sensing, to evaluate human-carnivore conflict in a system involving a top predator, livestock, people and a protected area, in a heavily human-altered landscape. As a case study, we considered a large cat, the common leopard *Panthera pardus*, in a mountainous,
but densely populated area of Pakistan. This system provides a useful example to assess the effects of human-caused prey loss on human-carnivore conflict. Pakistan has experienced a huge deforestation over the last millennia: currently, just c. 2% of the country is covered by forest, with an annual rate of decrease since 1990 of c. 400 km²/year: the highest deforestation level in Asia (FAO 2009). Conversely, in the last 50 years, the human population has shown a 300% increase, with c. 182 million people in 2013 (Khan 2015). Loss of forest and excessive hunting have resulted in the extinction of some iconic species (e.g., the Bengal tiger Panthera tigris tigris, the Asiatic lion Panthera leo persica and the Iranian cheetah Acinonyx jubatus venaticus), and significant declines of others (e.g., common leopard) (Roberts 1997). In mountainous areas, wild ungulates e.g., grey goral Nemorhaedus goral, musk deer Moschus chrysogaster and barking deer Muntiacus vaginalis have either declined, or been locally extirpated, thus significantly reducing prey availability for large carnivores (Anwar et al. 2011; Shehzad et al. 2014).

The common leopard is “critically endangered” in Pakistan (Sheikh and Molur 2004; “vulnerable” at the international level: http://www.iucnredlist.org/details/15954/0, accessed on 17.07.2017). This large carnivore (body weight: female 28–60 kg, male 37–80 kg; Nowak 1999) can use a wide range of habitats, from sub-desertic to equatorial/boreal ones (Nowak 1999), and feed on a wide spectrum of prey (Lovari et al. 2013a, for Asia; Hayward et al. 2006, mainly for Africa). In the absence of a diverse array of substantial wild ungulate prey, this adaptable large cat can survive on domestic livestock and smaller wild prey (Shehzad et al. 2014). Under these circumstances, conflicts with human activities would be expected to develop (Khan 2015). Habitat degradation and loss, human encroachment of forested areas, depletion of wild prey, and poaching, are major threats to the conservation of leopard. Moreover, absence of a sustainable financial mechanism and a policy framework to compensate livestock owners for losses due to depredation, result in retaliatory killing by local communities, thus further endangering the survival of this carnivore. In turn, appropriate measures to mitigate the conflict with humans must be implemented.

We studied leopard-human conflict in a densely inhabited, mountainous area of northern Pakistan. The common leopard is the top predator in this area, and because wild ungulates are virtually absent, domestic (goats, sheep, cattle and dog) and small wild species (rhesus monkeys, small-to-meso carnivores, rodents and birds; Shehzad et al. 2014; Khan 2015) are the only available prey. To propose effective mitigating solutions, we evaluated the (i) food habits of common leopards, (ii) livelihood approach of local communities, livestock depredation and economic values of losses, (iii) forest loss over the last two decades, (iv) ranging movements of the leopard, and (v) direct conflicts (i.e., human casualties and retaliatory killing).

Materials and methods

Study area

Our study area included a portion of the Western Himalayan Ecoregion in the Abbottabad District (c. 1967 km²) of Pakistan. Our core study area (c. 328 km², 1000–2800 m a.s.l., Fig. 1) encompassed the Ayubia National Park (ANP), Khyber Pakhtunkhwa Province (KP), the Murree Forest (MF, Punjab Province) and the Changla Gali-Koza Gali area (CGKG, between Ayubia and Murree). ANP is a protected area (c. 3300 ha), and is the largest forest patch within the study area; MF and CGKG have higher anthropogenic

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activities and smaller forest patches fragmented by cultivated fields and villages and ham-
lets. Forested areas include temperate, tropical and sub-tropical pine forests, with elements
of subalpine meadows also present. The main tree species are blue pine *Pinus wallichiana*,
Chir pine *Pinus roxburghii*, fir *Abies pindrow*, Himalayan yew *Taxus wallichiana*, deodar
*Cedrus deodara*, morinda spruce *Picea smithiana*, horse chestnut *Aesculus indica*, oak
*Quercus incana* and *Quercus dilatata*, *Rhododendron arboreum* (Khan 2015).

