

Common and snow leopards share prey, but not habitats: competition avoidance by large predators?

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Keywords

coexistence; resource partitioning; food habits; *Panthera uncia*; *Panthera pardus*.

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Editor: Jane Waterman

Received 25 January 2013; revised 27 May 2013; accepted 30 May 2013

doi:10.1111/jzo.12053

Abstract

Resource exploitation and behavioural interference underlie competition among carnivores. Competition is reduced by specializing on different prey and/or spatio-temporal separation, usually leading to different food habits. We predicted that two closely related species of large cats, the endangered snow leopard and the near-threatened common leopard, living in sympatry, would coexist through habitat separation and exploitation of different prey species. In central Himalaya, we assessed (2006–2010) habitat and diet overlap between these carnivores. The snow leopard used grassland and shrubland, whereas the common leopard selected forest. Contrary to our prediction, snow leopard and common leopard preyed upon similar wild (Himalayan tahr, musk deer) and domestic species (*Bos* spp., dogs). Dietary overlap between snow leopard and common leopard was 69% (yearly), 76% (colder months) and 60% (warmer months). Thus, habitat separation should be the result of other factors, most likely avoidance of interspecific aggression. Habitat separation may not always lead to the use of different prey. Avoidance of interspecific aggression, rather than exploitation of different resources, could allow the coexistence of potentially competing large predators.

Introduction

Resource availability influences food habits, which, in turn, may lead to interspecific competition for scarce key resources (de Boer & Prins, 1990). Competing species may show evolutionary responses to each other, leading to ecological divergence (Pianka, 1973; Schoener, 1974). Competition among carnivores may include resource exploitation and behavioural interference, especially through interspecific killing and kleptoparasitism (Palomares & Caro, 1999; Donadio & Buskirk, 2006). Interspecific killing is widespread among carnivores, with negative effects on the population size of victim species: interactions depend on interspecific differences in body size/diet and taxonomic relatedness (Palomares & Caro, 1999; Donadio & Buskirk, 2006).

Resource exploitation can be avoided by specializing on different prey species (e.g. Karanth & Sunquist, 2000; Hass, 2009). Interference may be decreased by spatial/habitat/temporal segregation (e.g. Schaller, 1972; Palomares *et al.*, 1995), but also by preying on different species (Karanth & Sunquist, 1995; Mills & Gorman, 1997). Assessing the potential for interspecific competition may help devising appropriate conservation measures for threatened species (Caro & Laurenson, 1994; Creel & Creel, 1996).

We studied the coexistence of two large cats of conservation concern, the endangered snow leopard *Panthera uncia* and the near-threatened common leopard *Panthera pardus* (Henschel *et al.*, 2008; Jackson *et al.*, 2008), in a predator–prey system where also the main prey species (Himalayan tahr *Hemitragus jemlahicus* and Musk deer *Moschus chrysogaster*) are threatened (Bhatnagar & Lovari, 2008; Wang & Harris, 2008).

The common leopard (body weight: female 28–60 kg, male 37–80 kg; Nowak, 1991) occurs over a wide range, in Africa and Asia. The slightly smaller snow leopard (body weight: female 25–40 kg, male 45–75 kg; Nowak, 1991; Jackson, 1996) lives from Afghanistan, Pakistan, India, Himalayas, Tibet, up to Mongolia and Russia (Fox, 1989). These species look so similar that living populations, as well as fossil remains of common leopards have been wrongly identified as snow leopards (Hemmer, 1972). While the common leopard is a highly adaptable species, from sub-desert habitats to tropical/boreal forests (Nowak, 1991), the snow leopard is a cold-adapted inhabitant of open bushy/rocky areas (Hemmer, 1972; Fox, 1989).

These leopard species have comparable diets (Lovari, Ventimiglia & Minder, in press) and mainly crepuscular/nocturnal activity (snow leopard: McCarthy, Fuller & Munkhtsog, 2005; common leopard: Bailey, 1993; Karanth & Sunquist,

2000). Very few data are available on the spatial behaviour of these species. Information on diet overlap, when in sympatry, is also not available. Donadio & Buskirk (2006) showed that (1) larger species usually kill smaller ones; (2) at small and large differences in body size, interactions are less likely to occur, whereas, at intermediate differences, the rate of aggression increases according to diet overlap; and (3) aggression tends to occur more frequently between species of the same family than between species of different families. One could predict that competition will arise between sympatric common and snow leopards, with the former being dominant over the latter. The adaptable, larger common leopard may replace the snow leopard in areas of its southern distribution range, because of the upward shift of the upper tree line triggered by climate change (Lovari *et al.*, in press). The potential for competition between these species may be best clarified in their areas of sympatry.

