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Food habits of two leopard species, competition, climate change and upper treeline: a way to the decrease of an endangered species?

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For carnivore species, spatial avoidance is one of the evolutionary solutions to coexist in an area, especially if food habits overlap and body sizes tend to coincide. We reviewed the diets of two large cats of similar sizes, the endangered snow leopard (*Panthera uncia*, 16 studies) and the near-threatened common leopard (*Panthera pardus*, 11 studies), in Asia. These cats share ca 10,000 km² of their mountainous range, although snow leopards tend to occur at a significantly higher altitude than common leopards, the former being a cold-adapted species of open habitats, whereas the latter is an ecologically flexible one, with a preference for woodland. The spectrum of prey of common leopards was 2.5 times greater than that of snow leopards, with wild prey being the staple for both species. Livestock rarely contributed much to the diet. When the breadth of trophic niches was compared, overlap ranged from 0.83 (weight categories) to one (main food categories). As these leopard species have approximately the same size and comparable food habits, one can predict that competition will arise when they live in sympatry. On mountains, climate change has been elevating the upper forest limit, where both leopard species occur. This means a habitat increase for common leopards and a substantial habitat reduction for snow leopards, whose range is going to be squeezed between the forest and the barren rocky altitudes, with medium- to long-term undesirable effects on the conservation of this endangered cat.

KEY WORDS: carnivore evolution, coexistence, sympatric species, diet, *Panthera uncia*, *Panthera pardus*.

INTRODUCTION

Two basic types of competitive interactions for resources have been recognised, interference and exploitation (MILLER 1967). The former is defined as any activity

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directly or indirectly limiting the access of a competitor to a necessary resource, while the latter concerns the reduced availability of a resource after being accessed and used by the superior competitor (MILLER 1967). Carnivores compete with each other not only through resource exploitation, but also through interspecific killing: a common key determinant of the abundance and distribution of carnivore species (DONADIO & BUSKIRK 2006). As a consequence, the use of space, activity patterns and social behaviour of the inferior competitor may be altered (PALOMARES & CARO 1999; HAYAWARD & SLOTOW 2009). Spatial avoidance is one of the evolutionary solutions for carnivore species to coexist in an area (HUNTER & CARO 2008), although coexistence may also be achieved by selecting prey belonging to different weight classes or taxa (e.g. BERTRAM 1982; BOTHMA et al. 1984; KARANTH & SUNQUIST 2000; HAYWARD & KERLEY 2008).

The common leopard *Panthera pardus* is a near-threatened large cat (IUCN 2012; body weight: female 28–60 kg, male 37–90 kg; NOWAK 1991) occurring over a very wide distribution range, including most of Africa and large parts of Asia, from the Near East to the Indian subcontinent, throughout most of Southern China down to the Malaysian Archipelago and up to the Amur Region. From the latest Early (some 0.9 Ma ago) to Late Pleistocene, it was present also in South Europe (TURNER & ANTON 1997). The slightly smaller snow leopard *Panthera uncia* is an endangered species (IUCN 2012; body weight: female 25–40 kg, male 45–75 kg; NOWAK 1991; JACKSON 1996) and it has never moved from Asia (TURNER & ANTON 1997), where it occupies a region of ca 1,230,000 km² (FOX 1989), from North Afghanistan, Pakistan, India and regions bordering the Himalayas, up to Mongolia and Russia. These species may appear so similar at first glance that living populations, as well as fossil remains, of common leopards have been wrongly taken for snow leopards (HEMMER 1972).

While the evolutionary history of the common leopard is well known (e.g. TURNER & ANTON 1997), that of the snow leopard is a mystery, as this cat suddenly appears in the lower Pleistocene (HEMMER 1972; TURNER & ANTON 1997). Molecular studies would suggest a close relationship of the snow leopard to another large cat found only in Asia: the tiger *Panthera tigris*, having diverged about two million years ago (O'BRIEN et al. 2008).

