

## Short report

# Predation may counteract climatic change as a driving force for movements of mountain ungulates



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## ABSTRACT

Temperature variations are expected to influence altitudinal movements of mountain herbivores and, in turn, those of their predators, but relevant information is scarce. We evaluated monthly relationships between temperature and altitude used by a large mountain-dwelling herbivore, the Himalayan tahr *Hemitragus jemlahicus*, and its main predator, the snow leopard *Panthera uncia*, in an area of central Himalaya for five consecutive years (2006–2010). In contrast to expectations, there was no significant direct relationship between altitude of tahr sightings and temperature. The mean altitude of tahr sightings decreased by c. 200 m throughout our study. As expected, snow leopard movements tracked those of tahr, although the core area of the snow leopard did not move downwards. Tahr remained the staple of the snow leopard diet: we suggest that the former did not move upwards in reaction to higher temperature to avoid encounters with the latter. Avoidance of competition with the larger common leopard *Panthera pardus* at lower altitudes could explain why snow leopards did not shift their core area downwards. Apparently, interspecific interactions (predation; competition) influenced movements of Himalayan tahr and snow leopards more than climatic variations.

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## 1. Introduction

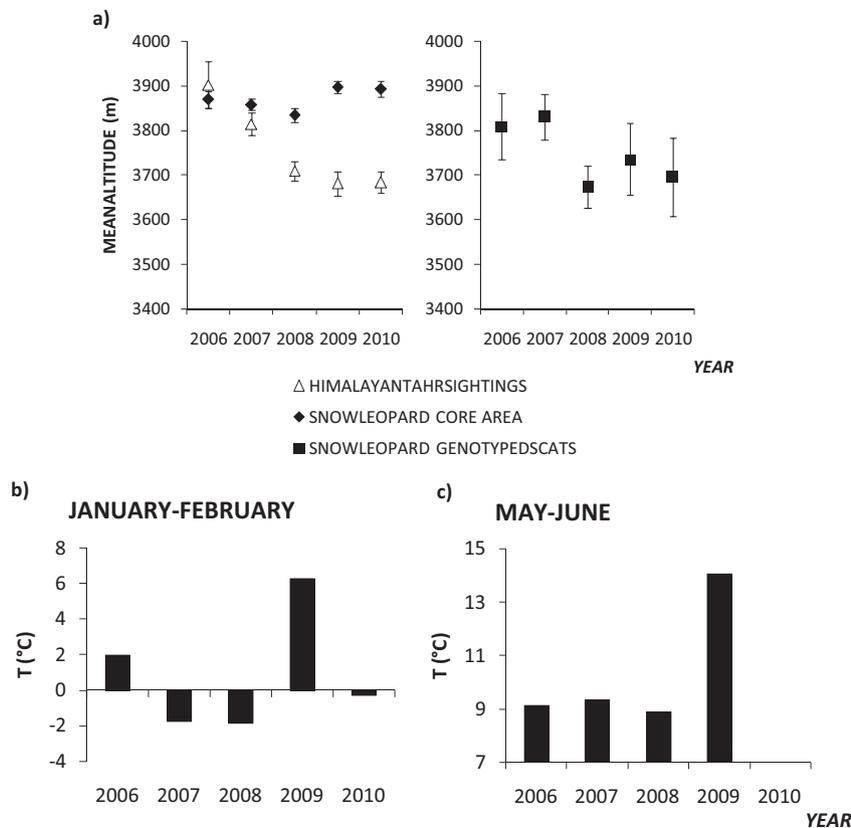
Current climatic changes are influencing the distribution of organisms (e.g. Walther et al., 2002; Parmesan and Yohe, 2003). Plant and animal species living in cold or strongly seasonal ecosystems, e.g. in mountain habitats, should be amongst the first ones to be affected (e.g. Gottfried et al., 2012; Telwala et al., 2013). Effects on plants, herbivores and carnivores can potentially generate cascading consequences across trophic levels (e.g. Walther et al., 2002). In mountainous areas, numbers and movements of large herbivores and carnivores should be greatly influenced by climatic changes because of thermoregulation (e.g. searching for cooler places in the warm season), snow cover and/or altitudinal shifts of respective food resources, but relevant evidence is scarce (e.g. Georgii and Schroeder, 1983; Grignolio et al., 2004; Lovari et al., 2006; Mason et al., 2014). Mountain ungulates need to increase their body reserves throughout the warm season to enhance their chance of survival during the following winter (e.g. Festa-Bianchet,

1988; Côté and Festa-Bianchet, 2001; Pettorelli et al., 2007). In the long-term, climatic variability should affect plant distribution (e.g. Gottfried et al., 2012) and phenology, in turn influencing movements and survival of herbivores (e.g. Pettorelli et al., 2007). Accordingly, movements of carnivores should be expected to track those of their prey.