In the District of Abbottabad, human population size is 881,000, and increasing (ERRA
2007). Livestock is abundant (249,268 cattle, 222,472 goats and 58,038 equids, with 269
livestock km\(^{-2}\), AAVV 1998). Wild ungulates are nearly absent, except for wild boar *Sus
scrofa* and grey goral which are very rare. The common leopard is the top predator in
this area. Seven individual leopards were genotyped (cf. Janečka et al. 2008; Lovari et al.
2009), but this is considered a minimum number because at least as many were removed by
humans for retaliation, during our study period, in ANP and its neighbourhoods. Smaller
carnivores present included the leopard cat *Prionailurus bengalensis*, the golden jackal
*Canis aureus*, the red fox *Vulpes vulpes*, the yellow-throated marten *Martes flavigula*,
and civets *Paguma larvata* and *Paradoxurus hermaphroditus*. Potential wild prey included the
rhesus monkey *Macaca mulatta*, the Indian crested porcupine *Hystrix indica*, flying squir-
els and galliform birds Phasianidae.

Usually, snow occurs from November to March, rainfall peaks from June to September
and again in February–March. December, January and February are the coldest months
(minimum temperature up to \(-7.5^\circ C\)) and May, June and July are the warmest (maximum
temperature up to 32 \(^{\circ}C\)) (Khan 2015).

**Food habits**

Diet composition of the common leopard was estimated through analyses of food remains
in scats (*n* = 525). Sample size was much greater than that considered adequate to describe
diet diversity in felids (*n* = 11–44, Hass 2009; Lovari et al. 2013b; Lyngdoh et al. 2014;
Lovari et al. 2015; cf. below). Scats were collected monthly (November 2010–October 2011) and bimonthly (November 2011–May 2013) along the same itineraries (total length: 83 km). A scat was conservatively identified on the basis of several features (e.g., smell, position, size, contents and presence of tracks: Lovari et al. 2009, 2015) to reduce the risk of collecting scats of species such as jackal, leopard cat, civets or domestic dogs. No one feature alone is species specific, but the combination of them can be quite effective (Lovari et al. 2009). The absence of sympatric large predators reduced the probability of error in the identification of leopard scats. Dubious cases were genotyped (n = 130) and 82% were confirmed as from leopards. A total of 525 scats was analysed to identify prey items, following Lovari et al. (2009, 2015; see Online Resource 1 for details).

Data were tabulated as absolute frequency of occurrence (AO, n. occurrences of each prey species/total n. scats × 100); relative occurrence (RO, n. occurrences of each prey species/total n. occurrences × 100); volume of each prey item was estimated by eye for each scat (estimated volume of each prey species/total estimated volume × 100, Kruuk and Parish 1981). Estimated volume, when present (%), was plotted versus the frequency of occurrence (%) of the prey species, to show the relative importance of prey items (e.g., Kruuk and Parish 1981).

Besides uncertainties affecting the calculation of biomass consumed, from scats (cf. Chakrabarti et al. 2016; Lumetsberger et al. 2017), it is usually impossible to know (i) the age-sex class that was preyed upon; (ii) whether other carnivores (e.g., jackals and foxes), also fed on a carcass; or (iii) whether it fed alone or with conspecifics, e.g., a pair or a female with cubs. Thus, we limited our analyses to frequencies of occurrence and estimated volume.

Diet diversity was determined using the standardized index of trophic niche breadth ($B_{sta}$; Krebs 1999):

$$B_{sta} = (B - 1)/n - 1,$$

where

$$B = 1/p_i^2$$

B is the Levin’s index of niche breadth (Krebs 1999), n is the total number of food categories and $p_i$ is the proportion of items in the diet that belong to category $i$. $B_{sta}$ range varies between 0 (minimum niche breadth) and 1 (maximum niche breadth).

