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Abstract: Twenty-five years ago, the snow leopard *Uncia uncia*, an endangered large cat, was eliminated from what is now Sagarmatha National Park (SNP). Heavy hunting pressure depleted that area of most medium-large mammals, before it became a park. After three decades of protection, the cessation of hunting and the recovery of wild ungulate populations, snow leopards have recently returned (four individuals). We have documented the effects of the return of the snow leopard on the population of its main wild prey, the Himalayan tahr *Hemitragus jemlahicus*, a 'near-threatened' caprin. Signs of snow leopard presence were recorded and scats were collected along a fixed trail (130 km) to assess the presence and food habits of the snow leopard in the Park, from 2004 to 2006. Himalayan tahr, the staple of the diet, had a relative occurrence of 48% in summer and 37% in autumn, compared with the next most frequent prey, musk deer *Moschus chrysogaster* (summer: 20%; autumn: 15%) and cattle (summer: 15%; autumn: 27%). In early summer, the birth rate of tahr (young-to-female ratio: 0.8-0.9) was high. The decrease of this ratio to 0.1-0.2 in autumn implied that summer predation concentrated on young tahr, eventually altering the population by removing the kid cohort. Small populations of wild Caprinae, for example the Himalayan tahr population in SNP, are sensitive to stochastic predation events and may be led to almost local extinction. If predation on livestock keeps growing, together with the decrease of Himalayan tahr, retaliatory killing of snow leopards by local people may be expected, and the snow leopard could again be at risk of local extinction. Restoration of biodiversity through the return of a large predator has to be monitored carefully, especially in areas affected by humans, where the lack of important environmental components, for example key prey species, may make the return of a predator a challenging event.

Restoring a keystone predator may endanger a prey species in a human-altered ecosystem: the return of the snow leopard to Sagarmatha National Park

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Keywords

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Abstract

Twenty-five years ago, the snow leopard *Uncia uncia*, an endangered large cat, was eliminated from what is now Sagarmatha National Park (SNP). Heavy hunting pressure depleted that area of most medium–large mammals, before it became a park. After three decades of protection, the cessation of hunting and the recovery of wild ungulate populations, snow leopards have recently returned (four individuals). We have documented the effects of the return of the snow leopard on the population of its main wild prey, the Himalayan tahr *Hemitragus jemlahicus*, a ‘near-threatened’ caprin. Signs of snow leopard presence were recorded and scats were collected along a fixed trail (130 km) to assess the presence and food habits of the snow leopard in the Park, from 2004 to 2006. Himalayan tahr, the staple of the diet, had a relative occurrence of 48% in summer and 37% in autumn, compared with the next most frequent prey, musk deer *Moschus chrysogaster* (summer: 20%; autumn: 15%) and cattle (summer: 15%; autumn: 27%). In early summer, the birth rate of tahr (young-to-female ratio: 0.8–0.9) was high. The decrease of this ratio to 0.1–0.2 in autumn implied that summer predation concentrated on young tahr, eventually altering the population by removing the kid cohort. Small populations of wild *Caprinae*, for example the Himalayan tahr population in SNP, are sensitive to stochastic predation events and may be led to almost local extinction. If predation on livestock keeps growing, together with the decrease of Himalayan tahr, retaliatory killing of snow leopards by local people may be expected, and the snow leopard could again be at risk of local extinction. Restoration of biodiversity through the return of a large predator has to be monitored carefully, especially in areas affected by humans, where the lack of important environmental components, for example key prey species, may make the return of a predator a challenging event.

Introduction

There is a delicate balance between the numbers of prey and predators in undisturbed pristine areas, with the prey outnumbering predators that subtly regulate prey dispersion and quality (e.g. Errington, 1956; Mech, 1970; Kruuk, 2002). The mechanisms of regulation of prey numbers by carnivores are unclear (Bowyer, Person & Pierce, 2005), but predation is assumed to be a density-dependent event, unlikely to lead a prey population to extinction (Ballard & Van Ballenberghe, 1997, but see Kavanagh, 1988). When predators and prey are large mammals, predator–prey systems become even more complicated, for example because of time lags in the numerical responses of both

predator and prey, weather effects and variation in the availability of alternative prey (Festa-Bianchet & Côté, 2008). Disease may also play a relevant role by increasing mortality or abortion rates and by depressing the fertility of males (e.g. Caughley & Sinclair, 1994; Tompkins *et al.*, 2002). These systems may become especially complex in areas where humans have altered the local ecological parameters, for example by removing some prey species or by introducing an alien predator (Macdonald & Thom, 2001; Courchamp, Chapuis & Pascal, 2003). The initial impact of a predator on naïve wild prey may be substantial (Haller, 1992; Poulle, Carles & Lequette, 1997). Moreover, when predation by a large carnivore concentrates on one particular species, for example because other prey have declined or

disappeared, the risks of a local negative impact will increase (e.g. Munoz, 1982; Sweitzer, Jenkins & Berger, 1997; Kamler *et al.*, 2002). Most likely, livestock depredation will also increase (Meriggi & Lovari, 1996; Kolowski & Holekamp, 2006) with the depletion of wild prey. There may be particularly heavy conservation costs when one or both taxa (the predator and the prey) are threatened, unless a long-term balance is reached between them.

High-altitude ecosystems are delicate and often their communities of large mammals are relatively depauperate, making them particularly sensitive to removal or addition of species. In turn, this may lead to management problems, especially when species of conservation concern are involved.

Fragmentation of continuous populations of wild mountain ungulates may not be manifest as lethal effects over relatively short time periods. However, the risk of rapid extinction will increase when stochastic predation by specialist carnivores impacts small, isolated populations (Festa-Bianchet *et al.*, 2006). In fact, predator–prey equilibria may only develop at large geographic and temporal scales, especially when strongly phylopatric prey are concerned, for example *Caprinae* (*Bovidae*) and *Cervidae* species. Even prey populations with a biomass theoretically sufficient to sustain predators may suffer severe negative effects, eventually leading to near extinction, when predation is systematically eliminating females (Festa-Bianchet *et al.*, 2006) or the annual recruitment from a population (Haller, 1992).