We tested the hypothesis that two large carnivores of approximately the same size and activity pattern will coexist by preying on different species, either in the same (1) or in different (2) habitats, when in sympatry. The latter would also prevent interference.

Materials and methods

Study area

Sagarmatha (Mt. Everest) National Park (SNP; 1148 km², north-east Nepal; Fig. 1) 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 includes mixed *Betula-Rhododendron-Abies* spp. forest, replaced at 4000–5000 m by *Juniperus* spp. and *Rhododendron* spp. Beyond 5000 m, mosses, lichens and Alpine grasslands comprise the climax vegetation (Buffa, Ferrari & Lovari, 1998; further details, in Buffa *et al.* (1998). The Park

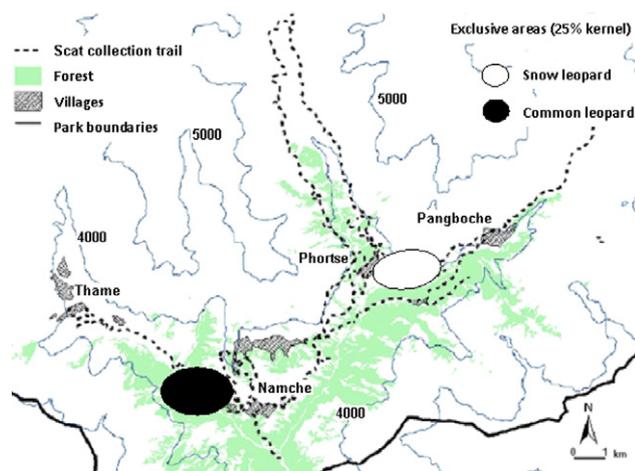


Figure 1 Map of the study area, in the Sagarmatha National Park, Nepal.

hosts a rich avifauna (e.g. Laiolo, 2003), with a relatively depauperate community of large mammals. Dholes *Cuon alpinus*, wolves *Canis lupus* and golden jackals *Canis aureus* were eliminated over two decades ago by human persecution (Brower, 1991). The only large predators living in the Park are snow leopards and common leopards (minimum densities: *c.* 3 snow leopards; *c.* 3 common leopards/1000 km², see Results). The Himalayan tahr (*c.* 100–150 individuals; Lovari *et al.*, 2009b), the relatively abundant musk deer (*c.* 300 individuals/1000 km²; Aryal *et al.*, 2010) and the rare Himalayan serow *Capricornis sumatraensis* inhabit the Park (Lovari, Ale & Boesi, 2005). Brower (1991) and Ale & Lovari (2005) reported that domestic yak *Bos grunniens* and their hybrids with zebu cattle *Bos indicus* (*c.* 2000 individuals) occur in the Park. Often, these cattle are left unguarded above the tree line, in small groups (<10 individuals). At night, they may return to rudimentary sheds. The main study area (3440–4750 m a.s.l.) lies between the villages of Namche, Phortse and Gokyo Lake.

Collection of signs of presence

Scrapes, hairballs and scats were recorded and georeferenced monthly (May–November 2006; September 2007–October 2010) along one fixed trail (*c.* 140 km), through the main valleys of SNP (Namche: 15.0 km²; Pangboche-Phortse: 18.3 km²; Gokyo: 33.2 km²; Thame: 20.0 km²).

A selection of scats was made on the basis of smell, position, size, contents and presence of pugmarks, to decrease the risk of collecting scats of red foxes, Bengal cats and dogs (Karanth & Sunquist, 1995; Lovari *et al.*, 2009b). A total of 515 scats were sun dried and preserved in polyethylene bags for diet analyses. Approximately 1 cm³ of each fresh scat (no moulds, still soft when prodded with a twig, not covered with dust) was preserved in 80% ethanol solution for DNA analyses.

Genotype identification

Total DNA was extracted from 176 ethanol-preserved scats and 29 hairballs using guanidinium thiocyanate and diatomaceous silica particles (Gerloff *et al.*, 1995). 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). Fragments were separated on an ABI Prism 3130XL and analysed using Sequencing Analyses 5.2 and SeqScape 2.0 (Applied Biosystems, Foster City, CA, USA). BLAST software (<http://www.ncbi.nlm.nih.gov/>) was used to compare results with Genbank sequences, to identify the species (GenBank accession nos EF551002, EF056507, EF056506, *P. pardus*; DQ097339, EF551004, D28904, *P. uncia*).