In Asia, at present, the distribution range of the common leopard and that of the snow leopard overlap on the southern slopes of the Himalayas and along river valleys penetrating into the Tibetan Plateau (Fig. 1), but they likely lived in sympatry over a much wider area, e.g. in the Karakorum, up to a relatively recent past (SCHALLER 1977). According to the altitudinal limits of both species provided by the International Union for Conservation of Nature (IUCN) red list – up to 5200 m in the Himalayas, for the common leopard (HENSCHEL et al. 2008); down to 3000 m, for the snow leopard (JACKSON et al. 2008) the two leopard species reach an altitudinal range overlap in a strip of 2200 m, all along the Himalayan range (2400 km long): a substantial area of ca 10,000 km².

While the common leopard is a highly adaptable species, living in habitats from sub-desertic to tropical forest and taiga (NOWAK 1991), the snow leopard is a cold-adapted inhabitant of open bushy and rocky areas (HEMMER 1972; FOX 1989). Because of their comparable body size – with the common leopard being the larger species – and morphology, one could expect competitive interactions to have occurred between these leopards in areas of geographic overlap.

In this work, we attempt to carry out a review of the food habits of the snow leopard and the common leopard in Asia. We discuss the results of our analysis in respect to the potential competition between these large cats especially in the past,
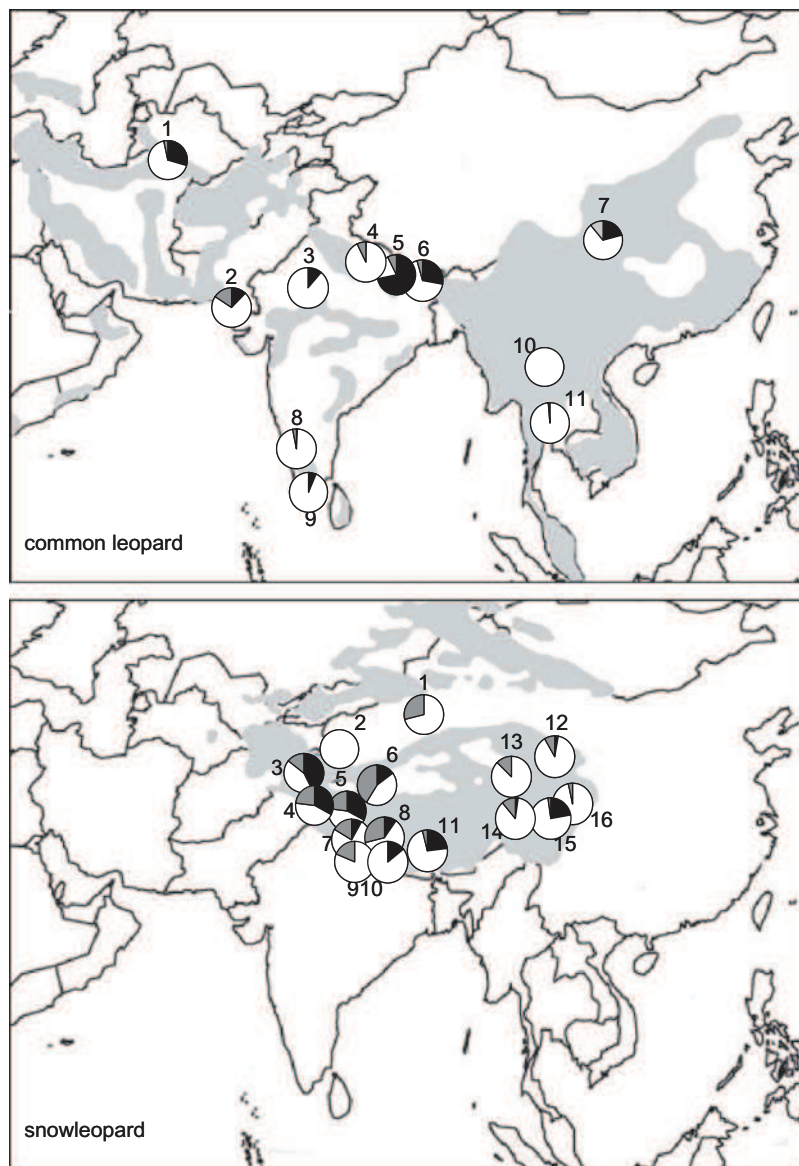
Fig. 1. — Diet composition in terms of frequency of occurrence of domestic prey (black), wild prey i.e. mammals and birds (white) and other prey e.g. amphibians, reptiles etc. (grey) in common leopard (*Panthera pardus*) and snow leopard (*Panthera uncia*) with respect to study sites and distribution range (IUCN 2012, modified). Study areas: CL, 1 – LUKAREWSKY 1988; 2 – SCHALLER 1977; 3 – KHANDAL & SRIVASTAVA (unpublished); 4 – WEGGE et al. 2009; 5 (Deurali area); 6 (Sagarmatha) – LOVARI (unpublished); 7 – JOHNSON et al. 1993; 8 – Bandipur area (JOHNSINGH 1992; KARANTH & SUNQUIST 1995; ANDHERIA et al. 2007); 9 – SATHYAKUMAR 1992; 10 (Doi Mon Jong) – LOVARI (unpublished); 11 – RABINOWITZ 1989. SL, 1 – SCHALLER et al. 1988b; 2 – SCHALLER et al. 1987; 3, 7, 8 – SCHALLER 1977; 4, 5 – BAGCHI & MISHRA 2006; 6 – CHUNDAWAT & RAWAT 1994; 9 – JACKSON 1996; 10 – OLI et al. 1993, 11 (Sagarmatha) – LOVARI (unpublished); 12, 13, 14, 15, 16 – SCHALLER, REN & QIU 1988. Shaded area: distribution range.