**Household surveys**

In our core study area (328 km$^2$), a household level survey (n = 1016 households) was conducted in May–July 2012. To select specific households for interviews, data on the number of households were obtained from union councils in the study area. Then 13 Union Councils (administrative units of a district) were selected which encompassed 36024 households. A multistage sampling technique was then adopted: a random sample of villages was selected from each union council; in each village, a number of households proportional to population was selected through systematic sampling. Finally, from each village, every fifth household was interviewed (Online Resource 3). Interviews of households included questions on (i) type/number of livestock raised; (ii) their livelihood approach; (iii) their perception of the most frequent cause of livestock losses in their region (leopard depredation/disease or winter severity/other causes), i.e. to assess the general perception of factors determining livestock losses; (iv) whether they suffered livestock losses in the previous
year; (v) which type of livestock they lost, and (vi) what they believed was the cause of their livestock loss.

We used generalised linear models with binomial errors (GLMs, Crawley 2007) to assess whether the probability of attribution of losses to leopards differed between general perception and responses of households on their own losses. Cause of loss was the response variable (leopards: 1; other causes: 0); “Question” was the predictor (general perception of factors determining livestock loss; cause of loss of their own livestock). Moreover, we evaluated whether the probability of leopard depredation differed across livestock types. In GLMs with binomial error, cause of loss was the response variable (leopard: 1; other: 0); type of livestock (goat; cattle) was the predictor. Dogs and equids were not included in this last analysis because of the small sample size of losses (dog: n = 23; equid: n = 2) relative to losses of goats (n = 723) and cattle (n = 108).

Economic losses for households

Economic rates of various jobs were inquired from the local markets and departments, and salary ranges were defined to calculate the economic losses and income of communities. Values of domestic animals were also assessed based on market rates around ANP and MF. The average value of a goat was taken as 80 USD (ranging from 60 to 100 USD) in the study area. The price of a cow ranged from 400 to 500 USD (average: 450 USD) and the price of an ox or a bull ranged from 500 to 700 USD (average: 600 USD1).

Verified livestock depredation to households

In ANP and the villages surrounding the Park, data were collected on depredation by the leopard on livestock and other domestic animals. A trained observer regularly visited the villages and maintained contact with local people, forest rangers and wildlife watchers, to collect any depredation reports. Upon receiving a report of depredation, the site was visited to confirm the kill (e.g., through examinations of carcasses, presence of pugmarks, faeces or scrapes). Only verified information was recorded along with the name of the owner, village, type of animal, GPS location, and place of depredation.

The place of depredation was recorded as one of three categories: protected forest (reserve forest or National park), private land (privately owned forest), and house (tied in the courtyard or locked in a hut adjacent to the house). Time of depredation was also recorded and classified as “night” (6:00 pm–6:00 am) or “day” (6:00 am–6:00 pm). When recording location and time, a surplus killing (i.e. cases when more than one livestock individual was killed) was considered as a single predation event.

Interviews to nomadic livestock herders

A total of 73 nomadic livestock herds were recorded in 2012–2014 in ANP and neighbouring areas. These herds move south from northern Pakistan during early summer and return in early autumn. Nomads were interviewed on the causes of losses of their animals during their stay in the study area.

1 One United States Dollar (USD) = 100 Pakistani Rupee (Rs.) at the time of the study.
Human-leopard casualties

Data on leopard attacks on humans (June 2005–January 2015) and common leopard mortality (1998–January 2015) were collected from the Khyber Pakhtunkhwa Wildlife Department, WWF-Pakistan and verified newspaper reports. We interviewed relevant families of the deceased or survivors, to clarify the details of the attack.

Land use changes

Land cover was assessed in 1990 and 2011, to determine any changes. Temporal satellite images (spatial resolution: 30 m, Landsat TM) were downloaded from the United States Geological Survey (www.usgs.gov). Histogram Equalize and Standard Deviation Stretch were applied for classification of land cover classes. These algorithms enhanced the low contrast of satellite images and made them more interpretable for further processing. Moreover, the brightness and contrast utility and different false colour composites (FCCs) were used to enhance and differentiate the features of the same colour tone. Three land cover categories were defined: Forest, Human settlements/agriculture; Other (i.e., bare rocks, open grasses and water channels).

