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Original article

Snow leopard *Panthera uncia* predation on livestock and wild prey in a mountain valley in northern Nepal: implications for conservation management

Per Wegge, Rinjan Shrestha & Øystein Flagstad

The globally endangered snow leopard *Panthera uncia* is sparsely distributed throughout the rugged mountains in Asia. Its habit of preying on livestock poses a main challenge to management. In the remote Phu valley in northern Nepal, we obtained reliable information on livestock losses and estimated predator abundance and diet composition from DNA analysis and prey remains in scats. The annual diet consisted of 42% livestock. Among the wild prey, bharal (blue sheep/naur) *Pseudois nayaur* was by far the most common species (92%). Two independent abundance estimates suggested that there were six snow leopards in the valley during the course of our study. On average, each snow leopard killed about one livestock individual and two bharal per month. Predation loss of livestock estimated from prey remains in scats was 3.9%, which was in concordance with village records (4.0%). From a total count of bharal, the only large natural prey in the area and occurring at a density of 8.4 animals/km^2 or about half the density of livestock, snow leopards were estimated to harvest 15.1% of the population annually. This predation rate approaches the natural, inherent recruitment rate of this species; in Phu the proportion of kids was estimated at 18.4%. High livestock losses have created a hostile attitude against the snow leopard and mitigation measures are needed. Among innovative management schemes now being implemented throughout the species' range, compensation and insurance programmes coupled with other incentive measures are encouraged, rather than measures to reduce the snow leopard's access to livestock. In areas like the Phu valley, where the natural prey base consists mainly of one ungulate species that is already heavily preyed upon, the latter approach, if implemented, will lead to increased predation on this prey, which over time may suppress numbers of both prey and predator.

Key words: bharal, blue sheep, diet, genetic sampling, naur, Panthera uncia, predation, Pseudois nayaur, scat analysis, snow leopard, wildlife conflict

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In a human-dominated world, conserving viable populations of large carnivores is becoming increasingly difficult because large carnivores prey on livestock, kill and injure humans and compete with humans by preying on attractive game species (Treves & Karanth 2003). Predation by snow leopards *Panthera uncia* on domestic stock is a typical example of the human-wildlife conflict (Bagchi & Mishra 2006), and it is considered a main challenge for developing proper management programmes for the species (Mishra et al. 2003, Jackson et al. 2010).

Snow leopards occur in fragmented populations throughout the mountain ranges of the Himalayas and Central Asia (Fig. 1) and are listed as 'endangered' by the World Conservation Union (IUCN 2006). The species feeds on a wide range of natural

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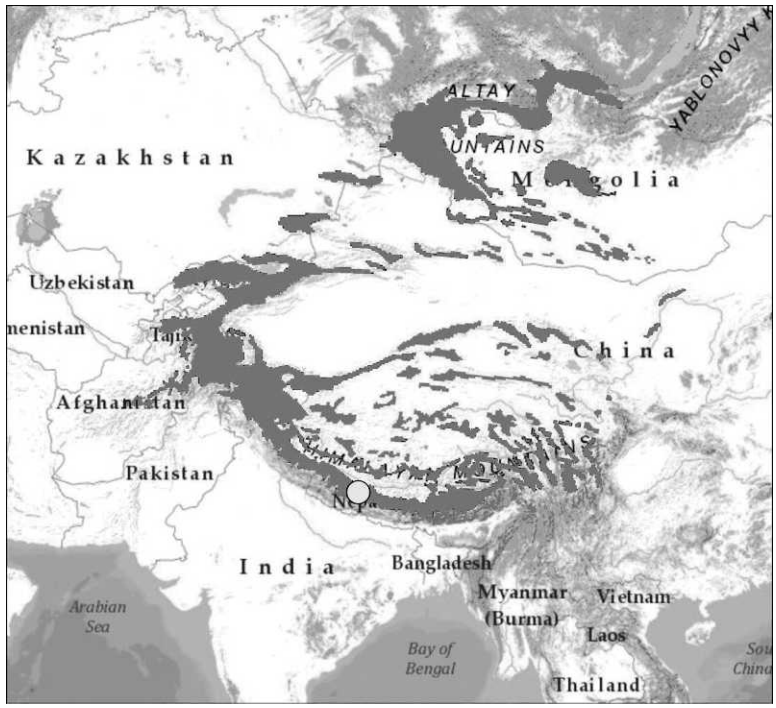


Figure 1. Global distribution of snow leopards, redrawn from Fox (1994). Our study area in Nepal is indicated by the circle displayed on the map.

prey, but like other large felids, it prefers larger ungulates because these confer most net energetic gain per unit effort expended. Thus, throughout its wide range, bharal (blue sheep/naur) *Pseudois nayaur* and Asiatic ibex *Capra ibex* constitute its preferred and stable, natural diet.