In the Sagarmatha (Mt. Everest) National Park (SNP), centuries-old efforts by the Sherpa people to decrease livestock losses to carnivores have reduced the populations of feline and canine predators (Brower, 1991). Furthermore, soldiers stationed at an Indian Army post, at 3500 m a.s.l., during the 1950s, are claimed to have overhunted birds and mammals (Brower, 1991). No data are available for predator densities in SNP before the 1960s. Since then, there have been several reports of the occasional presence of the snow leopard *Uncia uncia* in the Park and its environs, but with no resident population. The SNP was established in 1976 and, after three decades of protection measures, snow leopards have returned (Ale & Boesi, 2005; Ale & Lovari, 2005; Ale, Yonzon & Thapa, 2007). Reliable information on their numbers and population stability is not available. The present local spectrum of wild prey for the snow leopard is particularly narrow compared with other areas (e.g. Schaller, 1977; Oli, Taylor & Rogers, 1993; Jackson, 1996; Schaller, 1998): just two species of wild artiodactyls and several gallinaceous birds. Domestic sheep and goats were removed from the Park when it was established, but several thousands of cattle occur in the Park. Thus, this area provides a simplified predator–prey system, and offers an opportunity to analyse the initial pattern of predation and the effect of the return of a large predator on prey populations.

The snow leopard is an endangered large cat [2500–5000 breeding individuals in the wild] because of habitat loss and persecution (IUCN/SSC, <http://www.redlist.org>, accessed 24 March 2009]. Included in CITES Appendix I, the snow

leopard is also protected by national legislation across most of its range (Nowell & Jackson, 1996). Its distribution extends over a patchy and fragmented habitat in Central Asia (1.6 million km², most of which is in Tibet and other parts of China; Fox, 1994).

This large cat inhabits the entire Himalayan range, albeit at low densities (five to 10 individuals per 1000 km²; Nowell & Jackson, 1996). In Nepal, its numbers range from 100 individuals per 1000 km² in the Langu Valley to one to five individuals per 1000 km² in most other areas, with an approximate total number of 350–500 individuals [Department of National Parks & Wildlife Conservation (DNPWC), 2005]. Livestock depredation, retaliatory killing, poaching and habitat loss due to the high density of livestock all threaten the long-term viability of this large cat in Nepal (DNPWC, 2005), where it has had protected status since 1973 (National Parks and Wildlife Conservation Act 2029, 1973).

There have been only two long-term (≥ 2 years) studies on its biology, mainly dealing with ranging movements (Jackson, 1996; McCarthy, Fuller & Munkhtsog, 2005). Several studies have examined food habits, but with sampling limited to 1 year of collection (Oli *et al.*, 1993; Bagchi & Mishra, 2006; Sharma *et al.*, 2006) or to just one season (Schaller, 1977; Schaller, Ren & Qiu, 1988). No study has quantified the effects of snow leopard predation on prey populations, although information on these aspects could help predict, understand and possibly prevent conservation problems elicited by predation on livestock. Here we document the effects of the return of the snow leopard on the population of Himalayan tahr *Hemitragus jemlahicus*, a near-threatened caprin (IUCN/SSC, <http://www.redlist.org>), in SNP. The Himalayan tahr and the snow leopard coexist in a part of the distribution range of the former, but alternative, preferred prey, especially the blue sheep *Pseudois nayaur*, are usually present, thus reducing predation on tahr (Oli *et al.*, 1993; Jackson, 1996).

In particular, we have examined whether (A) the predator tends to concentrate predation on one sex or age class of the prey; (B) predation can severely alter the population structure of the prey.

Methods

Study area

SNP lies in the Solu-Khumbu district of north-east Nepal and encompasses the upper catchment of the Dudh Kosi River system (Fig. 1). It includes several of the highest mountains in the world (Everest, Lhotse, Cho-oyu: all over 8000 m high), as well as valleys < 3000 m.

The Subalpine belt of vegetation in the SNP includes forests of *Abies* spp., *Betula utilis* and *Rhododendron* spp., replaced higher up by the Alpine zone (4000–5000 m) with *Juniperus* spp. and *Rhododendron* spp. Beyond 5000 m, mosses, lichens and Alpine grasslands comprise the climax vegetation (Buffa, Ferrari & Lovari, 1998). The Park has a rich avifauna (e.g. Laiolo, 2003), with a relatively depauperate community of large mammals. The dhole *Cuon alpinus*,