The land cover categories were extracted using Object Based Image Analysis (OBIA) (Flack 1995). In this process, boundaries of the dominant objects were extracted at fine and coarse scales. For interpretation and processing, Digital Image Processing (DIP) software ERDAS Imagine 8.7® and Definien Developer 7.0® were used. All the maps were developed in ArcGIS 10.2.2®.

Ranging movements

An adult male leopard was trapped (1.09.2013), through a box-trap baited with live—but protected—goat, dog or chicken, alternatively. An intramuscular injection of a combination of Ketamine hydrochloride (5 mg/kg) and xylazine (2 mg/kg) was used to tranquillise the leopard, through a low pressure dart gun (Telinject USA, Inc.). Upon sedation, the leopard was measured and weighed (64 kg); its age (c. 5 years old) was estimated on the basis of tooth condition (Standers 1997). The leopard was fitted with a 620 g GPS/GSM collar (Pro Light 1, Vectronic Aerospace GmbH, Germany) and monitored from September 2013 to December 2014 (1 location/7 h; \( N = 1173 \) locations). Total home range size was estimated through the Minimum Convex Polygon, considering all the locations (MCP100%) and 95% locations (MCP95%), and through the fixed kernel method (Worton 1989), considering 95 and 50% locations (K95% and K50%, respectively), over the study period. We assessed the distance between locations and human settlements, considering different periods of the day: dawn (6:00–8:00 am, in winter; 3:00–5:00 am, in summer), day (i.e. from dawn to twilight), dusk (4:00–6:00 pm, in winter; 6:00–8:00 pm, in summer) and night (i.e. from dusk to dawn). We calculated the proportion of locations occurring in or out of the forest. Each season, we initially compared the number of locations in forest/non forest with the numbers expected on the basis of the relative proportions of these habitats in the MCP100% home range, through G-tests. Then, we compared the proportions of locations in each habitat (i.e. use) with the proportion of the seasonal MCP100% home range including forest/non-forest (i.e. availability), to calculate indices of selection, i.e. selection ratios (both non-standardised and standardised, Manly et al. 2002) and the Ivlev index (Ivlev 1961). We also used
a GLM with binomial errors to evaluate whether the proportion of locations occurring in forest differed between seasons and times of day: the habitat where locations fell was the response variable (forest: 1; non forest: 0), whereas Season (summer; winter) and Time of day (day; dusk; night; dawn) were predictors. Analyses were conducted using ArcGIS® 10.2.2 (Hawths tools with home range tool), ArcView GIS 3.1 (extension Animal Movement SAv2.04beta) and R software.

Results

Food habits

Sixty-six scats included two prey items (12.6%, N = 525) and two included three prey items (0.4%). Ten food categories were identified, inclusive of one of unknown remains: major prey species were listed individually and minor prey items (occurring less than five times) were grouped as ‘others’ (Fig. 2; Online Resource 2). Domestic prey was the most frequent prey of the common leopard (AO: 79.9%; RO: 71%), followed by wild species (AO: 21.7%; RO: 19%). Goats were the main prey, followed by domestic dog (Fig. 2). Canids accounted for c. 1/6 of diet, followed by plant material, small carnivores, cattle and monkeys (Fig. 2; Online Resource 2). Wild boar and goral remains were found in only five and four scats, respectively (Online Resource 2). Dietary breadth was narrow (Levins standardised index: 0.06).

Socioeconomic implications: household surveys

The 1016 households interviewed owned 4,967 domestic animals. Eighty-four percent of interviewed households were livestock owners: 92% of them reared livestock for domestic purposes, 7.5% kept it to sale extra milk or, occasionally, an animal, whereas only 0.5% of them kept livestock for livelihood/business purposes (Online Resource 3). Overall, 64.7% of respondents kept at least one goat (two goats: 32.2%; one goat: 25.2%); 45.1% kept at least one cattle; about 15% kept domestic dogs, whereas sheep and equids were rarely kept (<2%).

According to the general perception, leopard depredation was not the main cause of livestock losses (17.8% of respondents, N = 664), however, 47% of households which suffered losses attributed these to the leopard (GLM: B = 1.412, s.e. = 0.143, p < 0.001; Fig. 3). Goats were the most frequently lost livestock (84.5% of cases), followed by cattle (12.6% cases). The probability of depredation by leopards was greater for goats (50.8% of losses) than for cattle (16.7% of losses; GLM: B = 1.645, s.e. = 0.269, p < 0.001; Fig. 3).