We conducted a 5-year study (2006–2010) to assess relationships between variation in ambient temperature and altitudinal movements of Himalayan tahr *Hemitragus jemlahicus* (Artiodactyla: Bovidae) and its main predator, the snow leopard *Panthera uncia*, in a high altitude mountainous habitat in Central Himalaya, the Sagarmatha (Mt. Everest) National Park (SNP, Nepal). Numbers of predator and prey were shown to be linked, in the same area (Lovari et al., 2009a; Ferretti et al., 2014; Lovari and Mishra, in press). Snow leopards prey mainly upon meso-large wild mammals (e.g. Anwar et al., 2011; Shehzad et al., 2012; for reviews: Lovari et al., 2013b; Lyngdoh et al., 2014), i.e. the Himalayan tahr in our study area (Lovari et al., 2013a), and should be particularly vulnerable to climatic changes (Forrest et al., 2012; Lovari et al., 2013b). As 2009 was exceptionally warm in respect to the other years (Fig. 1a), we collected data to test whether a shift in altitudinal movements of tahr and, in turn, snow leopards occurred. For SNP, Lovari (1992) and Ale (2007) reported the core area of tahr distribution at almost 4000 m a.s.l. in 1989 and 2004–06, respectively.

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**Fig. 1.** (a) Altitude (mean  $\pm$  standard error) of genotyped scats ( $N=72$ ) and core area ( $N$  of snow leopard scats and scrapes,  $N=1019$ ), as well as sightings of Himalayan tahr ( $N=593$ ) and mean temperature in (b) January–February and (c) May–June, in Sagarmatha National Park, in 2006–2010. Temperature data for 2010 were not available.

We wished to test the following predictions: (i) there should be a positive relationship between temperature and altitude of sightings of tahr, expected to use sites at higher altitudes in the warmest year, i.e. 2009, than in the other years, to search for cooler places; (ii) snow leopards should follow tahr and use areas at higher altitudes in the warmest year.

## 2. Materials and methods

### 2.1. Study area

Our study area (Sagarmatha National Park, 1148 km<sup>2</sup>, 27°20'N, 86°45'E) lay mainly between the villages of Namche, Phortse and Gokyo Lake (3440–4750 m a.s.l., cf. Lovari et al., 2013a). Vegetation included mixed *Betula-Rhododendron-Abies* spp. forest (below 4000 m); *Juniperus-Rhododendron* spp. (4000–5000 m); mosses, lichens, Alpine grasslands (above 5000 m). Beside the Himalayan tahr, c. 300–350 individuals in 2003 and c. 100 individuals in 2010 (e.g. Lovari et al., 2009a, b; Ferretti et al., 2014) and the relatively abundant forest/shrubland dwelling musk deer (c. 300 individuals/1000 km<sup>2</sup>; Aryal et al., 2010), only the Himalayan serow *Capricornis sumatraensis* was present, but with a sparse, localised distribution in the forest (Lovari et al., 2005). Himalayan tahr was the staple prey of snow leopards (>55% of diet, Lovari et al., 2013a), which returned as a breeding species to SNP on 2003 (Lovari et al., 2009a, 2013a: 2–5 individuals/year). Intense predation by snow leopards on tahr, especially on kids, led to the heavy decline of the latter (see Lovari et al., 2009a for the discussion of potential alternative factors limiting the tahr population). Domestic yak *Bos grunniens* and their hybrids with zebu cattle *Bos indicus* (c. 2000 individuals) also occurred (cf. Lovari et al., 2013a). The common leopard *Panthera pardus* was the only other large predator living

permanently in SNP (Brower, 1991; Lovari et al., 2013a: 1–2 individuals/year) below the upper treeline, c. 3500–4000 m a.s.l., where it preyed mainly on musk deer, whereas the snow leopard occurred mainly above it, up to c. 5000 m asl (Lovari et al., 2013a). Himalayan tahr was the third prey of the common leopard (c. 20% of diet), which showed a substantial dietary overlap with the snow leopard (c. 70% of diet), suggesting a potential competition between these large cats (Lovari et al., 2013a).