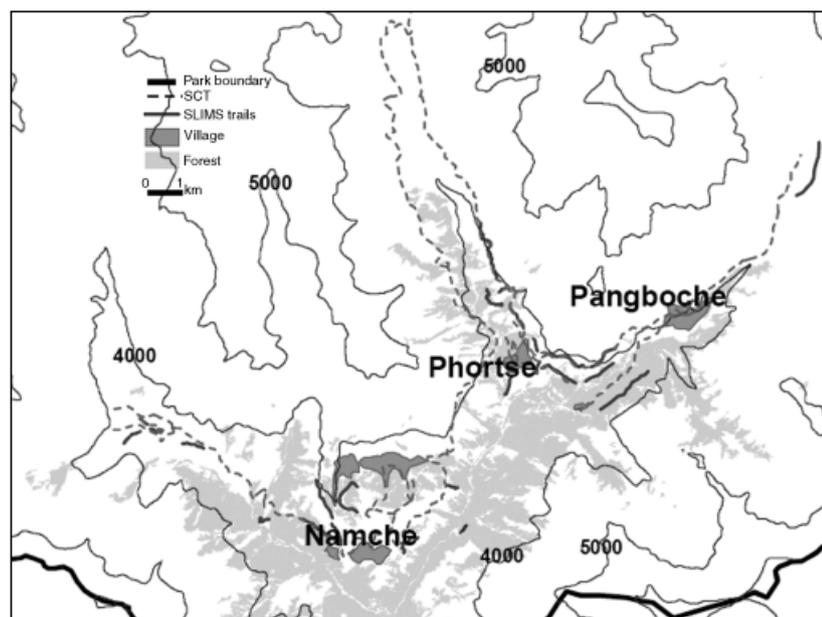


Figure 1 Study area, in Sagarmatha National Park (114 800 ha, 86°30'53"–86°99'08"E and 27°46'19"–27°6'45"N), with forest distribution, as well as valley trails used for scat collection (SCT) and Snow Leopard Information Management System (SLIMS).

the wolf *Canis lupus* and the golden jackal *Canis aureus* were present formerly, but were eliminated over two decades ago due to human persecution. Presently, the only large predators living in the Park are the snow leopard and the common leopard *Panthera pardus*, the former occurring above 3500 m, in the open areas, and the latter in the forest, usually at lower altitudes. Among ungulates, the Himalayan tahr (*c.* 300–350 individuals, until 2003; Lovari *et al.*, 2009), the relatively abundant musk deer *Moschus chrysogaster* and the rare Himalayan serow *Capricornis sumatraensis* inhabit the Park (Lovari, Ale & Boesi, in press). With respect to livestock, 2000 domestic yak *Bos grunniens* and their hybrids with zebu cattle *Bos indicus* occur in the Park (Brower, 1991; Ale & Lovari, 2005). Often, these cattle are left unguarded above the upper tree line, in small groups (usually <10 individuals). At night, they may return to rudimentary sheds.

The main study area lies between the villages of Namche (3440 m a.s.l.), Phortse (3849 m a.s.l.) and Gokyo Lake (4750 m a.s.l.), where a minimum density of one to three snow leopards per 1000 km² was estimated in November 2004 (Ale & Lovari, 2005). For a detailed description of the main climatic and vegetational aspects of this area, see Buffa *et al.* (1998).

Assessment of presence

We used the techniques recommended in the Snow Leopard Information Management System (SLIMS, Jackson & Hunter, 1996) to assess the presence of the snow leopard. Signs (scrape, scat, rubbing site, pugmark and spray/urine) were recorded monthly along fixed trails, about 18 km long in total, from 3500 to 5000 m a.s.l., through the four main valleys of SNP (Namche: 15 km²; Pangboche-Phortse: 18.3 km²; Gokyo: 33.2 km²; Thame: 20 km²), from June to

November 2005 and from May to November 2006. For each sign, we recorded its location through a global positioning system and the date of collection. The number of signs in an area is assumed to provide an indication of the presence and numbers of this large cat (Jackson & Hunter, 1996).

Scat collection and analyses

Scats were collected monthly along a fixed trail, about 130 km long, in the region where snow leopard signs were found (the four main valleys of SNP) during the study period. The trail was located primarily (98%) in the open, upper habitats. A thorough, conservative selection of scats to be collected was made on the basis of different features (e.g. smell, position, size, contents and presence of tracks) to decrease the risk of collecting scats of other species, for example the red fox, the Bengal cat and domestic dogs. No feature alone is species specific, but the complex of them can be quite effective. Mistakes may occur especially with scats of the common leopard, but the habitat separation between this large cat and the snow leopard should minimize the probability of errors, if scats are collected well above the upper tree line. Furthermore, the presence of hair in scats of felids is commonly used to assess the identity of the cat species. One hundred and six scats of assumed snow leopards were sun dried and preserved in polyethylene bags to identify food habits. Approximately 1 cm³ of each fresh scat (a scat with no moulds, still relatively soft when prodded with a twig, not covered with dust, *n* = 30) was preserved in 80% ethanol solution for genetic analysis.

DNA extraction

Total DNA was extracted from 30 ethanol-preserved faecal samples using guanidinium thiocyanate and diatomaceous

silica particles (Gerloff *et al.*, 1995). DNA extracted from faeces is often dilute, degraded and rich in PCR inhibitors, and so careful laboratory procedures were applied to obtain reliable individual genotypes. All DNA extractions were carried out in an isolated room with strict precautions: exclusively reserved coats, pipets and sterilized lab tools were used after a chemical decontamination of the workbench with commercial bleach. Negative controls, in which no DNA is present, were used to check for contamination.

Mitochondrial DNA

Species identification was assessed through the amplification of a 219 bp region of the mitochondrial cytochrome *b* gene using Cyt *b* (F) and Cyt *b* (R) primers (Buckley-Beason *et al.*, 2006). Amplification reactions were performed in an isolated room under a hood with a HEPA filter, after a decontamination with UV light. PCR products were purified using ExoSap (GE Healthcare, formerly Amersham Biosciences, Piscataway, NJ, USA) and sequenced with the forward primer using the BigDye Terminator kit v.1 (Applied Biosystems, Foster City, CA, USA). Fragments were separated on an ABI Prism 3130XL and analysed using Sequencing Analyses 5.2 and SeqScape 2.0 (Applied Biosystems). BLAST software (<http://www.ncbi.nlm.nih.gov>, accessed 24 March 2009) was used to compare results with Genbank sequences in order to identify the species for each sample (GenBank accession nos EF551002, EF056507, EF056506, *P. pardus*; DQ097339, EF551004, D28904, *U. uncia*).