Socioeconomic implications: verified livestock depredation

Four hundred and ninety verified cases of depredation by leopards were recorded (goat: 76.1%, cattle: 5.5%, dog: 17.5%, equid: 0.8%), in 446 predation events. Surplus killing occurred in 32 cases (7.2%), and always concerned goats, with the number of individuals killed ranging from two to five. The large majority (66.6%) of predation events occurred during the day. Attacks on livestock occurred mainly in the protected forest (60.1%), followed by houses/private land (39.9%, e.g., livestock tied in the courtyard or locked in a hut adjacent to the house). Out of 307 georeferenced depredation events, most occurred
within a 500 m zone from the forest border (Fig. 4). In particular, about 35% of depredation events in private land \((n = 134)\) occurred within 100 m from the forest border; c. 70% events occurred within 500 m from the border and, overall, about 90% of events occurred within 1000 m from the border. As to predations occurring within the protected forest \((n = 173)\), < 10% occurred at a distance > 500 m from the forest border (Fig. 4).

**Socioeconomic implications: economic losses to households**

Income levels were assessed for the top three represented categories, i.e. irregular (labour, work in hotel, driver, work in factory, security guards, work in shop, tailoring), private
employment, and government employment. About 57% of people were dependent on irregular sources of income (level: 80–120 USD per month), whereas 8.6 and 15.9% of interviewed households had private or government jobs, respectively (income levels: 100–150 USD per month, and 150–200 USD per month, respectively) (Online Resource 4). Less than 1% of interviewed households depended solely on livestock and poultry production (Online Resource 4).

On average, a goat owner lost 2.3 goats/year and a cattle owner lost 1.4 cattle/year. Considering local practices of livestock rearing, where female goats are strongly preferred to males, it has been assumed that 80% of the goats were females. So, 294 goat females are estimated to be lost by 128 households and 74 males by 32 households each year (Table 1). To calculate the percentage of economic losses in terms of the annual income, we considered 80–200 USD as limits for salaries of goat owners and 150–200 USD for cattle owners (Table 1), because the latter had a higher income than the former. A goat owner who suffered losses was likely to lose 8–37% of annual income, while a cattle owner lost 45–92% of annual income, depending on the sex of the individual preyed on (Table 1).

**Socio-economic implications: interviews to nomadic livestock herders**

A total of 23788 livestock were owned by 73 nomadic herders (Online Resource 5). Only 16% out of 577 losses were attributed to leopards, of which, 90% concerned goats. Out of 483 livestock losses caused by diseases or other factors, 86% also concerned goats. In
general, most losses were determined by disease or other causes for all livestock, except for guard dogs, all of which had been killed by leopards (Online Resource 5).

**Socioeconomic implications: human-leopard casualties**

Between June 2005 and January 2015, 19 leopard attacks on people were reported (c. 2 events/year), with 1 casualty/year ($n = 10$, c. 1 out of 2 attacks was lethal). At least 17 attacks occurred in daylight with 6 occurring within 100 m from houses. In 2005, six women were killed with two consumed. On 2011, a leopard killed two children, and both were partially eaten.

Between 1998 and January 2015, 40 leopards were killed by humans (c. 2.5 leopards/year), plus eight which ended up in captivity, in Abbottabad District alone. Available data for this period for the whole of Pakistan provided an alarming number of 105 leopards killed or ending up in captivity, i.e. c. 6 leopards/year.