For further information on genotype identification, see Lovari *et al.* (2009b).

Habitat overlap

Carnivores tend to scent mark in strategic areas, especially near home range/territory boundaries (e.g. Bailey, 1993; Roper

et al., 1993; Sillero-Zubiri & Macdonald, 1998). We assessed the habitat features selected by the two species of leopards for marking, within the whole study area and within their respective exclusive areas, by using territorial signs (scats, scrapes). Yearly habitat selection and overlap were estimated and compared at these two spatial scales. At the study area scale, we compared the proportion of genotyped scats/hairballs collected in each habitat to the availability of habitat types across our itinerary. We assessed exclusive areas through kernel analyses (Worton, 1989) applied to locations of genotyped scats. For both species, we ran 95% kernel analyses, then decreased the probability level of kernel utility distribution by 5%, until no spatial overlap occurred. Exclusive ranges (Fig. 1) corresponded to kernel 25% areas: for each species, we compared the proportion of scats and scrapes recorded in each habitat to the availability of each habitat type across segments of the itinerary. All scrapes within a species-exclusive area were assumed to belong to that species, as no overlap occurred between 25% ranges of these two cats (Fig. 1).

Habitat selection was estimated through selection ratios and Bonferroni confidence intervals (Manly *et al.*, 2002). For a habitat type i and for each species, the ratio was:

$$w_i = o_i / \pi_i$$

where: $o_i = n$. signs of presence (study area scale: genotyped scats; exclusive areas scale: scats and scrapes) in the habitat i /total n . signs collected; π_i ($i = 1, \dots, M$) = extent of habitat i along itineraries (within a buffer of 10 m at each side of them)/total extent of all habitats along the itineraries.

Confidence intervals were estimated through the formula (Manly *et al.*, 2002):

$$w_i \pm a2n \text{ se}(w_i)$$

where $\text{se}(w_i) = \sqrt{[o_i \times (1 - o_i) / u\pi_i^2]}$, with u = total number of observations/habitat i .

Intervals overlapping 1 indicate habitats are used proportionally to availability. Intervals with the lower limit >1 indicate selection, whereas those with the upper limit <1 indicate avoidance (Manly *et al.*, 2002). We considered the following habitats: closed (i.e. dense) forest; open (i.e. sparse trees with bushes) forest; closed shrubland (i.e. treeless, thick undergrowth); open shrubland and alpine meadows (i.e. subalpine grassland/scrubland); cultivated fields; rocks/scree.

Symmetric habitat overlap was assessed through the Pianka index (Pianka, 1973):

$$P = \frac{\sum_{i=1}^M o_{iF} o_{iR}}{\sqrt{\sum_{i=1}^M o_{iF}^2 \sum_{i=1}^M o_{iR}^2}}$$

where o_{iF} and o_{iR} denote the proportions of snow leopard and common leopard signs of presence (study area scale: genotyped scats; exclusive area scale: scats and scrapes) in the i -th habitat, respectively. We also estimated asymmetric habitat overlap of the common leopard on the snow leopard, through the MacArthur and Levins index (MacArthur & Levins, 1967):

$$I_{FR} = \frac{\sum_{i=1}^M o_{iF} o_{iR}}{\sum_{i=1}^M o_{iR}^2}$$

We assessed the habitat selection of snow leopards in relation to that of common leopards, in exclusive areas, through generalized linear models, with binomial errors and both fixed and random effects (Crawley, 2007). The presence of each leopard species (1 = snow leopard; 0 = common leopard) was associated to season, year, habitat, altitude, slopiness, aspect, distances from cliffs, from the border of the forest, from the nearest village and from the river (fixed effects). Segments of the itinerary were fitted as random effects. No multicollinearity occurred ($r_s > |0.6|$, Green, 1979; cf. Sergio, Marchesi & Pedrini, 2003) between continuous explanatory variables. All variables were entered in a global model. Minimum adequate models were estimated by removing the least significant term at each step, starting from the highest level of interactions, until the elimination of terms caused a significant increase in the residual deviance, assessed through chi-squared deletion tests (Crawley, 2007). This analysis was not carried at the study area scale, because of the small sample size of genotyped scats of common leopards. Analyses were carried out through ArcView GIS 3.2 (ESRI, 1999) and R 2.9.1 (R Development Core Team, 2009) software.