Microsatellite loci

Single amplifications of nine microsatellite loci were attempted for all 30 samples using published primers (Fca126, Fca132, Fca139, Fca161, Fca26, Fca43, Fca77, Fca8 and Fca96) screened from domestic cat (Menotti-Raymond *et al.*, 1999). Each forward primer (which reads from 5' to 3' on the DNA strand) was labelled with 6-FAM or HEX ABI dye. PCR amplifications were performed in a Perkin-Elmer Model 9700 thermocycler (Applied Biosystems) using the following set of conditions: denaturation of 10 min at 94 °C, a touchdown cycle of 94 °C for 30 s, 55 °C for 30 s decreased by 0.5 °C in the next cycle for 10 cycles, 72 °C for 30 s, then 35 amplification cycles of 94 °C for 30 s, 50 °C for 30 s and 72 °C for 30 s, followed by an extension of 10 min at 72 °C. Amplified products were separated on an ABI Prism 3130XL (Applied Biosystems) and analysed using Genemapper 4.0 and Genotyper 3.7 (Applied Biosystems).

Results of genotyping from faecal DNA are prone to several problems, particularly allelic dropout (ADO) and amplification of false alleles. Allelic dropout is caused by the stochastic amplification of only one of the two alleles at a heterozygous locus while false alleles are due to the amplification of nonspecific DNA. Both errors are caused by the low concentration of the DNA template and might lead to an error in the individual identification. To overcome these problems, genotypes were determined from four independent replicates of each locus in each sample. After compar-

ing replicates, a single locus genotype was accepted only if it showed a minimum of two identical heterozygous profiles or four identical homozygous profiles. Biological samples with identical multilocus genotypes were identified using Gimlet v.3.1 (Valière, 2002). ADO and PCR amplification success rates among replicates were calculated in accepted genotypes using Gimlet v.3.1.

The probability of identity, $P_{(ID)}$, is the probability that two individuals drawn at random from a population will have the same genotype at multiple loci (Waits, Luikart & Taberlet, 2001). Probabilities of identity in a population of unrelated individuals $P_{(ID)}$ or among siblings $P_{(ID)sib}$ were computed using GenAlEx v.6 (Peakall & Smouse, 2006).

Sex identification

Gender was identified using assessment of a short region of the zinc finger protein genes using primer P1-5EZ (Aasen & Medrano, 1990) and primer ZFXRb (Mucci & Randi, 2007). The P1-5EZ marker was labelled with 6-FAM dye. In cats, homologous sequences of ZFXR genes, located on X and Y chromosomes, differ by a few base pairs in length (Pilgrim *et al.*, 2005). A single fragment 177 bp long and two fragments 174 and 177 bp long were retrieved, respectively, in females and males. Fragments were separated on an automated ABI 3130XL and analyzed using Genemapper v.4 software and Genotyper v.3.7 software (Applied Biosystems). Four independent replicates of each locus were carried out in each sample.

Food habits

The snow leopard diet was assessed through the analysis of 106 scats. Scats were washed with tap water in a fine mesh sieve and undigestible remains of hair, teeth, hooves, bones, feathers and claws were oven dried at 60 °C for 24 h. Prey species were identified by comparison with a reference collection of slides and photographs of the structure of the cuticula and medulla of hair of potential prey species (cf. Teerink, 1991), at magnifications of $\times 100$ –400. Data were tabulated as absolute (number of occurrences of each food, when present/total number of scats $\times 100$) and relative (number of occurrences of each food, when present/total number of occurrences of all food items $\times 100$) frequencies of occurrence of each prey species (Lucherini & Crema, 1995; Lovari & Rolando, 2004). Seasonal differences in the absolute frequency of main prey items in faecal samples were tested by the χ^2 -test.

Counting Himalayan tahr

A steep and rugged terrain poses particular problems for population counts of large mammals because such a terrain precludes the use of strip or line transects or quadrat counts (Harris, 1994). In the mountainous regions of Asia, Himalayan tahr, as well as other caprin species, are difficult to count, because they inhabit terrain inhospitable to ground-based investigators and because they often gather together in loose groups, which occasionally shift, move and regroup

(Harris, 1994). Especially in the warm season, Himalayan tahr tend to inhabit open areas, only rarely moving to forest habitats (Buffa *et al.*, 1998), which makes this caprin relatively easy to spot. Zeiss 10 × 40 binoculars (Zeiss, Oberkochen, Germany) and a Nikon spotting scope RaII 15 × 45 (Nikon, Tokyo, Japan) were used to identify the sex and age class of Himalayan tahr (Lovari *et al.*, 2009). Every year (2004–2006), two to three standardized repeated counts were carried out by walking a > 100 km route in early summer and/or in November. Searching efforts were concentrated on the valleys of Namche and Pangboche-Phortse, that is, *c.* 70% of the distribution range of the tahr in the Park, where the greatest concentration of this caprin in SNP was located (over one-third of the tahr population, Lovari, 1992). These south-facing areas (xerophytic grasslands and shrublands dominated by *Juniperus* bushes) were located *c.* 10 km from each other, measured in a straight line, separated by the Imja Kola river. These counts were carried out within a long-term research project on reproductive behaviour of tahr (Lovari *et al.*, 2009), started in 1989, to assess the group structure and the minimum number of individuals present in the area (Lovari, 1992). We totalled the maximum number of each sex and age class sighted during surveys throughout the year.

After the birthing season, the proportion of ungulate females seen with a calf may be used as an approximate measure of birth rate (e.g. wapiti *Cervus canadensis*: Eberhardt *et al.*, 1996; white-eared kob *Kobus kob*: Fryxell, 1987; moose *Alces alces*: Laurian *et al.*, 2000). This method may not be fully reliable in closed habitats (Bonenfant, Gaillard & Klein, 2005), but it is widely used to monitor the viability of ungulate populations in an open terrain.