**Land use changes**

From 1990 to 2011, the area covered by Human Settlements increased by 25.4% (1990: 30.6 km²; 2011: 38.4 km²), while that covered by Forest decreased by 6.6% (1990: 219.4 km²; 2011: 205 km²). The category ‘Other’ increased by c. 1.5% (1990: 418.2 km²; 2011: 424.8 km²). Deforestation occurred mainly in peripheral forested areas (Figs. 1, 4).
| Animal       | Average price | Assumption                  | Milk                                      | Economic value | N individuals lost | Economic loss | Percentage of annual income (%) |
|--------------|---------------|-----------------------------|-------------------------------------------|----------------|-------------------|---------------|---------------------------------|
| Goat female  | 80 USD        | 80% goats were females      | On average: 0.5 l milk per day; Rs. 40/kg; 73 USD/year | 153 USD        | 2.30/household    | 351 USD       | 15–37                           |
| Goat male    | 80 USD        | 20% goats were males        | –                                         | 80 USD         | 2.31/household    | 185 USD       | 8–19                            |
| Cattle female| 450 USD       | 50% cattle were females     | On average: 2 l per day; Rs. 70/l; 510 USD/year | 960            | 1.7/household     | 1658 USD      | 69–92                           |
| Cattle male  | 600 USD       | 50% cattle were males       | –                                         | 600            | 1.8/household     | 1080 USD      | 45–60                           |
Ranging movements

The radio-tagged leopard moved across a total area of 102.2 km² (MCP100%), ranging from 967 to 2454 m a.s.l., encompassing 29112 households in 70 hamlets. Home range size was 91.5 km² (MCP95%), 72.6 km² (Kernel 95%) and 4.2 km² (Kernel 50%). Distances between locations and human settlements ranged between 2.5 and 1063 m, being the closest at dusk and the farthest at dawn, with mean values of 159-256 m (Table 2). Overall, 38% of locations (N=1173) occurred in the forest (summer: 41%, n= 568; winter: 36%, n=605). In both seasons, the number of locations in each habitat differed from that expected on the basis of the relative proportion of forest/non forest (summer: G_adj = 42.307, df = 1, p < 0.001; winter: G_adj = 62.239, df = 1, p < 0.001), indicating a non-random use of forested versus non forested areas. All indices suggested a mild preference for forested areas (selection ratio: 1.57–1.67, standardised selection ratio: 0.66–0.67, Ivlev index: 0.22–0.25). Non-forested areas were approximately under-utilised or used according to their availability (selection ratio: 0.80–0.81, standardised selection ratio: 0.33–0.34, Ivlev index: −0.11/−0.10). The proportion of locations in the forest was the lowest at dusk, and being slightly lower—but not significantly—in winter than in summer (Online Resource 6).

**Table 2** Distance between collared leopard and houses with respect to time and season

| Season/time | Distance from the household in metres | Total fixes |
|-------------|--------------------------------------|-------------|
|             | Min. | Max. | Mean (SD) |             |
| Summer      |      |      |           |             |
| Sunrise     | 2.5  | 903  | 235 ± 154 | 72          |
| Sunset      | 13   | 736  | 187 ± 146 | 80          |
| Day         | 15   | 998  | 216 ± 147 | 270         |
| Night       | 13.5 | 959  | 204 ± 150 | 146         |
| Winter      |      |      |           |             |
| Sunrise     | 31.5 | 685  | 256 ± 136 | 74          |
| Sunset      | 4.1  | 848  | 159 ± 155 | 80          |
| Day         | 15.8 | 722  | 224 ± 134 | 173         |
| Night       | 4.7  | 1063 | 205 ± 131 | 278         |

Discussion

Our results suggest that a low diversity of prey species and the poor conservation status of their habitat emphasise the conflict between a large carnivore and humans by concentrating predation on livestock. In our study area, the absence of wild ungulates made domestic goats, followed by domestic dogs, the most available prey for leopards. In fact, this species tends to prey on meso- (i.e. 2–40 kg) and large mammals (Hayward et al. 2006, mainly for Africa; Lovari et al. 2013a, for Asia). Livestock as the staple of the leopard diet is uncommon (Hayward et al. 2006; Lovari et al. 2013a; Athreya et al. 2014; Shehzad et al. 2014: 4.5%, N=44 studies). In our study area, livestock were free to roam largely unguarded in daylight, but at night were usually locked in poorly constructed sheds. Most
predation events on goats occurred during the day, whereas dogs were often taken at night from sheds or from courtyards. Livestock density in the Abbottabad District was allegedly high (1998: 269 heads/km², AA.VV., 1998), and increasing (Khan 2015), making livestock depredation a viable prey for leopards.