In Nepal, the snow leopard is one of the least understood and most threatened wildlife species, with an estimated national population of 350-500 animals (Jackson et al. 2002). In this area, like elsewhere throughout its range, poaching for skin and killing by local farmers in retaliation for livestock losses constitute a major threat to its survival. In order to implement appropriate conservation and management programmes, knowledge of the impact that snow leopard predation has on its natural prey and of the role that livestock play in its diet is required.

In our study in a mountain valley in Nepal, we estimated the composition of the snow leopard's diet from the prey content in scats. We used individual identification by DNA profiles from the scats and combined the proportion of known livestock losses with the food requirements of snow leopards to arrive at two independent estimates of the number of snow leopards in the valley. From a census of the local bharal population, we then estimate the annual predation rates on bharal and livestock and discuss how these figures may have general implications for the conservation management of snow leopards.

Material and methods

Study area

We conducted our study within an area of ca 125 km^2 in the upper part of the Phu valley (28°46'N, 84°17'E) of Manang District in north-central Nepal. Running north-south, the rugged and narrow valley originates in the high mountains along the Nepal-Tibet border. The mountains in the north present a barrier to animal movement, and the lower part extends into lower-elevation conifer forests. Westwards, the valley connects to other mountain valleys with similar flora and fauna permitting animal movement, whereas the eastern border is quite rugged with a less readily exchange of animals. A small village of 33 households of Tibetan-speaking people in the middle of the valley subsists mainly on animal husbandry, herding nearly 2,000 livestock in the surrounding pastures between 3,500 and 4,500 m. a.s.l. As part of the Annapurna Conservation Area Project, the village has established a snow leopard conservation committee, which keeps a record of all livestock losses due to snow leopard predation. The valley has a relatively dense population of bharal, the principal

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natural prey of snow leopard, and about twice as many livestock (Shrestha & Wegge 2008a). Snow leopard and bharal are the only naturally occurring large, wild mammals.

Collection of scats

As part of a study of the relationship between domestic and wild ungulates (Shrestha & Wegge 2008a,b), a total of 59 putative snow leopard scats were collected opportunistically within 95 km^2 in the upper, central part of the valley. Of the 59 scats, 36 were subsequently preserved in 70% ethanol, whereas the rest were sun-dried and dry-stored. All samples were kept at room temperature in the laboratory until DNA and diet analyses could be undertaken.

DNA analysis

We extracted DNA from all samples using the PowerMaxTM Soil DNA Isolation Kit (MO BIO Laboratories, Carlsbad, California, USA), which is a DNA extraction method originally designed for isolation of genomic DNA from environmental samples. We diluted the DNA isolates five times prior to Polymerase Chain Reaction (PCR) amplification. For species determination of the samples, we amplified a 330 bp fragment of the mitochondrial cytochrome b (cyt b) gene (Irwin et al. 1991). We performed amplifications in 50 µl reactions containing 2.25 mM $MgCl_2$, 0.2 mM of each dNTP, 1.6 pmol of each primer, 2.5 µg of Bovine Serum Albumine (BSA), 1.5 units of HotStar DNA polymerase (Qiagen) and 2 µl of template. A 15-minute predenaturation step at 95°C was followed by 40 cycles of amplification with 30 seconds at 94°C, 30 seconds at 50°C and 1 minute at 72°C. A final 10-minute extension step was added at the end. PCR products were visualised on a 2% agarose gel. Successful amplifications were subsequently purified by E.Z.N.A. spin columns (Omega Bio-tek, Norcross, Georgia, USA) and sequenced using BigDye terminator cycle sequencing chemistry on an ABI 3130 instrument (Applied Biosystems, Foster City, Califoria, USA), following the protocol provided by the manufacturer.

We verified 41 samples as snow leopard scats, all of which represented one single snow leopard haplotype previously published in Genbank (Accession numbers D28904, EF551004, NC_010638, DQ097339). Of the scats, two represented a canid lineage, but species origin was difficult to assess conclusively due to $> 2\%$ divergence with previously published sequences. It may represent a previously unpublished lineage of the Tibetan wolf *Canis lupus chanco*, but domestic or feral dogs *Canis lupus familiaris* cannot be excluded. The remaining 16 samples were too degraded for reliable species determination.