Food habits

Scats were analysed and prey taxa identified following Lovari *et al.* (2009b). Data were tabulated as absolute (n. occurrences of each food when present/total n. scats $\times 100$) and relative (n. occurrences of each food when present/total n. occurrences of all food items $\times 100$) frequencies of occurrence of each prey taxa (Lucherini & Crema, 1995), as well as relative volume estimated by eye (e.g. Kruuk & Parish, 1981).

Food habits were determined from genotyped scats of snow leopards and common leopards. These results were compared (G-test, Sokal & Rohlf, 1995) with those from not-genotyped scats found in exclusive areas of each species. Thus, data were pooled to increase sample size. The adequacy of sample size was determined through a Brillouin diversity index (Hb, index range: 0–4.5; Brillouin, 1956; cf. Glen & Dickman, 2006; Hass, 2009):

$$Hb = (\ln N! - \sum \ln n_i!) / N$$

where N = total n. individual prey taxa in all samples and n_i = n. individual prey taxa in the i th category. A diversity curve was calculated by sampling with replacement over a range of 3–21 samples, in increments of two. Cumulative diversity (Hb) was plotted against n. scats. Adequacy of sampling effort was determined by examining the asymptote reached in the diversity curve.

Diet overlap was estimated through Pianka index (1973):

$$P = \frac{\sum_{i=1}^M o_{iF} o_{iR}}{\sqrt{\sum_{i=1}^M o_{iF}^2 \sum_{i=1}^M o_{iR}^2}}$$

where o_i is the proportion of prey item i in the diet of the snow leopard (F) and common leopard (R). Seasonal frequency of occurrence of prey items (colder months: November–March;

warmer months: April–October) of both leopard species were compared by the *G*-test.

Results

Seventy-six out of 176 ethanol-preserved scats were assigned to snow leopards, 48 to common leopards. Twenty-seven out of 29 hairballs were genetically assigned to a leopard species (snow leopard: $n = 24$; common leopard: $n = 3$).

Habitat overlap

Genotyped snow leopard scats ($n = 7$ individuals, 2006–2010), five individuals in 2007 (M : F, 1:1.5) and one pair in 2010 (M : F, 1:1), were found especially in open shrubland and alpine meadows, whereas those of common leopards ($n = 3$ individuals, 2006–2010, M : F, 1:2) were found especially in forests (Table 1).

Table 1 Number (percentage) of scats of snow leopard and common leopard found in each habitat, in Sagarmatha National Park

Habitat	Snow leopard	Common leopard
Rocks	1 (1.4)	0
Closed forest	1 (1.4)	13 (29.5)
Open forest	14 (36.4)	16 (36.4)
Closed shrubland	15 (20.8)	9 (20.5)
Open shrubland/Alpine meadows	41 (57.0)	6 (13.6)
Cultivated fields	0	0
Total	72	44

All habitat types were included in each exclusive area, in different proportions [*G*-test: $G = 27.157$; degrees of freedom (d.f.) = 5; $P < 0.001$]. Pooling closed and open forests ('forest') and closed shrubland, open shrubland and alpine meadows ('shrubland and grassland'), habitat selection differed between leopard species. Snow leopards selected shrublands and grasslands, used rocky areas according to their availability and avoided cultivated fields; the forest was used according to its availability (study area scale) or avoided (exclusive area scale; Fig. 2). Conversely, common leopards selected forest and avoided other habitats (Fig. 2).

At a finer habitat classification (i.e. considering separately closed forest, open forest, closed shrubland, open shrubland and alpine meadows), at the study area scale, snow leopards avoided closed forest and cultivated fields, whereas other habitats were used in proportion to their availability (Table 2). The common leopard selected open forest and avoided open shrubland and cultivated fields, whereas closed forest and closed shrubland were used according to their availability (Table 2).

At the exclusive area scale, the snow leopard ($N = 1019$ scats and scrapes) selected open shrublands, alpine meadows, as well as closed shrublands, but avoided forests, cultivated fields and used rocky areas according to their availability (Table 2). Conversely, the common leopard ($N = 145$ scats and scrapes) selected closed forest, used open forest according to its availability and avoided closed shrubland and open habitats (Table 2).