Co-occurrence of humans and leopards led to (i) relevant economic losses to human communities, (ii) direct threats to human life, and (iii) retaliatory killing of leopards. Further negative consequences for the conservation status of the leopard (“critically endangered” in Pakistan, Sheikh and Molur 2004) will continue unless sound conservation measures are urgently implemented. The common leopard is an elusive large predator, rarely seen in daylight, but our data suggest that, despite this, it can remain undetected at a very close range (up to 15 m) to human habitations (see also Athreya et al. 2013). Enhanced predation on livestock may occur, as well as on humans (35% of human attacks occurred within 100 m from houses, in daylight).

Although literature on this topic is limited, the frequency of attacks on humans in our study area (2 events/year) was lower than in other areas, but the percentage of attacks leading to a lethal outcome (c. 50%) was greater than elsewhere (1.6–17 events/year; percentage of lethal attacks: 0–36%, Treves and Naughton-Treves 1999; Athreya et al. 2010, 2013). These events elicited retaliatory killing, with the loss of 2.5 leopards/year, in the Abbottabad District alone, and 6 leopards/year at the national level (105 individuals from 1998 to 2015). These figures indicate that carnivore impacts on human welfare have serious and direct ramifications for leopard conservation.

Livestock depredation is often the proximate consequence of ultimate determinants which range from human habitat manipulation to depletion of wild prey communities (e.g., Meriggi and Lovari 1996; Bagchi and Mishra 2006). Financial compensation for livestock losses may not solve the ultimate determinants of livestock depredation. In our study area, the near-absence of wild ungulates exacerbates livestock depredation (e.g., Meriggi and Lovari 1996; Bagchi and Mishra 2006). Wild ungulates (e.g., goral, wild boar and musk deer) are potential prey for common leopards (Lovari et al. 2013a), but are unavailable in our study area. In Pakistan, the goral is listed as ‘Vulnerable’ (IUCN Red List of Pakistan, Shiekh and Molour 2004) and is threatened because of poaching, habitat loss, disease and competition with livestock (Chaiyarat et al. 1999; Abbas et al. 2009; Perveen et al. 2013). While the wild boar is present in our study area, although rare, the musk deer has been extirpated. In turn, the reintroduction and enforced legal protection of wild ungulates are urgently required. These operations are challenging, because of several limitations: (i) availability of source areas from which a sufficient number (n > 30 individuals) of founders may be taken; (ii) availability of a suitable habitat to reintroduced prey; (iii) prevention of poaching, especially in the initial stages of reintroduction; (iv) transportation, release and appropriate monitoring (e.g., radio-tracking) of the founders; (v) financial support and commitment of government functionaries (cf. IUCN 2012). Survival of wild ungulates can only be ensured if the size of the area under effective legal protection is appropriate and if free livestock grazing is restricted, to limit potential for competition and disease transmission (e.g., Mishra et al. 2001; Bagchi et al. 2004).

In our study area, people kept a relatively small number of livestock and did not depend on them for their livelihood, but for domestic purposes (e.g., to have milk for the family). Nearly 20% of households lost livestock to leopards (13.4% of total heads) over a study period of 12 months, with a relevant economic loss of 8–37% and 45–92% of annual income for goat or cattle owners, respectively. Not surprisingly, interviews of households indicated that the perception of human-leopard conflict was greater among respondents who suffered losses than it was among people who did not suffer them. Our figures still
suggest a remarkably high depredation level (cf. 2.3–4.5% of livestock losses and c. 3–19% of economic value, Oli et al. 1994; Butler 2000; Patterson et al. 2004; Wang and Macdonald 2006; Holmern et al. 2007). Financial compensations were very low and were given on an ad hoc basis, which is likely to have no positive impact on the conflict between human communities and leopards (Khan 2015). We suggest that effective protection measures for livestock (i.e. leopard-proof sheds) and a sound scheme for financial compensation of losses be urgently implemented to limit the economic impact of livestock depredation and mitigate the conflict, in the short-term (e.g., Wang and Macdonald 2006; Mishra 2016). Measures preventing intensive depredation are important even if wild prey becomes available again through reintroductions. Livestock depredation will not decrease considerably if goats/cattle are kept readily available to leopards and are not properly guarded (Suryawanshi et al. 2013).