with implications for the evolution of the snow leopard. Furthermore, we predict a conservation problem for this endangered large cat along the Himalayan range, because of a decrease of its habitat to the increase of that of the common leopard, elicited by recent climate changes.

STUDY AREA

The cold-adapted snow leopard has a fragmented distribution associated with intact mountain chains and patches of mountainous habitat. Snow leopards are mostly associated with arid and semi-arid shrubland, grassland or steppe. They are generally found at altitudes between 3000–4500 m above sea level (a.s.l.), although they occasionally reach up to 5500 m in the Himalayas, whereas at the northern limits of their range they can be found between 600–1500 m (e.g. HEMMER 1972; FOX 1989). Steep open terrain broken by cliffs, ridges, gullies and rocky outcrops is their preferred hunting ground, with exceptions (SCHALLER 1977; JACKSON & AHLBORN 1989). Their camouflaged fur blends very well into this background, whether it be scree or snow (SCHALLER 1977). In the Himalayas, the snow leopard's main potential wild prey include bharal *Pseudois nayaur*, Himalayan tahr *Hemitragus jemlahicus*, argali *Ovis ammon*, possibly the serow *Capricornis sumatraensis*, goral *Naemorhedus goral*, musk deer *Moschus* spp., primates and smaller species, e.g. marmots *Marmota* spp., pikas *Ochotona* spp. and large gallinaceous birds. On other mountain ranges, e.g. Karakoram, Tian Shan and Altai, wild goats (e.g. Siberian ibex *Capra ibex sibirica*, markhor *Capra falconeri*, bharal and wild goat *Capra hircus*) and wild sheep (e.g. urials *Ovis vignei*), as well as musk deer and smaller prey, are available (e.g. SCHALLER 1977; SUNQUIST & SUNQUIST 2002).

The common leopard has a wide habitat tolerance, with the world's largest distribution of any wild large cat (TURNER & ANTON 1997). Leopards occur mainly in forest, from tropical rainforest to the temperate deciduous and alpine coniferous (up to 5200 m in the Himalaya), as well as in dry scrubwood and tall grassland (NOWELL & JACKSON 1996), as they depend on vegetation cover to stalk their prey successfully (BAILEY 1993; KARANTH & SUNQUIST 1995).

The large variety of habitats occupied by common leopards provides a wide spectrum of potential prey, from small mammals and birds to the ungulate community (small and medium-sized deer, the young of wild cattle and larger deer), as well as primates (HAYWARD et al. 2006).

Locally, both species may prey on domestic animals, especially livestock.

METHODS

Twenty-seven food habit studies (16 for the snow leopard, 11 for the common leopard) were reviewed from a wide range of habitats between 26–42°N and 31–58°W and 200–5000 m altitude (Fig. 1). Differences in the use of altitude ranges between common leopard and snow leopard, across different studies, were assessed by the Mann-Whitney U-test (ZAR 1999).

