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PREY BEHAVIOR LEADS TO PREDATOR: A CASE STUDY OF THE HIMALAYAN TAHR AND THE SNOW LEOPARD IN SAGARMATHA (MT. EVEREST) NATIONAL PARK, NEPAL

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ABSTRACT

Rare, elusive predators offer few sightings, hindering research with small sample sizes and lack of experimentation. While predators may be elusive, their prey are more readily observed. Prey respond to the presence of a predator, and these fear responses may have population- and community-level consequences. Anti-predator behaviors, such as vigilance, allow us to sidestep the difficulty of direct field studies of large predators by studying them indirectly. Here we used a behavioral indicator, the vigilance behavior of the Himalayan tahr, the snow leopard's main local prey, to reveal the distribution and habitat use of snow leopards in the Mt. Everest region of Nepal. We combined techniques of conventional field biology with concepts of foraging theory to study prey behavior in order to obtain insights into the predator's ecology. The Himalayan tahr's vigilance behavior correlates with the distribution of snow leopard signs. Tahr actually led us to six sightings of snow leopards. We conclude that behavioral indicators provided by prey offer a valuable tool for studying and monitoring stealthy and rare carnivores.

Keywords: Vigilance, fear, behavioral indicator, predator, prey, snow leopard, Himalayan tahr, Mount Everest

INTRODUCTION

Rare, elusive predators offer few sightings. This hampers research because of small sample sizes and lack of opportunities for experimentation. Consequently, field studies of large carnivores often reside outside of mainstream ecology, and our understanding of the role of these animals in ecosystems remains unclear and contentious (Soule and Terborgh, 1999). Unlike predators, prey are generally more abundant, and their behaviors can be more readily observed. Foraging theory considers how prey should adopt adaptive foraging strategies that reduce or eliminate predation risk (Brown, 1988; Lima and Dill, 1990; Abrams, 2000). Prey respond to the presence of a predator (Elgar, 1989; Caro, 2005), and these fear responses have population- and community-level consequences (Sinclair and Arcese, 1995; Schmitz et al., 1997; Brown et al., 1999; Brown and

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Kotler, 2004; Kotler et al., 2004; Valeix et al., 2009). Such adaptive behaviors may be subject to strong selection (Stephens and Krebs, 1986). Prey foraging behavior can indicate the status of individuals and populations, the suitability of habitats, and the extent to which individuals face danger from predators; the latter may lead to information about the status of predator populations (Kotler et al., 2007; Morris et al., 2009).

Here we use vigilance behavior of Himalayan tahr, *Hemitragus jemlahicus*, the prey, to reveal distribution of snow leopards, *Uncia uncia*, the predator. Behavioral responses, such as vigilance, allow us to sidestep the difficulty of direct field studies of large predators by studying them indirectly through their prey. Behaviors in response to predation risk have been studied before, particularly in relation to understanding prey responses to predators (Caro, 2005, for a review). No field studies, however, have yet used prey behaviors to assess the presence and distribution of a rare and cryptic predator species within large mammal communities. Here we show that vigilance behavior of Himalayan tahr (hereafter tahr) to infer indirectly the distribution and habitat use of snow leopards in the Everest region of Nepal.

The permanent occurrence of snow leopards had not been reported from Nepal's Everest region since the 1960s, although occasional isolated individuals may have passed through the region from time to time (cf. Brower, 1991) without forming a stable population. Tourism has flourished since the first ascent of Mt. Everest in 1953, bringing both prosperity and some adverse ecological impacts to the region. In 1976, the Everest region (area of 1,148 km^2) was designated as the Sagarmatha (Mt. Everest) National Park (hereafter Sagarmatha) to better balance the opportunities from tourism with the need for conservation. By the late 1980s, anecdotal reports indicated the presence of snow leopards. Since the onset of the millennium, the snow leopard's permanent return was confirmed (Ale et al., 2007). This event has provided an opportunity to assess the effect of the return of a large predator, the snow leopard, on a prey, the tahr, which apparently thrived in the region without the stable presence of predators (Lovari et al., 2009*a*). Assuming that the continuous presence of a predator influences prey behavior, here we show that tahr behavior, in turn, reveals information on leopards' distribution and abundance.