Serosurvey of Himalayan tahr for selected pathogens

Diseases may play a role in the population dynamics of wild sheep and goats by inducing hypo-fertility, abortion or neonatal-juvenile mortality (Williams & Barker, 2001), although they do not seem to lead to their extinction (Tompkins *et al.*, 2002). In November 2004, blood samples were obtained from a group of 20 adult Himalayan tahr (3–11 years old) in the Namche area (Dematteis *et al.*, 2006). Their sera were analysed for antibodies to the six groups of pathogens most likely to determine reproductive disorders and juvenile mortality in wild sheep and goats (Gillespie & Timoney, 1981; Williams & Barker, 2001). Laboratory methodologies are provided in Table 1.

Results

In November 2003, one of us (S. L.) found a scat similar to that of a large cat, containing remains of a kid of Himalayan tahr, at 3800 m a.s.l. In December 2003, one of us (R. B.) photographed a snow leopard approximately in the same area. When standard itineraries were devised and walked to record signs of snow leopards, in 2004–2006, many signs of presence were found in SNP throughout the year, showing

Table 1 Pathogens, serological methods and positivity cutoffs (numbers indicate the dilution of blood sera used for analyses) for the serosurvey of Himalayan tahr *Hemitragus jemlahicus* ($n=20$)

Pathogen(s)	Method	Cutoff
<i>Brucella</i> spp.	CFT	1/20
Herpesviruses/BHV1-IBR	SN	1/2
Pestiviruses/PSC-BVDV-BDV	ELISA	1/4
<i>Chlamydia</i> spp.	CFT	1/16
Paramyxoviruses/PPR-BP	HI	1/8
<i>Rickettsia</i> spp.	IFI	1/40

BHV1-IBR, infectious bovine rhinotracheitis; PSC-BVDV-BDV, ruminants pestivirus; PPR-BP, paramyxovirus (small ruminants); CFT, complement fixation test; SN, serum neutralisation; ELISA, enzyme-linked immunosorbent assay; HI, haemagglutination inhibition; IFI, indirect immunofluorescence.

that a large cat had been permanently present (3.2–4.5 signs of presence km^{-1}). An approximate number of one to two snow leopards was estimated by SLIMS methods (Ale, 2007), with a density of 4 individuals per 1000 km^2 .

Population assessment through genetic analysis

The results of genetic analyses are reported in Table 2. For each faecal sample, species, genotype and sex were assessed using molecular tools. Five out of the 30 samples failed to amplify for all the molecular tests and have not been shown in Table 2. Six different individuals were identified.

Species identification

A sequence comparison between common and snow leopard sequences (219 bp) showed 6.85% divergence. The analyses of the cytochrome *b* provided positive results on species identification in 21 out of 30 samples (70%; Table 2). Of these, 16 (76.2%) belonged to snow leopards, nearly all collected in the open habitats of the higher altitudes. Only five samples of common leopard were found, and these had been collected on a 3 km trail segment along the upper tree line and discarded from the food habit study.

Genotype identification

We obtained microsatellite genotypes from 15 samples (50%; Table 2). Allelic dropout was low (mean = 0.0189), occurring in only two samples. The PCR amplification success rate showed high values in successfully genotyped individuals (mean = 0.83). Higher ADO values and lower success rate were detected when all 30 biological samples were considered (respectively, mean = 0.123 and mean = 0.48). Irrelevant values of false alleles were identified. Four snow leopards and two common leopards were detected. Several individuals were resampled in different sessions (Table 2). Identical genotypes always showed concordant mtDNA haplotypes (Table 2).

$P_{(ID)}$ and $P_{(ID)sib}$ calculated in snow leopards were, respectively, 2.00×10^{-5} and 8.32×10^{-3} . PI accuracy,

Table 2 Species, individual and sex detection and resampling of snow leopard *Uncia uncia* and common leopard *Panthera pardus* in Sagar-matha National Park, in the sampling periods

Faecal sample	Species identification	Genotype	Sex
	(mtDNA cytochrome <i>b</i>)	(nine microsatellite loci)	determination (ZFX genes)
June–November 2005			
1	Snow leopard	Low reliability	–
2	Common leopard	# 1	F
3	Common leopard	low reliability	–
4	Common leopard	# 2	M
5	Snow leopard	# 4	M
6	Snow leopard	# 5	F
7	–	–	M
8	Snow leopard	# 3	F
May–November 2006			
9	–	–	M
10	–	–	F
11	Common leopard	–	F
12	Snow leopard	–	–
13	Snow leopard	Low reliability	F
14	Snow leopard	# 4	M
15	Snow leopard	# 4	M
16	Snow leopard	# 4	M
17	–	# 5	–
18	Snow leopard	# 5	F
19	Snow leopard	# 6	–
20	Snow leopard	–	–
21	Snow leopard	–	F
22	Common leopard	# 1	F
23	Snow leopard	# 5	F
24	Snow leopard	# 5	–
25	Snow leopard	# 6	M

–, no results; #, individual; M, male; F, female.

however, might not be correctly estimated using only a few individuals and a large sample size appears to be necessary to make these results reliable. We estimated a density of 7 snow leopards per 1000 km².

Sex identification

Sex identification was obtained in 18 (60%) samples (Table 2). We found three females (# 1, 3 and 5) and three males (# 2, 4 and 6) belonging to two cat species: two males (# 4 and 6) and two females (# 3 and 5) of the snow leopard, and one female (# 1) and one male (# 2) of the common leopard. Determination was consistent in samples with the same genotype.