JOHNSINGH (1992), KARANTH & SUNQUIST (1995) and ANDHERIA et al. (2007) collected data on food habits of common leopards in the same Bandipur area, in different years: we have pooled together and averaged their data to avoid pseudoreplication. Original data were also included from two study areas in Nepal (2006–2008: Deurali area; 2005–2008: Sagarmatha) and one area in NW Thailand (1986–1987: Doi Mon Jong) (all referred to as S. LOVARI, unpublished data), obtaining

a total number of 16 diet studies for the snow leopard and 11 for the common leopard. Data collection and analyses were similar across all studies, making it possible to compare results.

As authors used different categories to describe the diets of leopards, we grouped the listed prey into two sets of categories, without including the "unidentified hair" values. The first set assigned the species or taxonomic group to the categories wild ungulates, domestic ungulates, other wild prey, other domestic prey, other prey (inclusive of unusual prey found in scats, e.g. reptiles, crustaceans and insects) and plant material. As to the second set, six categories of prey were assessed on the basis of the mean weight (cf. below) of each species or higher taxonomic group: "very small" < 2 kg; "small" 2–25 kg; "small-medium" 26–50 kg; "medium-large" 51–75 kg; "large" 76–100 kg; "very large" > 100 kg) (see Table 1). The weight of each mammalian species (NOWAK 1991) was averaged by the following formula:

$$(\text{max. weight} + \text{min. weight}) / 2 \tag{1}$$

We have referred to weights of populations included in the distribution range of each leopard species for prey which occur over a wider area than those of these large cats in Asia, unless the relevant weights were pointed out in the reviewed papers. The weights of domestic forms and those of *Phasianidae* were taken from internet sources and our own data (S. LOVARI, unpublished data).

For each study, data were worked out as relative frequencies of occurrence of each prey category (number of samples with occurrence of food category *i* over the total number of occurrences of all categories × 100) (LUCHERINI & CREMA 1995; LOVARI & ROLANDO 2004), because absolute frequencies were not available in all studies. We used the standardized Levins B index (B$_{sta}$: COLWELL & FUTUYMA 1971) to evaluate the diet niche breadth of both predators (low niche breadth = 0; great niche breadth = 1):

$$B_{sta} = \left(1 \middle/ \sum p_i^2 - 1\right) \middle/ (B_{max} - 1) \tag{2}$$

where *p* is the proportion of each food category (i) and B$_{max}$ is the total number of food categories.

The Pianka's index (PIANKA 1973, no overlap = 0, max. overlap = 1) was applied to calculate the overlap of diets between the leopards:

$$O_{jk} = \sum (i = 1 \ldots n) \, p_{ij} \, p_{ik} \middle/ \left(\sum p^2_{ij} \sum p^2_{ik}\right)^{1/2} \tag{3}$$

where p$_i$ is the percentage of prey item "i" in the diet of species "j" and "k".

A linear regression was calculated on the frequency of occurrence of wild ungulates (independent variable) and domestic ungulates (dependent variable). We considered wild ungulates as the independent variable. Leopards evolved in association to wild prey, while it is reasonable to assume that the use of domestic animals is a consequence of relatively recent domestication and habitat alteration (cf. MERIGGI & LOVARI 1996). For this purpose, we used only data from studies conducted in areas where domestic ungulates were present (15 studies for the snow leopard; nine studies for the common leopard).

The Kendall concordance correlation coefficient (W) was used for the main prey category set, as well as for the weight category set, to express the association of diet composition between study sites (cf. VIRGÓS et al. 1999). The coefficient of concordance, from 0 (no association of prey occurrences) to one (complete association), is a function of the degree of variance (SIEGEL & CASTELLAN 1988).

Statistical analyses were carried out using SPSS 12.0 (Inc.,USA).

Table 1.

Occurrence of prey in the common leopard *Panthera pardus* (CL) and the snow leopard *Panthera uncia* (SL) diets, food niche breadth (Levins standardized index, B_{Sta}) and weight of prey. Food items have been ordered by increasing weight. Data from studies listed in Fig. 1.