The absence of predators for decades may cause the loss of some anti-predator behaviors (Diamond, 1990). The consequences of such loss may be profound if predator-naïve species re-encounter their predators (Berger et al., 2001). Prey may, however, respond to re-establishing predators (e.g., Ripple and Beschta, 2004; Berger, 2007). Can the tahr's response to fear facilitate monitoring the spatial distribution of snow leopards based on their signs? We answer this question by combining "mud-and-boots" field biology (i.e., searching for signs—Schaller, 1977; Fox et al., 1991; Jackson and Hunter, 1996) with techniques and concepts from foraging theory (Stephens and Krebs, 1986; Brown et al., 1999), that is, observing and quantifying prey vigilance behavior.

Assuming that food resources (Jarman, 1974; Carbone and Gittleman, 2002) and predator pressures (Hunter and Skinner, 1998) and their interactions (Brown et. al., 1999; Brown and Kotler, 2004) govern animals, foraging theory predicts that: 1) terrains and habitats exhibiting heightened tahr-vigilance should reveal a higher number of snow leopard signs, and 2) valleys with the most alert tahr should have higher snow leopard signs.

MATERIALS AND METHODS

The Sagarmatha National Park (86°30′53″–86°99′08″ E; 27°46′19″–27°6′45″ N), in northeast Nepal, encompasses the upper catchments of the Dudh Kosi River system. Our study area consisted of four survey blocks, a total of c. 86 km^2. These survey blocks represent the four main valleys of Sagarmatha: Namche (15 km^2), Phortse (18 km^2), Gokyo (33 km^2), and Thame (20 km^2), with elevations ranging from <3,000 m to >5,000 m, within our study area. Vegetation consists of open forest (mixed stands of *Abies* spp., *Betula utilis*, and *Rhododendron* spp.) and scrubland with such major constituent species as *Juniperus* spp. and *Rhododendron* spp., interspersed with grasses and sedges (for vegetation details, see Buffa et al., 1998).

Tahr, a gregarious caprin in the Himalayas, is the largest prey of snow leopards (tahr adult females: 62 kg on average, see Dematteis et al., 2006; Lovari et al., 2009a). Himalayan musk deer, *Moschus chrysogaster*, is the second largest natural prey (Ale et al., 2007; Lovari et al. 2009a). In 2005–2006, tahr constituted snow leopard's staple diet, consisting of up to 60% of relative frequency of occurrence, besides five other species including musk deer (Lovari et al., 2009a). In addition, the area supports several thousand domestic animals (cattle, yak, and yak-cattle hybrids). During the daytime, these animals are often allowed to graze unguarded above the tree-line, returning at night to rudimentary sheds in areas of human habitation. The last wolf was reported to have been killed in the late 1980s (Stevens, 1993). The presence of common leopard in the lower elevations has been recently confirmed (Lovari et al., 2009a). Albeit most of our study area was above the habitat of common leopards, there may have been some overlap with leopard habitats.

OBSERVATION OF TAHR VIGILANCE BEHAVIOR

From August to November 2005, we followed tahr on foot, closely observing their anti-predator vigilance behavior. We quantified scanning (vigilance) and feeding behaviors of tahr, in different terrains (cliff, broken, and rolling), and in different vegetation types (scrubland and open forest), across all four valleys. We grouped the vegetation habitat into (alpine and subalpine) scrubland and subalpine open forest. Scrubland, in Sagarmatha, consists of grasses, sedges and forbs interspersed with patches of shrubs comprising species like *Juniperus* and *Rhododendron*. Below scrubland lies the zone of open [pine] forest – this is, more or less scrubland, but with stands of trees in it. In the Himalayas, one can easily differentiate between patches of alpine and subalpine scrublands, on the one hand, and open forests that grade scrublands in lower elevations on the other, but it may be relatively difficult to distinguish terrain types based on the degree of their ruggedness, . We carefully categorized terrain types (within a 20 m radius around the sign site), following Jackson and Hunter (1996) and McCarthy (2000), into cliffs, areas of at least 100 m^2 with slopes greater than 50°; rolling terrain, land characterized by smooth, rolling surfaces with gentle slopes (<25°); and broken terrain, areas between cliffs and rolling terrain that are interspersed with boulders and rocks.