Disease, winter severity and other minor causes contributed to livestock losses more than leopards (Fig. 3). Improved management practices have the potential to reduce the impact of alternative mortality factors, e.g., suitable winter sheds and/or an appropriate health management of livestock, including financial incentives to veterinary service or livestock insurance plans (Dickman et al. 2011) to offer long-term solutions to reduce losses. A decrease of overall losses may also limit the perception of the negative effects of livestock depredation by leopards.

Prey depletion has been linked to forest exploitation. A rapid increase in loss of forested areas has been a major consequence of the growth of human population. Also in strongholds of leopards, communities are highly dependent on natural resources for fuel wood, fodder collection, medicinal herbs, livestock grazing, construction material, water and other non-timber forest products, all of which increase the probability of human-leopard conflicts. Our results show that deforestation is emphasised at peripheral forested areas and that depredations are likely to occur close to forest borders, which makes deforestation a further factor in human-leopard contacts. The common leopard is an ambush/stalking predator (e.g., Kruuk and Turner 1967; Bailey 1993; Karanth and Sunquist 1995, 2000) which inhabits mainly forested habitats (e.g., Karanth 2013; Lovari et al. 2013b). Home range size can be expected to be an inverse function of habitat quality/quantity, in particular prey abundance (Harestad and Bunnell 1979). If so, habitat manipulation has caused the impoverishment of habitat quality for leopards, as suggested by the large size of the area used by the radio-tracked individual (91.5 km²; MCP95%; 72.6 km²; Kernel 95%; vs. c. 17–50 km² for males, with different estimators/time scales, in Asia: Rabinowitz 1989; Grassman 1999; Karanth and Sunquist 2000; Odden and Wegge 2005; Simcharoen et al. 2008; Odden et al. 2014). The area used by the radio-tagged individual in our study was c. 2–3 times larger than the whole protected area (Ayubia National Park), and the leopard was located regularly very close to human settlements. Male cats do not travel only to search for prey, but also for territory patrolling. Moving across a large area may increase energy costs (e.g., Wang et al. 2017; Wilmers et al. 2017; Smith et al. 2017). In an area intensively used by people, all this tends to increase the consumption of domestic prey and exacerbates conflict with humans (e.g., Smith et al. 2016; Wang et al. 2017). If this decreasing trend of forested areas continues, contact between humans and leopards will initially increase, thus in the end increasing the frequency of lethal encounters, for both humans and leopards.

Our results emphasise the role of wild herbivores in a mammal community as a buffer against livestock depredation (cf. Meriggi and Lovari 1996; Bagchi and Mishra 2006), provided that livestock is not made easily accessible to predators and suitable habitat is available. In turn, a positive feedback could be generated, favouring carnivore persistence and human well-being through the limitation of human-carnivore conflicts. Promoting
the conservation of herbivores and their habitat should be linked to livelihood improvement of communities (Jackson and Wangchuk 2004; Sillero-Zubiri and Laurenson 2001). Improvement of management measures for livestock (e.g., protection and access to veterinary facilities), livestock insurance and/or compensation would be important to limit losses and should come together with actions against the ultimate determinants of the conflict, i.e. habitat degradation and absence of wild prey. We strongly suggest that a bottom-up conservation approach, leading to the increase of local diversity of prey and to habitat improvement (i.e. forest protection/restoration), would indirectly favour the conservation status of the common leopard and would also protect communities against impacts of climate change, i.e. flash floods. As a consequence, the welfare of human communities would improve through (i) a reduced reliance on livestock by leopards, and (ii) a consequent decrease of lethal encounters with humans. Prey depletion, forest fragmentation and shrinking, human encroachment and the ensuing human-carnivore conflict jeopardise the survival of top predators. In spite of its great ecological flexibility (Stein et al. 2016), the common leopard makes no exception. If so, the conservation of different components of ecosystems, from plants to animals, will provide indirect benefits also to species which may not be the direct focus of implemented actions.

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