Food category	Occurrence		Relative frequency		Weight (kg)		Weight category
	CL	SL	CL	SL	Mean	Range	
WILD PREY							
Small mammals	6	8	0.057	0.098	1.05	0.1–2	<2
Phasianidae	4	7	0.038	0.085	1.5	*(unavailable)*	"
Martes foina	–	1	0.000	0.012	1.7	1.1–2.3	"
Atherurus macrurus	1	–	0.009	0.000	2.75	1.5–4	2–25
Vulpes spp.	1	1	0.009	0.012	3.65	1.8–5.5	"
Lepus spp.	5	5	0.047	0.061	4.15	1.3–7	"
Paguma larvata	2	–	0.019	0.000	4.3	3.6–5	"
Moschiola meminna	2	–	0.019	0.000	4.35	0.7–8	"
Ailurus fulgens	1	–	0.009	0.000	4.5	3–6	"
Marmota spp.	–	11	0.000	0.134	5.25	3–7.5	"
Hylobates lar	1	–	0.009	0.000	6	4–8	"
Macaca spp.	3	–	0.028	0.000	9.25	2.5–16	"
Hystrix spp.	7	–	0.066	0.000	9.35	0.7–18	"
Manis spp.	2	–	0.019	0.000	10	*(unavailable)*	"
Arctonyx collaris	3	–	0.028	0.000	10.5	7–14	"
Canis aureus	1	–	0.009	0.000	11	7–15	"
Arctictis binturong	2	–	0.019	0.000	11.5	9–14	"
Moschus spp.	2	2	0.019	0.024	12	7–17	"
Presbytini	7	–	0.066	0.000	14.5	5–24	"
Cuon alpinus	1	–	0.009	0.000	15.5	10–21	"
Tetracerus quadricornis	2	–	0.019	0.000	19	17–21	"
Muntiacus muntjak	3	–	0.028	0.000	23	14–28	"
Naemorhedus goral	2	–	0.019	0.000	28.5	22–35	26–50
Canis lupus	1	–	0.009	0.000	31.5	18–45	"
Elaphodus cephalophus	1	–	0.009	0.000	33.5	17–50	"
Hyaena hyaena	1	–	0.009	0.000	40	25–55	"
Gazella bennettii	1	–	0.009	0.000	48.5	12–85	"
Pseudois nayaur	–	12	0.000	0.146	52.5	25–80	51–75
Axis spp.	4	–	0.038	0.000	68.5	27–110	"
Hemitragus jemlahicus	2	2	0.019	0.024	75	50–100	"
Sus scrofa	7	–	0.066	0.000	80	40–120	76–100

(*Continued*)

Table 1.

(*Continued*)

Food category	Occurrence		Relative frequency		Weight (kg)		Weight category
	CL	SL	CL	SL	Mean	Range	
Capra spp.	–	5	0.000	0.061	91	32–150	"
Capricornis sumatraensis	1	–	0.009	0.000	95	50–140	"
Ovis spp.	2	1	0.019	0.012	110	20–200	>100
Ailuropoda melanoleuca	1	–	0.009	0.000	117.5	75–160	"
Cervus spp.	5	2	0.047	0.024	135	130–140	"
Boselaphus tragocamelus	1	–	0.009	0.000	205	169–241	"
Budorcas taxicolor	1	–	0.009	0.000	275	150–400	"
Bos spp.	1	–	0.009	0.000	720	540–900	"
Bubalus bubalis	1	–	0.009	0.000	800	700–900	"
DOMESTIC PREY							
Felis catus	1	–	0.009	0.000	3.9	3.3–4.5	2–25
Canis familiaris	2	1	0.019	0.012	10.5	1–20	"
Sheep and goats	6	10	0.057	0.121	15	5–25	"
Equus asinus	–	3	0.000	0.037	125	100–150	>100
Equus caballus	1	4	0.009	0.048	225	150–300	"
Bos grunniens	7	7	0.066	0.085	350	300–400	"
Camelus bactrianus	1	–	0.009	0.000	400	300–500	"
Total occurrences	105	82	1.000	1.000			
Food niche breadth B_{sta}			**0.511**	**0.215**			

RESULTS

Snow leopards occurred at a significantly higher altitude (range 3200–5000 m a.s.l.; median 4200 m) than common leopards (range 200–3840 m a.s.l.; median 800) (Mann-Whitney U-test, $U = 2$, $P < 0.0001$).