The symmetric habitat overlap (Pianka index) was 0.58 (study area) and 0.33 (exclusive area). While at the study area scale, the asymmetric habitat overlap of the common leopard

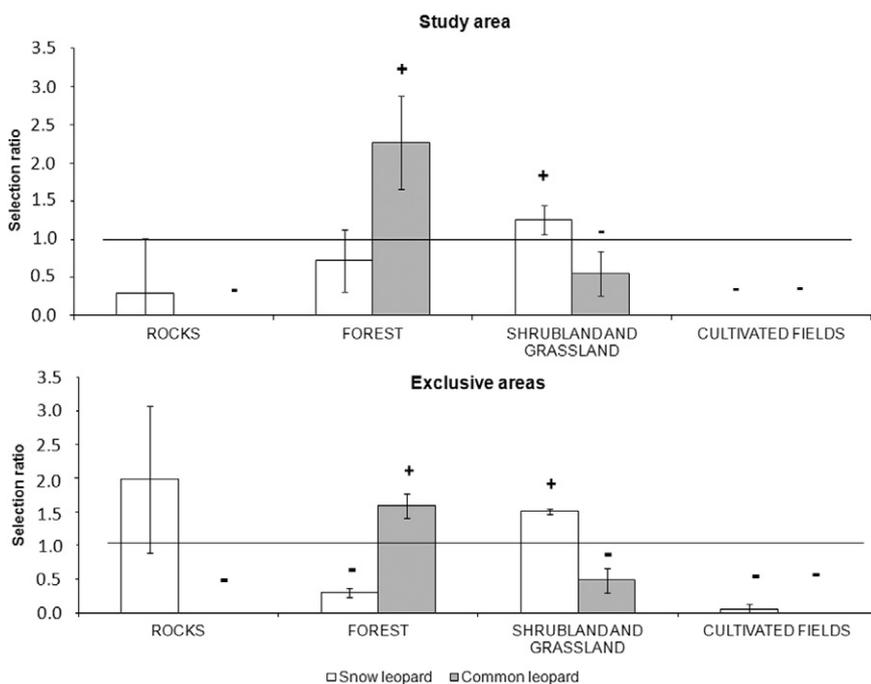


Figure 2 Yearly habitat selection by the snow leopard *Panthera uncia* and the common leopard *Panthera pardus*, in Sagarmatha National Park, estimated through counts of scats and scrapes and selection ratios (Manly *et al.*, 2002) with Bonferroni confidence intervals. (a) Habitat selection in the study area ($N = 72$ genotyped scats, for the snow leopard; $N = 44$, for the common leopard). (b): habitat selection in exclusive areas ($N = 1019$ scats and scrapes, for the snow leopard; $N = 145$, for the common leopard). + = positive selection; - = avoidance.

Table 2 Yearly habitat selection by snow leopards (SL) and common leopards (CL), in Sagarmatha National Park, estimated through counts of scats and scrapes and selection ratios (*W*) with Bonferroni confidence intervals (IC- = lower interval; IC+ = upper interval), in the study area (*N* = 72 genotyped scats, SL; *N* = 44, CL) and in exclusive areas (*N* = 1019 scats/scrapes, SL; *N* = 145, CL)

Species	Habitat	Study area				Exclusive area			
		<i>W</i>	IC-	IC+	Selection	<i>W</i>	IC-	IC+	Selection
Snow leopard	Rocks	0.289	-0.479	1.058	0	1.979	0.807	3.152	0
	Closed forest	0.068	0.113	0.249	-	0.368	0.269	0.467	-
	Open forest	2.235	0.801	3.669	-	0.115	0.023	0.207	-
	Closed shrubland	1.042	0.402	1.682	0	2.210	1.907	2.514	+
	Open shrubland/Alpine meadows	1.356	0.984	1.727	0	1.316	1.228	1.405	+
Common leopard	Cultivated fields	0.000	0.000	0.000	-	0.054	-0.018	0.126	-
	Rocks	0.000	0.000	0.000	-	0.000	0.000	0.000	-
	Closed forest	1.448	0.546	2.350	0	1.541	1.304	1.778	+
	Open forest	4.180	1.950	6.410	+	2.104	0.548	3.660	0
	Closed shrubland	1.023	0.209	1.836	0	0.501	0.230	0.771	-
	Open shrubland/Alpine meadows	0.325	-0.005	0.654	-	0.450	0.144	0.756	-
	Cultivated fields	0.000	0.000	0.000	-	0.000	0.000	0.000	-

+ = positive selection; - = avoidance; 0 = no selection/avoidance.