The samples that we identified as snow leopard scats were analysed further for individual identification using a panel of seven microsatellite markers, specially designed for the target species (Janecka et al. 2008). We used two multiplex panels of PCR amplification, i.e. (1) PUN82, PUN124, PUN327 and (2) PUN100, PUN132, PUN225, PUN229, in 10 µl reactions with conditions and profiles as described above for the cyt b amplification, except for annealing temperature (55°C), amount of DNA polymerase (0.9 units/reaction) and primer amount (Table 1). We ran all genotyping reactions in at least three independent replicates. A single-locus genotype was never accepted before it had showed at least three identical homozygote profiles or two identical heterozygote profiles, which is in accordance with Janecka et al. (2008). As an additional quality control, we calculated the quality index described by Miquel et al. (2006) for all samples. Following the recommendations of Miquel et al. (2006), we dis-

Table 1. Summary statistics for the microsatellite markers applied in our study. Levels of genetic diversity are given in terms of number of alleles. In the panels, A gives expected heterozygosity (H(exp)) and the observed heterozygosity (H(obs)) in the target population. Range refers to the total allelic range observed.

Panel	Marker	Primer[a]	Range	A	H(exp)	H(obs)
A	PUN82	7.5 pmol	110-116	3	0.59	0.50
A	PUN124	7.5 pmol	90-100	3	0.55	0.67
A	PUN327	5 pmol	81-89	2	0.41	0.50
B	PUN100	5 pmol	92-96	3	0.67	0.83
B	PUN132	5 pmol	113-121	3	0.68	0.83
B	PUN225	5 pmol	175	1	0.00	0.00
B	PUN229	10 pmol	107-113	3	0.55	0.67

[a] The primer refers to the amount of both forward and reverse primer.

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carded all samples with a quality index of < 0.625 from the data set.

We performed a sex determination test for all samples that were successfully amplified with the microsatellite markers. We used a Y-chromosome specific marker (SRY; Lyons et al. 1997) with the same PCR profile and conditions as for the cyt b amplification. We ran three replicates per sample and Y-chromosome-specific amplification products were interpreted as males. We used two scat samples from a male in Woodland Park Zoo, Seattle, USA, as positive controls for the sex determination.

Diet analysis

We obtained information on number and types of livestock from field counts and interviews with the livestock owners in the Phu village and with herders in the field. Similarly, we obtained animal losses due to snow leopards and other causes from interviews with all owners and double-checked with the records kept by the village snow leopard conservation committee. Due to strict regulations supervised by the village religious leader (i.e. the abbot), numbers lost, and their causes, were monitored carefully and not inflated for compensatory purposes. Some recently killed animals were found during fieldwork; these individuals appeared later in the village registry, thus confirming that proper records were kept.

We determined the total diet from an analysis of the content of 41 genetically verified snow leopard scats, collected over a period of 16 months. The analysed scats were distributed almost evenly between winter (November-April; N = 23) and the snow-free season (May-October; N = 18). We assigned scats that were considered old when collected during the first month of a season to the preceding season. For the diet analysis, we followed a modified version of the point-frame method originally developed by Chamrad & Box (1964, later modified by Ciucci et al. (2004); instead of using drop pins to select the prey items, we selected the prey items at each intersection (N = 50) in a gridded tray with a pair of tweezers and examined these under a dissecting microscope, or a high power microscope if needed for reliable identification. Bone fragments and a photographic key of mammal hair of most prey species occurring in the area, prepared by Oli (1993), aided us in species identification.

Snow leopard abundance

Two independent sources of information provided estimates of the number of snow leopards in the valley: DNA in scats, and diet composition and loss of livestock.

DNA in scats

We counted the number of unique multilocus genotypes in our final data set, leading to a direct count estimate of the number of snow leopards in the valley. The entire sample collection period was two years, but all animals were identified from samples collected within a five-month period (i.e. January-May). This is still a relatively long sampling period, which likely would violate an assumption of population closure, if we had chosen a capture-mark-recapture approach to estimate snow leopard abundance (e.g. Kendall 1999, Boulanger & McLellan 2001). Given these limitations and considering the rather limited sample size, we chose to use the simple direct count estimate as a measure of snow leopard abundance in all subsequent analyses.