The number of taxa preyed upon by the common leopard was 42, whereas only 17 taxa were reported for the snow leopard (Table 1). Thus, niche breadth was much larger for the former (Levins standardized index: 0.54) than for the latter (0.22). Domestic prey were mainly *Bos* spp., goats *Capra* spp. and sheep *Ovis* spp. for both leopards. Wild boar *Sus scrofa*, *Presbytini* monkeys and porcupine *Hystrix* spp. were the most frequently used wild prey by common leopards, whereas bharal and marmots were the staple of the diet of snow leopards.

Wild prey was the main category in the diet of both predators (Fig. 1) with a median relative frequency of 89% (Q_1–Q_3: 68–95%) for the common leopard and 75% (Q_1–Q_3: 60–87%) for the snow leopard, whereas domestic prey rarely occurred with

high relative frequencies [common leopard (CL) median = 11%, Q_1–Q_3: 1–24%, snow leopard (SL) median = 9%, Q_1–Q_3: 0–22%]. The category "other" included mainly plant material, which was apparently more frequently found in faecal samples of snow leopards (median: 13%, Q_1–Q_3: 4–23) than in those of the common leopard (median: 3%, Q_1–Q_3: 1–7). This category was excluded from further analyses, as plant material is not digested by the unsuitable digestive system of large cats, thus being a poor food source for energy or nutrition (e.g. VAUGHAN 1986; MACDONALD 1992), although it may be occasionally ingested for sanitary reasons (BAILEY 1993), e.g. for cleaning the digestive tract from hair and possibly aiding in the removal of gut parasites.

When prey were grouped into main food categories (wild ungulates, domestic ungulates, other wild prey, other domestic prey, birds, other prey), niche breadth was similar for both leopards (O_{jk} = 0.998). Wild ungulates were the most used category, followed by other wild prey and domestic ungulates (Table 2). Other domestic prey were found in only two studies on the common leopard and one study on the snow leopard. Individual studies showed extreme variation in the use of domestic prey (e.g. common leopard: Fig. 1, sample 5, snow leopard: Fig. 1, samples 3–5). Apart from extreme cases, livestock did not constitute the bulk of the diet of either leopard species (Fig. 1). When comparing occurrences of food categories used by each species, "other" prey was used only by the common leopard.

As to weight categories, snow leopards used mainly medium-large prey (51–75 kg) and small prey (2–25 kg), whereas the diet of the common leopard consisted chiefly of small, as well as some very large (> 100 kg), prey (Fig. 2). In fact, very large (> 100 kg) and large (76–100 kg) prey occurred apparently more often in the diet of the common leopard (Fig. 2). Despite these differences, there was an extensive niche overlap in the diet of the two leopard species (O_{jk} = 0.91).

The proportion of wild ungulates in the diet of the common leopard influenced negatively the presence of domestic ungulates (linear regression, $n = 9$, y = 42.38 – 0.48x; SEE (standard error of estimate) = 0.19; R^2 = 0.489; F = 0.69, P = 0.036), but not in the diet of the snow leopard ($n = 15$; y = 29.93 – 0.27x; SEE = 0.22; R^2 = 0.107; F = 1.55, P = 0.235).

Occurrence of prey in the diet in relation to main food categories, as well as to weight categories of prey, was slightly more variable between study sites in the common

Table 2.

Relative frequency of occurrence (%) of main prey categories in the common leopard *Panthera pardus* ($n = 11$) and the snow leopard *Panthera uncia* ($n = 16$) diets (median, quartiles and range).