Table 3 Factors affecting the habitat selection in exclusive areas by snow leopard with respect to common leopard

Variable	Coefficient value	SE	<i>P</i> value
Altitude	0.005	0.002	0.000
Distance from forests	0.019	0.004	0.000
Distance from cliffs	-0.010	0.003	0.000
Intercept	-17.821	5.344	0.001

Effects were estimated by means of generalized linear models with binomial errors and both fixed and random effects. 1 = presence of snow leopard; 0 = presence of common leopard. SE = standard error.

over the snow leopard was high ($I = 0.70$), at the exclusive area scale, it decreased by half ($I = 0.35$).

In their exclusive areas, snow leopards selected areas at a greater altitude, farther from forest margins and closer to cliffs than common leopards (Table 3).

Food habits

Absolute frequencies of occurrence of prey did not differ significantly between genotyped scats ($N = 44$, snow leopards; $N = 33$, common leopards) and not-genotyped ones, collected in the exclusive areas ($N = 139$ samples of snow leopards; $N = 41$ samples of common leopards; G -test: $P > 0.05$). Thus, these data were pooled for further analysis (snow leopard: $N = 183$; common leopard: $N = 74$). For both leopard species, the diversity curves of the respective diets reached an asymptote at 11–13 samples (Fig. 3), suggesting that our sample sizes were adequate.

Snow leopards and common leopards shared similar wild (Himalayan tahr, musk deer) and domestic (*Bos* spp. and dogs) prey species. The Himalayan tahr was the staple of snow leopards (56.3% absolute frequency), whereas the musk deer was the staple of common leopards (54.1%; Fig. 4). Scats often included only one prey species (mean volume, when

present: 91% for both cats). *Bos* spp. was the second most important prey of both leopards (absolute frequencies: *c.* 25%).

Within each species, there was no significant seasonal difference in diet (G -test: $P > 0.05$). Diet composition varied significantly between species, at both yearly and seasonal scales (G -test; year: $G = 46.070$, d.f. = 5, $P < 0.001$; colder months: $G = 15.306$, d.f. = 5, $P = 0.009$; warmer months: $G = 38.392$, d.f. = 5, $P = 0.000$; Figs 4 and 5). Yearly diet overlap was 0.69; seasonal overlap was 0.76 (colder months) and 0.60 (warmer months).

Both leopard species ingested plant material: *Myricaria rosea* was present in 14.2 and 12.0% of snow leopard scats and 9.6 and 6.8% of common leopard scats, in cold and warm months, respectively. Tamaricaceae species made up the bulk of hairballs and were found significantly more often for snow leopards than for common leopards (scats + hairballs, pooled together: snow leopards, 16.9% colder months, 15.3% warmer months; $N = 59$; common leopards, 4.1% colder months, 9.6% warmer months; $N = 10$; G -test: $G = 6.309$, d.f. = 1, $P = 0.012$).

Discussion

Jackson (1996) indicated a greater use of tree cover types by the snow leopard than in our study area, although these were 'extremely small and presumably used primarily for daytime bedding'. He used daylight radio-tracking data, thus emphasizing diurnal behaviour of snow leopards that is when they are the least active (Jackson, 1996; McCarthy *et al.*, 2005). Our data are based on genotyped scats, reflecting diel activities.

Common leopard and snow leopard adult males appear intolerant of conspecific males (Bailey, 1993; Jackson, 1996), suggesting territoriality. These authors remarked that female leopards tend to avoid one another, even when sharing the same area. As we used scats (marking signs), most likely we

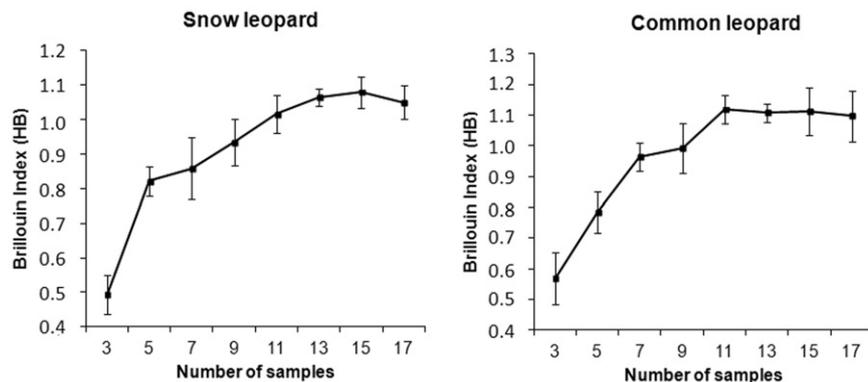


Figure 3 Diversity curves (mean \pm standard error) of food habits of snow leopards and common leopards, estimated through the Brillouin index (HB).