Diet composition and loss of livestock

The analysis of prey remains in scats provided information on the relative proportion of different livestock in the diet. Numbers and types of livestock lost to snow leopard predation were known due to the careful records kept by the local snow leopard conservation committee. Combining this information with the food requirement of snow leopards (see below), we generated an estimate of the number of snow leopards.

Prey abundance

We estimated the number of bharal within our study area from total counts in autumn using binoculars and spotting scopes from vantage points. Sex and age composition followed the criteria adopted by Wegge (1979), subsequently applied by Wilson (1981), Oli (1994) and Shrestha & Wegge (2008b) and was only recorded for groups where all individuals could be classified reliably. Care was exercised to avoid double-counts; because field observations were conducted for several months in the same drainages and animals occupying these rarely crossed over to adjacent major basins, they were readily identified and recognised over time.

Total counts were also conducted the following spring. However, this census took place immediately before and during the birth season, which therefore underestimated the total numbers during the year. Although observed numbers (958) compared closely with the autumn census (1,056), some likely double-

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counts made the spring census less reliable, and it was therefore not used in the final analysis.

Snow leopard predation rates

Food requirement

In order to estimate predation rates, the food requirement of the predator needs to be known as well as the proportion of the prey consumed. Jackson & Ahlborn (1988) estimated that an adult snow leopard required 1.3-2.0 kg of digestible food/day, a consumption rate also applied in other studies (Chundawat & Rawat 1994, Oli 1994, Bagchi & Mishra 2006). Higher values are reported for lowland leopards *Panthera pardus* (Bailey 1993, Hayward et al. 2006). From intensive radio-tracking of lowland leopards in Nepal, Odden & Wegge (2009) recently recorded a daily food intake of 3.3 and 4.3 kg for adult females and males, respectively. In Nepal, the two leopard species are very similar in body weight (adult snow leopards from Manang next to our study area weigh 47 kg for males and 42 kg for females; Oli 1994, and for lowland leopards 51 and 36 kg, respectively; Odden & Wegge 2009). The two species can therefore be assumed to have comparable food requirements. Because the estimate of Jackson & Ahlborn (1988) was based on indirect evidence and several assumptions, whereas that of Odden & Wegge (2009) was based on measurement from carefully monitored animals, we assume that the daily food requirement of adult snow leopards is close to 3.5 kg/animal/day. Because our identified animals consisted of mainly females and a few subadults (see section Results below), we adopted 3.2 kg as a mean estimate of the daily food requirement, which is equivalent to 1,168 kg per year of each snow leopard in the valley, and we used this figure in our calculations.

Proportions consumed of each prey

We took live weights of livestock species from Chundawat & Rawat (1994), Oli et al. (1994) and Mishra et al. (2004) in the following way: domestic yak *Bos* spp. (adult males excluded since they are not killed by snow leopard): 150 kg, horse: 110 kg, goat: 25 kg and sheep: 30 kg. We took live weights of different categories of bharal from Wegge (1979) and Oli (1994). According to our classified counts, the adult sex ratio was at parity, and kids and yearlings constituted 22 and 15.5%, respectively. We assumed that predation was random on sex and age groups and estimated the live weight of all bharal killed as the mean weight of all sex/age categories present in the population. The resulting mean weight was 34 kg. Royle's pika *Ochotona roylei* and other small mammals (mainly voles) were frequently detected in the scats, as were bird feathers and occasionally also egg shells. We assumed the mean live weights of small mammals and birds to be 0.3 kg. A few scats contained hairs that could not be classified reliably. We could exclude large livestock and bharal and supposed that they were from smaller predators like red fox *Vulpes vulpes* and mustelids (Oli et al. 1993), and we assigned a mean live weight of 2 kg to these items. Predators do not consume the whole ungulate carcass of large prey due to inedible parts like large skeletal parts, horns/antlers, rumen content and parts of the skin (Floyd et al. 1978). From careful measurements, Stander (unpubl. data cited in Stander et al. 1997) found that lowland leopards consumed 75% of prey > 25 kg live weight. In our study, we assumed that snow leopards consumed the same proportion of all bharal killed, but smaller fractions of the livestock prey. Like pointed out by Oli et al. (1994), herders usually retrieve the carcasses of livestock quickly after they are killed. Thus among livestock, proportions consumed are even smaller than predicted from their live weights. In our study, we therefore assumed that the leopards consumed the following proportional weights of livestock: yak (females and young) 50%, horse and cattle 60%, sheep and goats 70%. Of the small mammals and birds, we assumed that everything was ingested, whereas of the unknown items, we assumed that 90% was consumed.