Food habits

Himalayan tahr, musk deer and livestock (*Bos* spp.) were the most frequent prey, while other items, for example birds (mainly *Galliformes*) and voles, were eaten occasionally by snow leopards (Fig. 2a). In both seasons, summer and autumn 2005–2006, the Himalayan tahr was the staple of

the diet, accounting for *c.* 50% relative frequency of occurrence in the warm season, but declining to less than 40% in autumn (absolute frequency, on count data: $\chi^2 = 3.3$, d.f. = 1, $P < 0.08$; Fig. 2a). In autumn 2005, the Himalayan tahr frequency in diet declined to half of that in the summer of the same year, whereas, in summer 2006, it increased significantly to the previous level (Fig. 2b). On the other hand, there was a detectable, but non-significant reduction in the proportion of Himalayan tahr in snow leopard diets between summer and autumn 2006 (Fig. 2b). The absolute frequency of livestock and that of birds increased by 13 and 7%, respectively (pooled data, 2005–2006), from summer to autumn, especially in 2006 (livestock, from 16 to 30%; birds, from 3 to 14%). Musk deer was the third most frequent prey of this large cat in both years, following Himalayan tahr and livestock (Fig. 2a), except in the summer 2006, when musk deer was almost twice as frequent as livestock in the snow leopard diet (musk deer 31%, livestock 16%, absolute frequency).

Tahr population dynamics

In November 1991–1992, in the Pangboche-Phortse and Namche areas, the young-to-female ratio of tahr ranged around 0.6–0.8 (Fig. 3). In November 2002, this ratio declined to 0.2 in the Namche herd, whereas it was still 0.6 in Pangboche-Phortse. Since then, the ratio in the Namche herd remained between 0.1 and 0.2, in autumn counts (Fig. 3). The Pangboche-Phortse herd also showed a steady decrease in the last 3 years, down to 0.1 in autumn 2006 (Fig. 3).

Every year, in both herds, most adult females produced kids in June–July (young-to-female ratio: 0.7–0.9), but the large majority of kids disappeared by November (young-to-female ratio: 0.1–0.3; Fig. 3). Following extirpation, the snow leopard was first observed and photographed in the Namche area, in December 2003, and in the Pangboche-Phortse valley in October 2004. In 2002, before the snow leopard was recorded in the Pangboche-Phortse valley, the local young-to-female ratio was 0.9 (June), decreasing to 0.6 in November.

The yearly decrease of kid numbers from birth to autumn might have been due to disease, but we found no seroreactor for four of the investigated pathogens and only a single one to *Chlamydia* spp. Conversely, antibodies to BHV1-IBR were found in seven Himalayan tahr (35%, $n = 20$), but their titres were ranging only between 1/2 and 1/4 (Table 1).

Discussion

The SNP valleys are bordered along their upper margins by high mountains (*c.* 7000–8000 m). Other mountains (5500–7000 m) border the easternmost and westernmost sides of the Park, with two high-altitude passes (>6000 m a.s.l.) to neighbouring valleys. A dense forest, unsuitable habitat for the snow leopard (Heptner & Sludskii, 1972, in Jackson, 1996; Fox, 1989; Jackson, 1996), grows in the valley bottoms. The density of snow leopards is low in

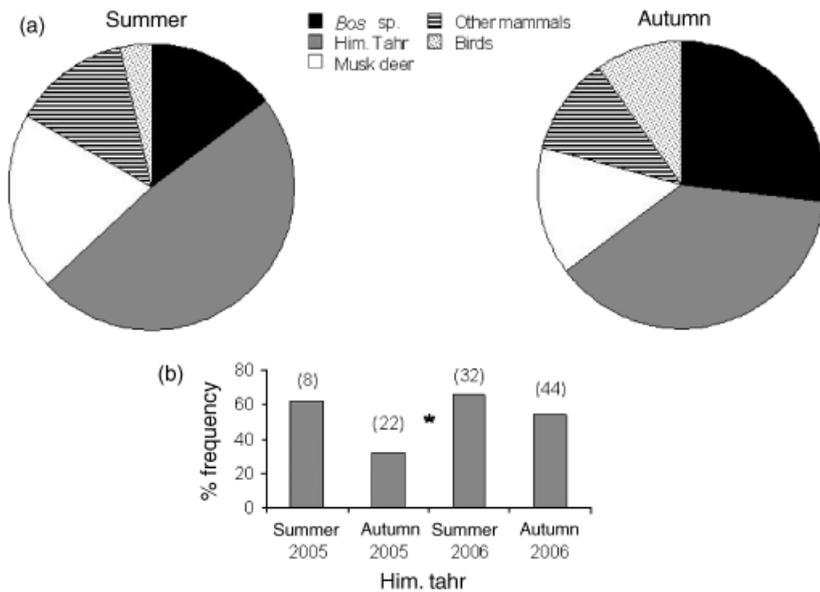


Figure 2 (a) Relative frequency of occurrence of prey in the diet of the snow leopard *Uncia uncia* in summer ($n=40$ scats) and autumn ($n=66$ scats) 2005–2006. (b) Absolute frequency of Himalayan tahr *Hemitragus jemlahicus* in faecal samples, in each season. Sample size in parentheses. $\chi^2=6.0$, d.f. = 1, $P<0.02$ (see text).

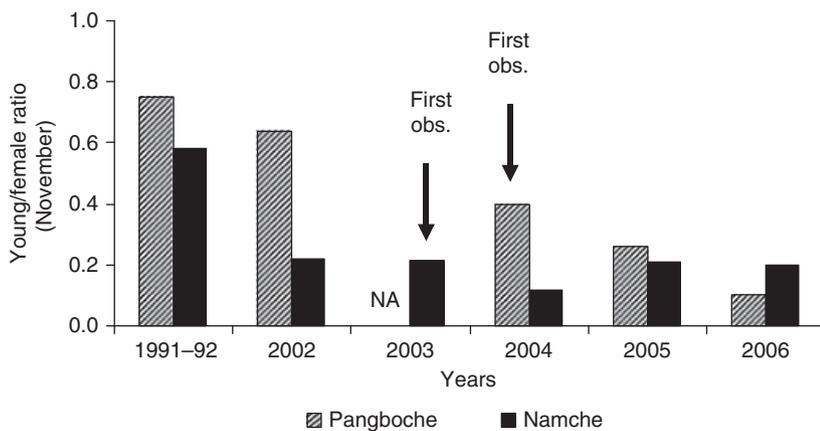


Figure 3 Ratio of number of young per female of Himalayan tahr *Hemitragus jemlahicus* in Pangboche-Phortse and Namche herds, in November 1991–1992 and 2002–2006. First sightings (obs.) of snow leopards *Uncia uncia* in these areas have been indicated by arrows. NA, data not available.