Once we locate a group of tahr, we used focal animal sampling (Martin and Bateson, 1986) to collect information on tahr foraging behavior. We watched each individual for 20 min (or until the animal moved behind a boulder or ridge), recording its activities in the following four categories: feeding (grazing or browsing), scanning (alert stance with raised ears, moving (walking, trotting, or running), and other (e.g., grooming). We then switched to another animal for another bout of observation. We made maximum efforts to sample both sexes equally. No young were selected for recording vigilance. Whenever possible, data were recorded from early in the morning (c. 7 am) until it was too dark to observe animals. We conducted 296 sessions of observation, each lasting a maximum of 20 minutes, a total of c. 95 hours. Sagarmatha supported adequate tahr for individual sampling (c. 300–350 tahr in the upper part of Sagarmatha: Lovari et al., 2009b).

Measures of scanning were expressed as the proportion of vigilant time per observation session. We transformed proportion (arcsine–square root transformation), but this did not improve its distribution. Our objective was to examine whether terrain, habitat type, and valley influence tahr vigilance, and interpret it vis-à-vis snow leopard habitat use based on the distribution of their signs. A one-way ANOVA was used—after we have tested the data for normality and homoschedasticity—to test for differences in scanning by tahr among terrain types, between habitat types, and across four valleys.

SNOW LEOPARD SIGN SURVEY

We used the sign-survey method, in which we searched for snow leopard signs—feces, pugmarks, scrapes, scent marks, and sites where the animals had rubbed against rock—to determine sites where snow leopards were active. This is a cost-effective method, commonly used for monitoring large predators, which has minimal impact on the species being studied (Wilson and Delahay, 2001). In 2005, we recorded snow leopard signs along "one-time" sign transects. We established sign transects along predictable travel lanes used by snow leopards (e.g., frequently used trails, river confluences, ridgelines, and cliff bases where cats are most likely to deposit signs: Jackson and Hunter, 1996). We established 29 transects in total: eight in Namche, ten in Phortse, six in Gokyo, and five in Thame, with a total length of 18.9 km (mean 652.5 m, *SE* = 0.33]. Prior to walking each transect, we randomly selected 6 to 8 sites per 1,000 m of transect to characterize the frequency of each terrain and habitat type (168 random sites in total). We used Ivlev's index of selectivity test (Ivlev, 1961) to examine whether snow leopards would show avoidance (negative values), active selection (positive values) or random selection (zero value) to terrain and habitat types.

"One-time" sign transects, in which researchers count signs along transects once a season or year (Jackson and Hunter, 1996), often yield few snow leopard signs, thereby hampering ecological interpretation of the data obtained. To complement the one-time sign transect survey, we trekked all four valleys extensively, visiting all locations where we judged snow leopards and tahr to occur, and recorded snow leopard signs (opportunistic-sign survey). This opportunistic sampling was conducted during September–

Table 1
Distribution of snow leopard signs along sign-transects across Sagarmatha's four valleys in 2005

Valley	Transect (km)	Scrape	Feces	Pugmark	Other	Total	Mean sign (all)/km	Mean scrape/km
Gokyo	4.6	9	0	1	1	11	2.4	2
Namche	3.6	21	6	4	3	34	9.4	5.8
Phortse	5.8	25	4	2	1	32	5.5	4.3
Thame	5	6	2	0	0	8	1.6	1.2
Total	19	61	12	7	5	85	4.5	3.2

Table 2
Distribution of sites with snow leopard signs and random sites along sign transects in Sagarmatha in 2005

	Sign sites (151)		Random sites (168)			
	Freq.	Prop.	Freq.	Prop	Ivlev's index	Selectivity
Terrain Type						
Broken	64	0.42	99	0.59	-0.16	Avoidance
Cliff	47	0.31	15	0.09	0.55	Selection
Rolling	40	0.26	54	0.32	-0.1	Avoidance
Habitat Type						
Open forest	79	0.52	21	0.13	0.61	Selection
Scrubland	72	0.48	147	0.88	-0.29	Avoidance

October 2004, August–November 2005, and May–June 2006.

For each sign encountered, we recorded the date, terrain ruggedness, habitat type, and location; the latter was determined using Garmin eTrex Venture global positioning system receivers (Garmin International Inc., Olathe, Kansas). We characterized 85 sign-sites along one-time sign transects in 2005 (Table 1), and 151 sign-sites during our opportunistic-sign survey from 2004 to 2006 (Table 2).