Predation rate estimation

Although subject to several sources of potential bias (Rühe et al. 2008), most studies attempting to quantify carnivore predation rates are based on analysis of scat contents. Frequency of occurrence of individual prey items are converted to biomass and numbers consumed according to the relationship between scat production and prey size (Floyd et al. 1978, Ackerman et al. 1984) in the following way: $Y = 1.980 + 0.035X$, where Y is the weight of prey consumed/scat and X is the live weight of the prey (in kg).

Derived from experimental feeding trials on cougar *Felis concolor* and widely used in diet studies of other felids (Wegge et al. 2009 and references therein), we used this equation to estimate the relative weights consumed and numbers killed of the different prey species in the diet. The village records provided an independent estimate, in our case believed to be realistic and not inflated, of the

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number of different livestock species killed by snow leopards. Comparing this estimate with the estimate from scats provided a quality control of the methods employed. The difference between the total food requirement of the number of snow leopards in the valley and the food contributed by livestock consisted of wild prey.

Results

Number of snow leopards

Estimate from scat DNA

Of the 41 positive snow leopard samples, 20 gave DNA of sufficient quality and quantity for reliable genetic identification analysis from a complete DNA-profile. The occurrence of genotyping error was low. On average, allelic drop-out occurred in 7.0% of heterozygous amplifications, whereas the presence of false alleles was negligible ($< 0.5\%$). The average quality index of samples that gave a readable DNA profile was 0.88. The genetically identified samples were distributed within ca 43 km^2 (Fig. 2).

From the 20 successfully genotyped scats, six individuals (four females and two males) were identified (see Fig. 2). Based on the observed allele frequencies of the applied loci, we estimated the probability of identity (PI) to be 4.8×10^{-6} for unrelated individuals and 0.03 for siblings, suggesting that different individuals could be distinguished reliably in the valley (*cf.* Waits et al. 2001). Among these individuals, six loci were polymorphic showing 2-3 alleles/locus (see Table 1). Averaged across the six polymorphic loci, the number of alleles (A) was 2.83 and the observed heterozygosity was 0.67. This level of genetic variation is intermediate between that found in two previously screened populations in northern India (A = 3.1 and Hobs = 0.75) and southern Mongolia (A = 2.5 and Hobs = 0.51; Janecka et al. 2008).

All six individuals in the Phu valley were identified from 14 scats collected during the course of five months. The positive male controls amplified consistently across all replicates, confirming that the sex determination protocol worked satisfactorily. Pugmarks of a female with large cubs was observed in the field during autumn prior to sample collection, and it is therefore likely that some of the animals observed in the sample were subadult animals. Of the identified females, one was represented in seven samples, and we hypothesise that she was the most likely resident female in the area. With only six identified individuals in our data set, we could not undertake statistically based relationship analysis. Nevertheless, inspection of the DNA-profiles from the identified individuals showed that the putative resident female could be the mother of several of the other individuals sampled within her range.