### 2.2. Data collection and analyses

Our study was conducted from May 2006 to October 2010. Mean daily temperatures were obtained from a weather station located in Namche Bazaar (c. 3300 a.s.l.). Sightings of Himalayan tahr were made through 10  $\times$  40 binoculars and a spotting scope 15  $\times$  45 and georeferenced by a GPS, from fixed trails crossing the study area, for a total length of c. 140 km, repeated monthly (see Lovari et al., 2013a). We also recorded and georeferenced scrapes, which are distinctive signs widely used to confirm leopard presence (e.g. Schaller et al., 1988; McCarthy et al., 2005). Locations of scrapes found along the trails (within the snow leopard core area, Lovari et al., 2013a; cf. below) and that of genotyped scats in and out of the snow leopard core area were georeferenced and used as a measure of snow leopard altitudinal movements; scats were also used to assess species identity, distribution and minimum number of individual leopards (Lovari et al., 2013a). The core area of snow leopards (i.e. the area used exclusively by them and not by common leopards) was assessed by Lovari et al. (2013a) and coincided with the kernel 25% area determined according to the locations of genotyped scats. See Lovari et al. (2009a, b, 2013a) and Ferretti et al. (2014) for further details on study area and data collection techniques.

**Table 1**

(a) Effects of the year on altitude of sightings of Himalayan tahr (total dataset: 2006–2010,  $N = 593$  sightings); (b) effects of temperature on altitude of tahr sightings (restricted dataset:  $N = 431$ ); (c) inter-annual differences in the altitudes of scats and scrapes in the core area ( $N = 1019$ ); (d) inter-annual differences in the altitudes of genotyped scats ( $N = 72$ ) of snow leopards in Sagarmatha National Park. Effects were estimated through general linear mixed models.

Response variable	Predictor	B	Standard error	P
(a) Altitude of tahr sightings	Intercept	3986.19	93.94	<0.001
	Year (2007)	−49.19	29.74	0.099
	Year (2008)	−115.89	30.88	<0.001
	Year (2009)	−141.49	32.05	<0.001
	Year (2010)	−105.60	31.11	<0.001
(b) Altitude of tahr sightings	Intercept	386.083	90.364	<0.001
	Temperature	2.123	1.969	0.297
(c) Locations of snow leopard scats and scrapes in the core area	Intercept	3917.37	51.17	<0.001
	Year (2007)	−21.71	21.94	0.323
	Year (2008)	−35.94	23.51	0.128
	Year (2009)	−11.10	22.06	0.615
	Year (2010)	−22.10	26.16	0.399
(d) Locations of snow leopard genotyped scats	Intercept	3786.64	107.22	<0.001
	Year (2007)	−32.11	61.64	0.605
	Year (2008)	−127.66	69.99	0.076
	Year (2009)	−31.79	70.88	0.656
	Year (2010)	−154.24	99.09	0.126

Inter-annual differences in the altitudes of tahr sightings were assessed through general linear mixed models (Crawley, 2007). The Altitude of each sighting was the response variable and the Year was the predictor. The altitude of tahr sightings is expected to vary across months because of monthly changes of temperatures and availability of food at different altitudes. In turn, the Month was fitted as random effect, to control for temporal autocorrelation and for the monthly variation of altitude of tahr sightings. We also included the identification code of each itinerary as random effect, to control for spatial autocorrelation of sightings made by the same trail.

Additionally, we evaluated the effects of temperature on altitudes of tahr sightings. The altitude was the response variable, the mean daily Temperature was the predictor while the Year, the Month and the location of itineraries were fitted as random effects. Inter-annual differences in the altitudes of the core area (i.e. location of scats/scrapes in the exclusive area, Lovari et al., 2013a) and the altitude of movements (i.e. location of genotyped scats) of snow leopards were evaluated through general linear mixed models. The Altitude of leopard scats/scrapes in the exclusive area and that of genotyped scats were the response variables, the Year was the predictor and the Month and locations of itineraries were random effects.

Eventually, we evaluated the relationships between the yearly mean altitude of the core area of snow leopards and that of tahr sightings, as well as the relationship between yearly mean altitudes of genotyped scats of snow leopards and that of tahr sightings, through general linear models. Statistical analyses were conducted through the 'lme4' package in the R 3.0.2. software (R Development Core Team, 2013).

### 3. Results

Throughout our study, the mean altitude of tahr sightings ( $N = 593$ ) decreased by c. 220 m, from 3901.8 m a.s.l. in 2006 (s.e. =  $\pm 51.8$  m) to 3683.6 m in 2010 (s.e. =  $\pm 24.9$  m) (Table 1; Fig. 1). The inter-annual decrease of altitude showed a significant, linear trend (general linear model:  $B = -56.940$ ; s.e. = 13.260,  $P = 0.023$ ). Considering data collected in days for which temperature values were also available ( $N = 431$  sightings), the altitude of tahr sightings was not significantly related to mean daily air temperature (Table 1).