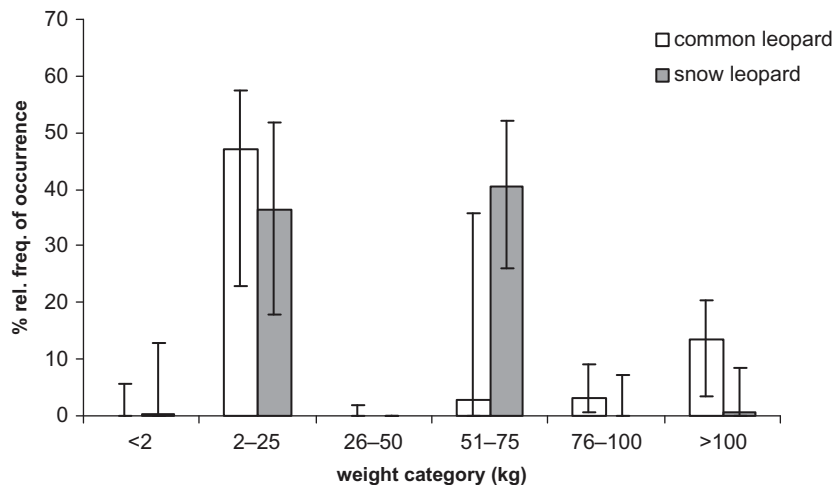| Prey category	% relative frequency of occurrence					
	common leopard			snow leopard		
	median	Q1–Q3	range	median	Q1–Q3	range
Wild ungulates	60	46–70	0–86	49	41–64	32–100
Domestic ungulates	11	1–21	0–64	12	0–24	0–50
Other wild prey	22	12–34	4–78	31	7–45	0–68
Other domestic prey	0	0–0	0–14	0	0–0	0–2
Birds	0	0–2	0–6	0	0–2	0–17
Other prey	0	0–2	0–11	0	0–0	0–0

Fig. 2. — Relative frequency of occurrence (%) of prey weight categories in the common leopard (*Panthera pardus*, $n = 11$) and the snow leopard (*Panthera uncia*, $n = 16$) diets (median, quartiles). $N_{CL} = 11$, $N_{SL} = 16$.

leopard ($W_{\text{main food categories}} = 0.32$; CL $W_{\text{weight categories}} = 0.54$) than in the snow leopard ($W_{\text{main food categories}} = 0.40$; $W_{\text{weight categories}} = 0.63$).

DISCUSSION

Our review has shown that the number of prey species of the common leopard is 2.5-fold greater than that of the snow leopard, which may be ascribed to the much greater variety of habitats and available prey, as well as the typically higher carrying capacity, of lower-altitude habitats used by common leopards compared to snow leopards. Similarly, differences in variability of prey categories between study sites were greater in the common leopard than in the snow leopard; i.e. the former tended consistently to feed on a more variable range of prey.

The common leopard is a species thriving in closed habitats (NOWAK 1991), while the snow leopard prefers open ones (HEMMER 1972; FOX 1989). Where these species live in sympatry, interspecific resource competition could develop at the junction of closed and open habitats, through the use of the same prey species, especially if their availability is limited. In fact, we found a substantial overlap in prey categories and prey sizes of these cats overall and in particular in the Sagarmatha National Park, where these species live in sympatry for 640 m of altitude ($O_{jk - \text{main food categories}} = 0.99$; $O_{jk - \text{weight categories}} = 0.67$; LOVARI et al. in prep.).

Our review suggests that the snow leopard uses mainly medium-large prey species and small prey. Apparently, the slightly larger common leopard feeds mainly on small and, to a lesser extent, on very large prey, but rarely on intermediate categories in Asia (Fig. 2). This finding is odd and perhaps due to a different data manipulation, as common leopards have been reported to kill mainly prey of small-medium body size in Africa and in several areas of the Indian subcontinent (HAYWARD et al. 2006). Usually, faecal analysis does not allow the determination of the age of ingested animals (but

see MATTIOLI et al. 1995) and information on the age of prey is lacking in all studies we reviewed. If we assume (KARANTH & SUNQUIST 1995; HENSCHEL et al. 2005; HAYWARD et al. 2006) that very large prey were mainly killed as young or subadult individuals, the prey size overlap of these cats would be even more extensive. On the other hand, one cannot rule out the scavenging of carcasses (e.g. BAILEY 1993; JACKSON et al. 1996; CORLETT 2011). Because of these contrasting limitations we have preferred not to make any assumptions.

Among carnivores, interspecific killing of an inferior competitor by a superior one is common and may lead to population reduction or even extinction of the former (PALOMARES & CARO 1999). DONADIO & BUSKIRK (2006) report that the frequency of attacks depends on differences in body size and on a close systematic position (DONADIO & BUSKIRK 2006): at small and large size differences, attacks are less likely to occur, whereas, at intermediate size differences (e.g. between common and snow leopards), killing interactions are frequent and related to diet overlap.