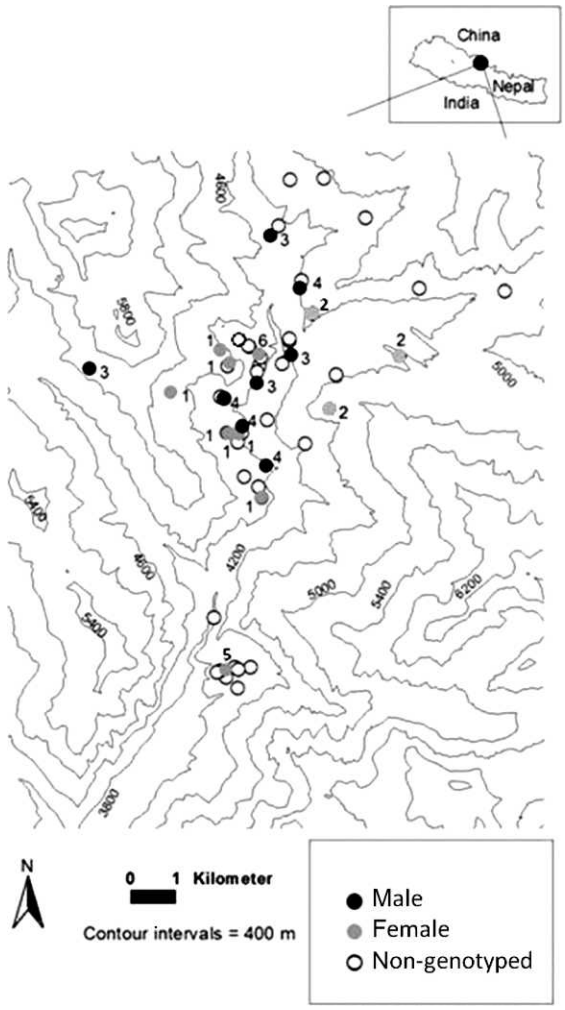


Figure 2. Distribution of the snow leopard scats identified by our DNA analysis in the upper Phu valley, north-central Nepal.

Estimate from livestock losses

During the study period, the village records reported an average annual loss of 78 livestock animals to snow leopards, of which the predator consumed an estimated 2,382 kg (Table 2). According to the diet analysis from scats, one snow leopard was estimated to consume 419 kg of livestock/year (Table 3). Thus, when combining these sources of information, the number of snow leopards causing this livestock loss

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Table 2. Annual consumption by snow leopards and their predation on livestock and wild prey in the Phu valley, Nepal, during 2002-2003, determined on the basis of scat analysis (SA) and village records (VR).[1]

Species	Total live population[2]	Consumed (kg)[3]		Numbers killed		Predation loss (%)[4]	
		SA	VR	SA	VR	SA	VR
Goat	650	660	744	37.7	42.5	5.8	6.5
Sheep	372	420	388	20.0	18.5	5.4	5.0
Yak	767	1224	1200	16.3	16.0	2.1	2.1
Horse	181	210	50	3.2	1.0	1.8	0.5
Livestock; total	1970	2514	2382	77.2	78.0	3.9	4.0
Bharal	1056	4051		159		15.1	
Others[5]		440		733			
Wild prey; total		4491		892			

[1] A snow leopard is assumed to consume 1,168 kg of food/year (see text for further details).
[2] Based on household interviews and village records (livestock) and autumn census (bharal).
[3] Net biomass consumed of prey live weight (see Table 1 and the text).
[4] Livestock estimated from total number of livestock species and the bharal from bharal census.
[5] Others include mainly Royle's pika, voles, Gallinaceous birds and smaller carnivores (see text).

was 5.68 animals. This estimate is nearly identical to the direct count estimate of six snow leopards based on our scat DNA analysis above.

Snow leopard diet

In the 41 verified snow leopard scats, we found 52 prey items (plant matter and snow leopard hair excluded). Only 11 scats contained > 1 prey, averaging 1.2 prey/scat. Plant material occurred in 62% of the samples, often dominating the scat content. When corrected for prey sizes, about 42% of the biomass killed consisted of livestock (see Table 3). Among this category, ca 56% was yak. Bharal made up for $> 90\%$ of the wild food, alone making up for ca 53% of the total biomass killed. Although $< 10\%$ of the biomass from wild food consisted of small mammals and birds, one snow leopard was estimated to consume > 110 such individuals annually. The corresponding numbers of livestock and bharal per snow leopard were 13.0 and 26.5, respectively (see Table 3), i.e. an average of about one livestock and two bharal per month.

The seasonal composition of the diets was quite similar, probably due to small seasonal samples ($\chi^2 =$

Table 3. Composition of livestock and wild prey in the diet of snow leopards in the Phu valley, northern Nepal, derived from scat analysis.

Prey item	FO[1]	Live weight (in kg)	Correction factor[2]	Biomass killed[3] (in %)	Number killed[3] (in %)	Weight consumed by one SL[4] (in kg)	No. consumed by one SL[5]
Goat	9.6	25	2.86	9.3	3.6	110	6.3
Sheep	5.8	30	3.03	5.9	1.9	70	3.3
Yak	9.6	150	7.23	23.4	1.5	204	2.7
Horse	1.9	100	5.48	3.5	0.4	35	0.7
Livestock; total	26.9			42.1	7.4	419	13.0
Bharal	50.0	34	3.17	53.4	15.1	675	26.5
Pika/voles	13.5	0.3	0.3	1.4	45.5	24	80.0
Birds	5.8	0.3	0.3	0.6	19.4	10	33.3
Others	3.8	2.0	2.0	2.6	12.6	40	22.2
Wild prey; total	73.1			58.0	92.6	749	162
						1168	

[1] Frequency of occurrence of prey item in the scats.
[2] As a basis of the correction factor, prey weight consumed = 1.98 + 0.035 (prey live weight) - Ackermann et al. (1984).
[3] Biomass killed was based on the obtained correction factors.
[4] Weight consumed by one snow leopard/year: from relative number and net weight of species killed, adjusted to daily food consumption of 3.2 kg (1,168 kg/year).
[5] Number consumed by one snow leopard/year was based on total weight consumed/species divided by its net live weight.