Conversely, the mean altitude of snow leopard scats and scrapes found along itineraries in the core area ( $N = 846$ ) varied by only c. 60 m throughout our study, with no significant linear trend across

years ( $B = 8.586$ ; s.e. = 7.936;  $P = 0.358$ ) and no significant inter-annual variation (Table 1; Fig. 1). The mean altitude of genotyped scats of snow leopards ( $N = 72$ ), i.e. reflecting leopard movements (see Methods), tended to decrease throughout years, being the lowest in 2008, with a negative, not significant inter-annual trend ( $B = -32.330$ ; s.e. = 16.81;  $P = 0.152$ ) (Table 1; Fig. 1).

The mean yearly altitude of snow leopard scats and scrapes found along itineraries in the core area was not associated to the mean yearly altitude of tahr sightings ( $B = -0.119$ , s.e. = 0.201,  $P = 0.596$ ). The mean yearly altitude of genotyped scats of snow leopards showed a positive, near-significant association to the mean yearly altitude of tahr sightings ( $B = 0.581$ , s.e. = 0.236,  $P = 0.091$ ).

### 4. Discussion

2009 was a markedly warmer year than the other study years, but Himalayan tahr did not move to areas at higher altitudes to search for cooler places (e.g. Grignolio et al., 2004; Mason et al., 2014). We suggest that two mechanisms could explain this result. First, after the return of snow leopards as a breeding species in SNP in 2003 (Lovari et al., 2009a), Himalayan tahr faced a heavy predation by these large cats (assessed by Lovari et al., 2009a, 2013a), which led to their 2/3 population decrease in less than one decade (Ferretti et al., 2014). In turn, tahr numbers plummeted in the area most intensively used by snow leopards, resulting in their sightings being located at lower elevations. Alternatively, tahr could have increased their anti-predatory behaviour, avoiding areas intensively attended by snow leopards (see Lovari et al., 2013a). In both cases, the presence of a large, specialist predator may have acted as a greater selective force on tahr than climatic variation. One could argue that the intensity of predation by snow leopards reduced population size of tahr so that there was ample habitat/food for remaining individuals and no need for upward movements. For the same study area, Lovari (1992) and Ale (2007) reported that the majority of tahr sightings were made around 4000 m a.s.l. respectively in 1989, i.e. well before the stable return of the snow leopard to SNP, and in 2004–05–06, i.e. just after its return. This would suggest the higher altitudes as the preferred ones for tahr.

The numbers of tahr decreased throughout our study, but snow leopards did not substantially increase their predation upon alternative prey, i.e. musk deer and livestock, but they kept focused on their main prey, the tahr (Ferretti et al., 2014). Snow leopards

increased their movements to the lower altitudes, most likely to reach tahr, who remained the staple of the leopard diet (Lovari et al., 2013a; Ferretti et al., 2014), but their core area remained at higher elevations, in spite of the local decrease of their main prey.

Interspecific interference – including killing – is widespread across carnivores, with negative effects on populations of inferior competitors (Palomares and Caro, 1999; Donadio and Buskirk, 2006). We suggest that avoidance of encounters with the larger common leopard at the lower altitudes (Lovari et al., 2013a,b) may have prevented snow leopards from moving their core area to slopes with a great availability of tahr. Snow leopards reacted to the reduction of their main prey by a decrease in numbers (Ferretti et al., 2014; Lovari and Mishra, in press). Increasing movements to lower altitude sites could trigger additional potential costs for snow leopards, e.g. (i) a greater energy expenditure, because of longer movements from/to their core area, to reach tahr at the lower altitudes; (ii) in turn, an increase of the risk of encounters with the common leopard. Prey species may seek refuge in buffer zones between territories of predators (deer/wolf *Canis lupus*: Mech, 1977; Mech et al., 1980) and the presence of common leopards in the forest at lower altitudes may have acted as a deterrent for snow leopards to move down permanently.

Thus, both our predictions turned out to be wrong. In our study system, interspecific interactions (predation; competition) appeared to be stronger selective pressures on movements of prey and predators than temperature variations, on a 5-year temporal scale (cf. Mason et al., 2014). As our study system is 8 year old (2003–2010), the two species could still be adjusting to each other. Several other factors (e.g. meteorological variations, insects, food resources, see below) could influence movements of a mountain ungulate and might deserve further attention. A longer time-series would help clarifying the effects of biotic (e.g. predator-prey relationships) and environmental (including climate) factors on movements of predator and prey. Our results suggest that climatic models predicting distributional changes of wildlife should not only consider climatic variables (cf. Forrest et al., 2012). However, the effects of climatic changes may be greater at longer temporal scales, especially if they act on vegetation availability (e.g. up-slope shifts of palatable plant associations triggered by the current climatic change, Gottfried et al., 2012; Telwala et al., 2013).

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