The bigger, adaptable common leopard, as the superior competitor, and the smaller, specialised snow leopard, as the inferior one, could fit in the above pattern. So far, no ecological study on these species has been carried out where they live in sympatry, but we should expect an extensive prey overlap and potential interference between them. Altitudinal and/or habitat separation help to avoid competition (SCHOENER 1974; CAUGHLEY & SINCLAIR 1994), but climate change is already pushing the upper forest treeline higher (e.g. WALTHER et al. 2002; DUBEY et al. 2003; BAKER & MOSELEY 2007). FORREST et al. (2012) indicated that an average of 30%, with a maximum of about 50%, of current snow leopard habitat in the Himalayas will be lost because of the shifting treeline and the consequent shrinking of the alpine zone. If so, one could expect that the common leopard will follow the forests, thus moving upslope its altitudinal distribution and invading the former range of the snow leopard (see below).

Rigorous environmental conditions, the resulting lower primary productivity and the limited habitat diversity of the ecologically poor areas which the snow leopard inhabits militate against highly variable prey communities in its distribution range (JACKSON et al. 2010). In fact, our review suggests that niche breadth and spectrum of prey species of the snow leopard are much smaller than those of the common leopard, confining the survival of the former to the availability of fewer prey species. A steno-species, e.g. the snow leopard, is more likely to be affected by an environmental change than a eury-species, e.g. the common leopard, all the more if a larger, adaptable competitor comes forward with the environmental change (cf. the spatial takeover of the larger and ecologically adaptable red fox to the expense of the smaller and less competitive arctic fox, HERSTEINSSON & MACDONALD 1992). If so, most likely, climate change will confine the snow leopard to a narrow range between the forest – an unsuitable habitat for this species – and the higher, barren rocky areas. This event could determine the loss of vast regions in the southern and southwestern parts of the distribution range of the snow leopard, e.g. along the Himalayas, with undesirable effects on the conservation of this endangered large cat.

One could expect even greater opportunities for competition to have arisen between these felids when, presumably, their distribution ranges overlapped greatly during the last glacial and interglacial periods (cf. SCHALLER 1977). According to palaeontological evidence, the snow leopard evolved much later than the common leopard, whose earliest fossil remains date back to the Early/Middle Pliocene (3.5 Ma ago, from Laetoli, Tanzania; TURNER 1990). Apparently, the common leopard spread from Africa to Asia during the Early Pleistocene (its oldest remains in Asia are from the

Indian Siwaliks at about 2 Ma ago; UPHYRKINA et al. 2001), whereas the earlier finds of the snow leopard date back to just 1.2–1.4 Ma ago (TURNER & ANTON 1997). Fossil records and its present distribution range suggest that the snow leopard never moved from Asia, with palaeontological remains from the Altai mountains, on the western borders of Mongolia, to the Siwalik region of northern Pakistan (TURNER & ANTON 1997). O'BRIEN et al. (2008) suggested that genetically the snow leopard is relatively close to the tiger, another entirely Asiatic species, which may support the hypothesis that the snow leopard evolved on this continent.

Open, cold, relatively homogeneous habitats, e.g. steppe, alpine moorland and tundra, are much less productive than warmer, heterogeneous habitats, e.g. temperate deciduous and riverine forests, and tall grassland. Accordingly, ungulate communities are richer in the latter than in the former (e.g. PFEFFER 1964; BOURLIÈRE 1973; SHACKLETON & BUNNELL 1989). One could predict that carnivore species will tend to concentrate on ungulate-rich areas, i.e. warmer, heterogeneous habitats, rather than areas with a low food supply, i.e. open, cold, homogeneous ones (cf. CORLETT 2011). If so, one could expect that extreme habitats will be colonized later than food-rich ones, by less competitive but well-adapted forms. We suggest that the snow leopard appeared later than most other species of large cats (TURNER & ANTON 1997), when these had already occupied the more food-rich warmer habitats in Asia. Thus, the snow leopard could have been compelled to adapt to a life in marginal habitats, with harsh climatic conditions and a low resource availability, which makes this specialised species particularly sensitive to environmental changes altering its habitat and bringing along a larger competitor.

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