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5.55, df = 6, $P > 0.475$). A higher proportion of livestock, and conversely, a smaller proportion of wild prey in winter was not significant ($P = 0.43$; Fisher's Exact Test). Voles and birds occurred more frequently and bharal less frequently during the snow-free season than in winter, but the differences were not significant ($P > 0.36$; Fisher's Exact Test). Pika was found almost exclusively in the winter scats.

Predation rates on livestock and bharal

According to the village records, 78 livestock out of a total stock of 1,970 animals were killed annually in 2002 and 2003; i.e. a predation rate of 4.0% (see Table 2). Among species, 6.5% of the goats, 5.0% of the sheep and 2.1% of the yaks were lost due to snow leopard predation. Our estimate based on scat analysis revealed a similar composition of the predation rates; the only difference was a slightly lower proportion of goats (see Table 2). We ascribe the higher estimate of horses to sampling bias due to their very low frequency. We recorded a total of 1,056 bharal, estimated to consist of 194 kids, 165 yearlings and 350 and 347 adult males and females, respectively, during the autumn census. Thus, the proportion of kids in the population was 18.4%. An estimated 159 animals were killed by snow leopard each year, equating an annual predation rate of 15.1% (see Table 2).

Discussion

Snow leopard is a low-density species occupying rugged terrain, which is not easily sampled. Due to the difficulty of obtaining adequate sample sizes and site-specific information on all the parameters that enter into the process of estimating diet and predator abundance, the results rest, unavoidably, on several assumptions. Nevertheless, potential errors are not expected to have affected our general outcomes and conclusions. For instance, our assumption of a higher daily food requirement than previously reported may, at first glance, have produced an inflated predation rate on bharal. However, our abundance estimate derived from the genetic analysis was quite conservative and compared closely with the number generated from the known losses of livestock. The six animals identified by the DNA analysis originated from scats collected within an area of ca 43 km^2. Converting this into a density estimate by use of the 'radial' method (Otis et al. 1978), using a mean radius of 2.06 km derived from home-range studies as shown by McCarthy et al. (2008), produced an area of 98 km^2, which corresponds closely to our ca 125 km^2 study area occupied by the sampled bharal population and the area grazed by livestock. Also, the estimated densities of ca 6.0 snow leopards/100 km^2 and 8.4 bharal/km^2 in the Phu valley compared closely with the densities recorded in the adjacent Manang valley by Oli (1994; snow leopard 4.8-6.7/100 km^2 and bharal 6.6-10.2/km^2).

We took the proportions of live weights assumed to have been ingested of the different prey species partly from secondary sources. For domestic stock, we used slightly lower percentages owing to the local practice of retrieving depredated animals shortly after they had been killed. The proportions we used for small stock could still have been too high, as carcasses of these were retrieved rather quickly by the attending herders. In our model, however, lower proportions of sheep and goats consumed would mean a higher number of snow leopards, which would push the estimated predation rate on bharal even closer to the balancing recruitment rate (see below).

All food studies in the Himalayas have shown that livestock constitutes an important part of the diet of snow leopards (Oli et al. 1993, Chundawat & Rawat 1994, Jackson et al. 1996, Ikeda 2004, Bagchi & Mishra 2006, Namgail et al. 2007, Lovari et al. 2009). Our results confirm this. In the Phu valley, it constituted about 42% of the biomass killed or 36% of the biomass consumed (due to smaller proportions of the livestock carcasses ingested). At two different study sites in the Indian Trans-Himalaya, Bagchi & Mishra (2006) reported 58 and 40% livestock loss to snow leopards. The higher proportion was obtained in an area with a higher density of livestock and a lower density of bharal compared to the Phu valley, whereas in the other area densities of both livestock and ungulate prey (ibex) was similar to our study area in the Phu valley.