east Nepal, where the SNP is located. In Tibet, greater densities seem to occur locally (*c.* 10 individuals 1000 km²; Schaller, 1998). Snow leopards could have immigrated to SNP from Tibet, through the Nangpa pass (5716 m), in 2002–2003, when the sharp decrease in the number of kids of tahr was first noticed.

Non-invasive genetic methods can be fruitfully used to detect the presence of elusive carnivores. Molecular analysis of faecal DNA allowed species identification, individual genotype and sex from 50 to 70% of the samples we collected in 2005–2006. Four genotypically distinct snow leopards (two males and two females), 3 individuals per year, were detected. An extended, genetically screened, sample collection will be needed to provide additional data (genotypes), to estimate individual ranges and population size, as well as to provide an estimate of the diets of snow leopards and common leopards.

In the 1960s, the snow leopard was thought to be eliminated from what is now SNP (Fleming, undated), but

occasional presence and poaching events have been subsequently recorded (G. Ahlborn & R. Jackson, unpubl.data; Brower, 1991). A snow leopard track, reported in Thame valley (SNP), in the winter of 1988–1989 (Brower, 1991), and a very low young-to-female ratio of Himalayan tahr, from 0 to 0.18, in different herds, recorded by Lovari (1992) in SNP, in October 1989, may suggest that predation events on tahr kids were occurring at that time as well. Conversely, a young-to-female ratio of about 0.6 has been reported for wild populations of Himalayan tahr (Schaller, 1973; Gurlung, 1995), in early spring that is before the birth season, thus accounting for mortality due to predation, as well as to winter rigours.

Also, infectious diseases inducing hypo-fertility, abortion or neonatal–juvenile mortality in ruminants (Gillespie & Timoney, 1981; Williams & Barker, 2001) may have determined the sharp decrease of this ratio from 0.9 in the birthing season to 0.1–0.2 in the autumn, but our results of serological screening do not support this hypothesis.

Our data suggest that snow leopard predation on Himalayan tahr has chiefly affected kids. After the return of the snow leopard, 70–90% of kids have disappeared every year during the summer compared with about 30% in previous years (Fig. 3). Although a snow leopard can kill a prey of 200–300 kg, smaller prey may be preferred for a variety of reasons. A young prey is less wary and easier to subdue than an adult one, which may be important especially in the rugged, steep terrain, where this large cat hunts. A smaller prey can also be more easily carried to the cubs in the den. In fact, when blue sheep (35–55 kg, females; 60–75 kg, males, Wang & Hoffmann, 1987) are present, they are the staple of the diet of snow leopards, even if other prey species are available (e.g. Schaller, 1977; Schaller *et al.*, 1988; Oli *et al.*, 1993; Chundawat & Rawat, 1994).

Another cause of mortality could have been food competition with livestock. In an intensively grazed rangeland, for example, blue sheep density was 63% lower and this population showed a lower young-to-female ratio than elsewhere (Mishra *et al.*, 2004). In our study area, livestock numbers have been stable and never abundant in the last two decades (i.e. 2.3 head per km²; Brower, 1991; Ale & Lovari, 2005). The sudden decrease of tahr kids during the summers of 2002–2003 and in the following years (Fig. 3) is unlikely to depend on livestock competition.

Although one cannot rule out the possibility that the dhole, wolf and golden jackal may have visited the SNP occasionally, no sightings or signs of these species have been reported in the last 20 years. It is also unlikely that scats belonging to these predators could be misidentified (see 'Methods'). The risk of a mistake is greater between scats of snow and common leopards, as indicated by our field misidentification of five samples (cf. 'Methods'), but the latter is rarely found above the upper tree line (Nowell & Jackson, 1996; our data), where our work was concentrated. Predation on kids of Himalayan tahr by the common leopard is probably negligible, as tahr (especially females with kids) are rarely found below the upper tree line, particularly during the warm season when kids disappear. Even if very few scats of the common leopard were included in our sample, they would be unlikely to substantially change our results on food habits of the snow leopard.

Implications for conservation

A snow leopard requires about 1.5 kg of meat per day or 548 kg per year (Schaller, 1977). Assuming a mean weight of 90 kg for Himalayan tahr (adult males: 100–130 kg, adult females: 62 kg, on average; Dematteis *et al.*, 2006), with about 50 kg of edible meat, a population of *c.* 200 tahr would represent about 10 000 kg of tahr meat theoretically available to snow leopards. If predation preferably targets kids (5–20 kg), many more individuals than adults will be necessary to provide enough food: conservatively, one may estimate a demand of approximately one kid killed every 4–5 days per snow leopard on a diet comprised only of tahr, which would make a total of six to seven kids per month per snow leopard, between July (birth season) and November

(Fig. 3). As there have been three snow leopards in the Park, each summer, a theoretical loss of >70 kids could be estimated. In practice, our data show (Fig. 2) that about 50% of the summer diet of the snow leopard is based on food resources other than tahr. If so, 30–35 kids may be preyed upon in the warm season. In SNP, 43 kids were born in 2005, whereas just eight young were counted in November of the same year, that is only 18% survived by the mid-autumn, which is consistent with our figures (cf. 'Results': Tahr population dynamics; Fig. 3).