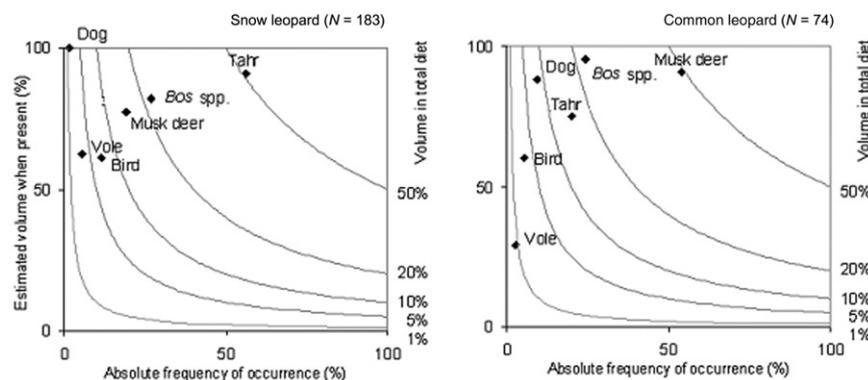


Figure 4 Food habits of sympatric snow leopards and common leopards, in terms of estimated volume when present (%) versus frequency of occurrence (%). Isopleths connect points of equal relative volume.

have mainly assessed the margins of territories, thus identifying their respective habitats.

Among carnivores, competitive interactions are related to diet overlap and body size, being less likely to occur when competitors differ greatly in size (presumably using different resources; Donadio & Buskirk, 2006). In carnivores, interspecific aggressive interference is frequent, which may lead to population reduction/extinction of the inferior competitor (Palomares & Caro, 1999, for a review). Between common and snow leopards, overlap of trophic niches ranges from 0.83 (weight categories of prey) to 1.0 (main prey categories) making them candidate species for competition (Lovari *et al.*, in press). Thus, one could expect that the bigger common leopard, as the superior competitor, may have an impact on populations of the slightly smaller snow leopard.

Our data confirmed the prediction that the two leopard species coexist by using different habitats. The exclusive areas of these cats were spatially separated, whereas at the study area scale there was some spatial overlap of the common leopard on the snow leopard, probably because of the great habitat adaptability of the former (Hemmer, 1972; Nowak, 1991; Fig. 2). This behaviour could enhance the takeover of the habitat of the snow leopard by the larger, ecologically flexible species. Conversely, presence of the snow leopard at the forest margins has been occasional and restricted to the breeding season, when individuals presumably roam around

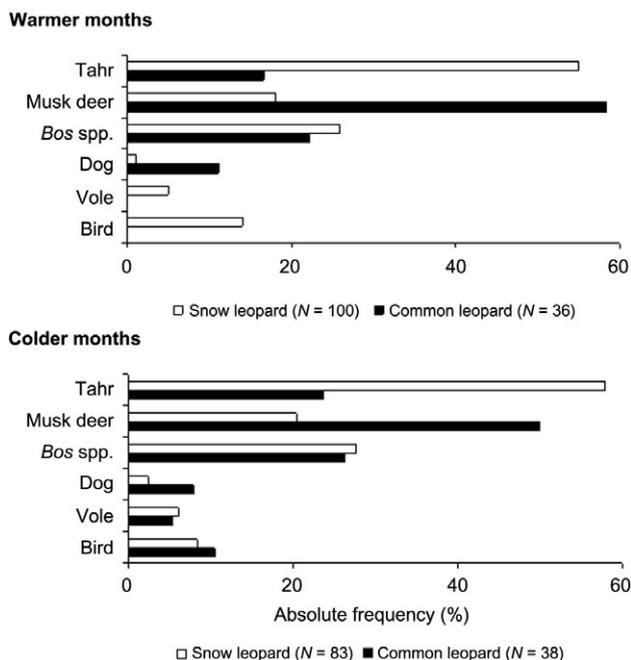


Figure 5 Seasonal diets of the snow leopard and the common leopard in terms of absolute frequency of occurrence.

searching for mates rather than looking for prey. Altitudinal and/or habitat separation help to avoid competition (Schoener, 1974; Caughley & Sinclair, 1994), but, on mountains, climate change is pushing up the upper forest tree line (e.g. Walther *et al.*, 2002; Dubey *et al.*, 2003; Baker & Moseley, 2007), with a predicted habitat decrease of the snow leopard (30–50% less, in the Himalayan Region, Forrest *et al.*, 2012). If so, one could expect that the common leopard will follow the forests, thus moving its altitudinal distribution upslope and locally invading the former range of the snow leopard (Lovari *et al.*, in press). If so, the potential for competition between these cat species will increase in *c.* 10–15% of the present range of the endangered snow leopard.