Our estimate of 3.9-4.0% livestock loss in the Phu valley due to snow leopard predation was higher than in the neighbouring Manang valley (2.6%) with a nearly equally abundant population of snow leopards (Oli et al. 1994). In monetary terms, such losses are quite substantial for poor mountain people. For the households in Manang, Oli et al. (1994) estimated the loss to represent nearly a quarter of the average annual Nepali national *per capita* income at that time. In the Phu valley, the average livestock holding was more than twice as large as in Manang (59.0 vs 26.6 animals/household,

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respectively), and people in the remote village Phu were more dependent on their stock animals for subsistence than in Manang. Thus, livestock losses due to snow leopards were clearly a serious problem in the valley, as it is in most areas where the species occurs.

Bharal is a monotocous species and rarely breeds before two years of age (Schaller 1977, Wegge 1979). With such a low inherent fecundity, annual mortality $> 20\%$ may exceed recruitment and lead to a population decline (Wegge 1997). According to our census data, the autumn population in the Phu valley consisted of 18.4% kids and the annual predation loss was estimated at 15.1%. Hence, the loss from predation by snow leopards was close to the balancing recruitment rate and was clearly a main mortality factor for the bharal population. If livestock were to be excluded as food and the snow leopards were to obtain this food instead from bharal, they would have to kill an additional 68 bharal, thereby raising the predation rate on this species to 21.5%.

Implications for conservation

The difficult task of finding a balance between conserving the endangered snow leopard and reducing the losses of poor mountain communities associated with livestock loss has recently been addressed by several innovative programmes throughout the species' range (Jackson et al. 2002, Mishra et al. 2003). Whereas earlier mitigation measures mainly consisted of preventing the livestock from being killed (e.g. corralling, stall feeding and improved herding practices), recent approaches focus more on compensation schemes and other incentive programmes (Mishra et al. 2003, Jackson et al. 2010).

Theoretically, reducing livestock grazing pressure by reducing stock numbers and/or expanding stall-feeding may improve pasture quality for the bharal and thereby raise their productivity. Similarly, increased predation on bharal (due to less available livestock) and thereby lowering their standing biomass may also improve range conditions. Such a response assumes (1) that ranges are overgrazed, (2) that bharal and livestock use the same habitats and food plants and (3) that the bharal population is regulated by density-dependent factors. Our recent studies of livestock-bharal relationships in the Phu valley (Shrestha & Wegge 2008a,b) showed that although the two species groups overlap in both habitat and food, competition is not acute due to resource partitioning. At the same time, the relatively low recruitment rate of 56 kids/100 females in autumn (Shrestha & Wegge 2008b) could reflect relatively poor range conditions, possibly mediated through overstocking by livestock (Mishra et al. 2004), or it could reflect a very high predation pressure on young animals.

From his study in Manang, Oli (1994) concluded that snow leopards killed livestock because they were abundant and easy to kill, not because they were an important food source. Oli (1994) went on to conclude that reducing access to livestock food is unlikely to affect the local predator population. We do not share this optimistic prediction. Livestock was found to make up for 35 and 42% of the snow leopard's diet in the two areas, respectively, and hence, this food base undoubtedly contributed to maintaining the large number of leopards. In the absence of livestock, other food sources will be required. In the Phu valley, bharal is abundant and the only optimum size of prey available. Other important natural prey species like marmots *Marmota himalayana* (Schaller et al. 1987) and the woolly hare *Lepus oiostolus* are absent, and the pika constitutes suboptimal prey. Thus, if access to livestock food is greatly reduced, snow leopards will most probably increase their predation on bharal, their principal natural prey. As the predation rate on this ungulate is already quite high, a further increase is likely to exceed the replacement rate and reduce their numbers in the valley. Concurrently, the conflict with the pastoralists is likely to escalate as during an interim period, the leopards will prey more intensively on livestock. A lower total food base means reduced carrying capacity, which over time will lead to fewer snow leopards in the valley. Such a scenario was recently well documented in a study of the relationship between the Eurasian lynx *Lynx lynx* and its main natural prey, the roe deer *Capreolus capreolus* in Poland (Schmidt 2008).

Current conservation of snow leopards focuses on compensation and incentive programmes and less on preventing livestock from being killed. Maintaining wildlife populations by supplementary, non-natural food is controversial, and allowing livestock to be killed for the purpose of conserving an endangered species such as snow leopard is certainly not a viable, ultimate solution. Thus, long-term conservation of this charismatic animal requires measures that can sustain local numbers without predation of livestock. This is a difficult challenge, particularly in areas like the Phu valley where the main wild prey consists of only one species and where this food source is already being exploited to near its sustainable limit.

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