Musk deer are small ungulates (12 kg on average; Nowak, 1991): their numbers are unknown in SNP, but the species is fairly common only in the forest, a habitat usually avoided by snow leopards (Fox, 1989). Conversely, pheasants and pikas *Ochotona himalayana* are relatively abundant where this large cat occurs, although they do not currently seem to be preyed upon frequently (Fig. 2).

Thus, several snow leopards could theoretically survive in the Park area, although the impact of their predation has altered the population of Himalayan tahr by systematically removing the large majority of the kid cohort every year. Small, isolated populations of wild *Caprinae* are quite sensitive to stochastic predation events by predators preying upon them (e.g. Haller, 1992: lynx *Lynx lynx* and Alpine chamois *Rupicapra rupicapra*; Festa-Bianchet *et al.*, 2006: cougars *Puma concolor* and bighorn ewes *Ovis canadensis*). Thus, predation by even a few snow leopards could sharply reduce the small population of Himalayan tahr in SNP, if the youngest age classes continue to experience heavy losses. The world's natural distribution of Himalayan tahr is confined to a narrow, fragmented strip along the Himalaya, mainly between 3500 and 4500 m a.s.l. (Schaller, 1977). In recent decades, its distribution has been increasingly disrupted by activities related to human encroachment (Wegge & Oli, 1997), thus making the survival of any sub-population important for conservation of a viable meta-population. In 1989, at least 350 tahr were estimated in SNP (Lovari, 1992); in 2005–2006, the numbers were down to *c.* 200–250 (Shrestha, 2006; Ale, 2007). In 2007, S. Lovari *et al.* (unpubl. data) estimated just over 100 tahr, with a young-to-female ratio of 0.3 in November.

There was evidence of a cross-transmission risk of BHV1-IBR between cattle and Himalayan tahr, although the seroprevalence of antibodies to BHV1-IBR (a virus with a livestock reservoir; Hudson *et al.*, 2002) was only moderate in tahr and does not suggest lethal levels of exposure. Under conditions of stress or reduced genetic variation, for example caused by predation concentrated on a small population, susceptibility to various diseases may increase (Lafferty & Gerber, 2002) and may result in a further decline of tahr.

Food habits of carnivores are strongly influenced by availability of food resources and cultural transmission, that is learning from the mother (Gilbert, 1999; Kitchener, 1999; Nel, 1999). If the numbers of Himalayan tahr plummet, it is probable that predation by the snow leopard will shift to alternative prey (livestock included), which in turn will allow the tahr to rebuild their numbers. Thus, a balance between population sizes of the snow leopard and

those of its prey, Himalayan tahr included, may be reached in time.

Predation on livestock can be predicted to increase, together with the decrease of Himalayan tahr, as it tends to be greater in areas where wild prey is scarce (Miller & Jackson, 1994; Schaller, Tserendeleg & Amarsanaa, 1994; Bagchi & Mishra, 2006).

The snow leopard is considered as one of the mountain deities by the Sherpas, who believe that these large cats kill livestock only because of the herder's negligence in appeasing these deities (Ale *et al.*, 2007). Nevertheless, retaliatory killing by local people should soon be expected, if livestock predation increases beyond tolerable limits, as has happened elsewhere in Nepal, for example in upper Mustang (DNPWC, 2005). In fact, there are indications that this process has already started in SNP (e.g. the alleged killing of a female snow leopard in the Phortse area, in May 2007).

Financial compensation for livestock losses may mitigate the conservation problem, but it will not solve it (Bagchi & Mishra, 2006; cf. also Lovari *et al.*, 2007, for the wolf *C. lupus*). Other concurrent solutions should be provided, for example the reintroduction (or benign introduction, *sensu* IUCN/SSC-Reintroduction Specialist Group) of other appropriate wild prey. Large areas at higher elevations in the Park could be suitable for blue sheep, and are not used by other ungulate species because of their different habitat requirements. In recent decades, this caprin has not been present in SNP, although it occurs in contiguous areas: Makalu-Barun National Park (Arun Valley, K. Thapa, *in litteris*, 13 May 2008), east of SNP; Lambagar Valley (K. Thapa, *in litteris*, 13 May 2008), between the Rolwaling and Langtang, west of SNP; just north of SNP, in the Qomolungma Conservation Area (Tibet). After an appropriate feasibility study (Soorae, 2008), if a viable population of blue sheep is established in the Park, the snow leopard will have another suitable prey, in addition to Himalayan tahr and musk deer. Establishment of blue sheep should decrease the probability of livestock predation by increasing the local community of wild herbivores (e.g. Meriggi & Lovari, 1996, for the wolf).

To better predict predator–prey relationships, basic information on population size and age structure dynamics is necessary for alternative prey species, as well as for tahr. In a protected area, a long-term monitoring programme of key species for conservation can provide useful insights into species recovery due to protection. This information is lacking for SNP, which makes it difficult to fully interpret and to predict the development of snow leopard–Himalayan tahr relationships. Our data suggest that there is reason to be concerned.

The restoration of biological diversity through the return of a large predator has to be monitored carefully especially in human-altered areas, where the lack of important environmental components, for example key prey species, may make the return of a large predator a challenging event. Prompt and appropriate conservation-oriented actions, for example through reintroductions of prey

species and adequate prevention/compensation measures, are required.

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S.L. planned this study, organized data collection and analyses, recorded data on tahr in 1991–1992 and wrote several drafts of this paper; R.B. collected data on tahr in 2002–2004 and carried out most scat analyses; I.M. carried out scat analyses and participated in writing drafts; E.R. and N.M. carried out genetic analyses and reported on them; A.D. collected and analysed sanitary data, as well as commenting on the health state of the tahr population; S.B.A. devised the local SLIMS collection of data, counted tahr and collected scats of snow leopards in 2005–2006.

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