Both leopard species can kill prey of large size (>50 kg; for a review: Lovari *et al.*, in press). Common leopards tend to concentrate on smaller prey (<25 kg), whereas the snow leopards do not show any preference up to 75 kg (Lovari *et al.*, in press, for Asia), although prey availability should influence prey selection (Sih & Christiansen, 2001).

We predicted that diet overlap would not have occurred or would be marginal. Conversely, the same prey – although at significantly different proportions – built up the staple for both leopards: tahr, musk deer and livestock (Fig. 4). The diet overlap was extensive in the colder and substantial in the warmer months (Fig. 5).

Especially in the warm season, Himalayan tahr tend to inhabit open areas, moving to forests/brushy habitats, for example in case of bad weather or disturbance (Schaller, 1977; Buffa *et al.*, 1998; Lovari *et al.*, 2009a). In the cold season, tahr move to the steep forest below 3500 m (Schaller, 1977), where they meet with common leopards more frequently than during the warm season. Conversely, musk deer live mainly in the forest (Buffa *et al.*, 1998; Aryal *et al.*, 2010), but also in grassland with bushes (Buffa *et al.*, 1998). In the former, they built the staple for common leopards, whereas in the latter they were available to snow leopards. Cattle are moved around from the open higher altitudes to the wood ecotone, in complex, seasonally changing patterns, according to land tenure, tradition, ritual regulation and dynamics of mountain vegetation (Brower, 1991). Both leopard species have access to them, especially as domestic animals are normally left unguarded.

Thus, throughout the year, all three main prey occur in the preferred habitats of both leopards, with tahr and musk deer switching roles as the staple, most likely because of their respective attendance in the habitats used by these cats (Fig. 4). Thus, partial sharing of the same resources occurred. Livestock held an intermediate position between tahr and musk deer in the diet of both leopard species. In spite of our monthly thorough search over 4 years (cf. Methods), our scat samples were relatively small, which reflects the low local density of both leopard species.

Food habits are strongly dependent on availability of potential prey. Presumably, common leopards and snow leopards could better differentiate their respective trophic niches in presence of rich prey assemblages. In respect to other Himalayan areas (e.g. eastern Himalaya: Schaller, 1977; Langu valley: Jackson, 1996; Manaslu: S. Lovari, unpublished data),

the meso-large mammal assemblage of SNP is relatively depauperate, especially when it comes to ungulates: *c.* 50% less species (Lovari *et al.*, 2009b). Potential competition between these large cats may vary according to local richness and abundance of prey species.

Competition between sympatric carnivores involves aggressive interference, which leads to interspecific killing (Palomares & Caro, 1999; Donadio & Buskirk, 2006). Temporal segregation in the same habitat and habitat separation also tend to make different prey available to carnivores, thereby both forms of competition are avoided. Predator–predator relationships are influenced by availability of prey (Harmsen *et al.*, 2011) and differences of body size between competing species (Donadio & Buskirk, 2006). Spatial segregation may occur when competing species have similar diets, but they differ greatly in body weight (i.e. >100%), with the smaller species avoiding the larger one (e.g. Mech, 1977; Palomares *et al.*, 1995). Our data have shown that habitat separation not always leads to the use of different prey, also when body weights of competitors nearly overlap. If so, avoidance of interspecific aggression (Donadio & Buskirk, 2006), rather than exploitation of resources, could be the major factor allowing the coexistence of potentially competing large predators.

Acknowledgements

We are grateful to National Academy of Sciences and Technology and especially to A. Da Polenza and the personnel of Ev-K2-CNR for backing our project; to K. Thapa, several students and especially to B.B. ‘Lalu’ Gurung for help in field work; to Lhakpa Sonam Sherpa and to Pema Sherpa, their families and their staffs for lodging and friendship. M. Festa-Bianchet provided advice on a previous draft. Three anonymous reviewers improved greatly our MS. Our work was financially supported by Project SHARE (Ev-K2-CNR, Italy) and the Italian Ministry of Foreign Affairs.

S.L. planned this study and wrote several drafts of this paper; I.M. and B.P. carried out diet analyses and participated in writing drafts; F.F. conducted some data analyses and cooperated in writing drafts; N.M. and E.R. carried out genetic analyses.

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