Differences in absolute sign frequency of snow leopards in different valleys, terrains, and habitat types were tested by simple χ^2 test.

RESULTS

Tahr exhibited the most heightened vigilance on cliffs ($F_{(2,293)} = 7.78$, $p = 0.001$; Fig. 1a). They were more alert in open forest than in scrubland [$F_{(1,294)} = 6.82$, $p = 0.009$; mean vigilance, 0.29 ($SE = 0.01$) in forest, and 0.16 ($SE = 0.009$) in scrubland]. Tukey post-hoc comparisons of the three terrain types indicated that vigilance on cliffs (0.24) was significantly higher than that in rolling terrain (0.18), $p = 0.019$. Comparisons between the vigilance on cliffs (0.24) and that in broken terrain (0.27) were not statistically significant at $p < 0.05$. The tahr's vigilance in broken terrain was significantly different than the vigilance in rolling terrain, at $p = 0.0001$.

Snow leopards used cliffs (χ^2=16.3, *d.f.=2, p* << 0.001; adjusted for overall transect length, Fig. 1b, Table 2) and open forest (χ^2=163, *d.f.=1, p* << 0.001, Table 2) more than expected by chance. Based on their vigilance behavior, the tahr perceived a higher predation risk in areas with cliffs and in open forest. As predicted (prediction 1), snow leopards biased their habitat use and activity towards cliffs and open forest, i.e., marking activity of snow leopards indicated a selection for cliffs and open forest.

Among the valleys studied, the tahr in Namche were the most alert ($F_{(3,292)} = 4.63$, $p = 0.003$; Fig. 2a), and as predicted (prediction 2), Namche provided the highest number of leopard signs per transect length ($\chi^2 = 19.5$, *d.f.* = 3, $p << 0.001$, adjusted for the overall transect length, Fig. 2b). Tukey post-hoc comparisons of the four valleys indicated that tahr-vigilance in Namche (0.26) and Thame (0.25) was significantly higher than that in Gokyo (0.17), $p = 0.002$. Comparisons between the vigilance in Phortse (0.23) and that in other three valleys were not statistically significant at $p < 0.05$.

The distribution of snow leopard signs among terrain types and between habitat types, within valleys, fits with tahr's alert behavior. The distribution of leopard signs across valleys, however, did not fit closely with tahr vigilance.

Group size did not influence scan duration ($F_{(25,270)} = 1.27$, $p = 0.17$). A factorial ANOVA showed no interaction effects except between habitat type and valley ($p = 0.023$).

DISCUSSION

Vigilance behavior of tahr correlated with the distribution of snow leopard signs among terrain and between habitat types, within valleys. The distribution of snow leopard signs

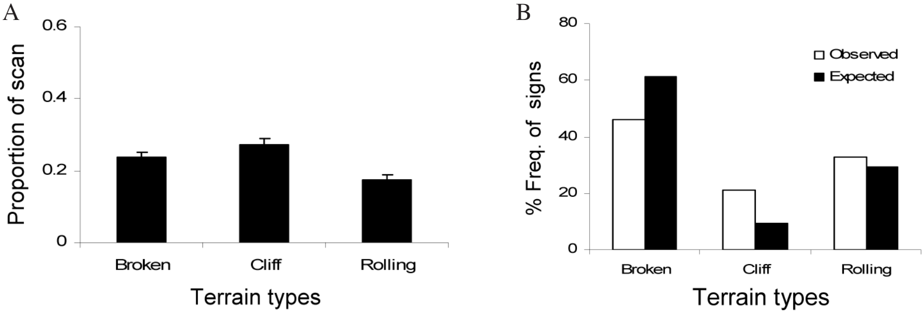

Fig. 1. A—Proportions (mean ± SE) of time spent scanning by tahr in different terrain types during 20 min foraging bouts (number of foraging bouts = 296). Tahr were most vigilant on cliffs ($p = 0.001$). The vigilance on cliffs (0.24) was significantly higher than that in rolling terrain (0.18), $p = 0.019$. The vigilance on cliffs was not significant when compared with that in broken terrain (0.27) at $p < .05$. B—Percentage frequency of snow leopard signs in three habitats along one-time sign transects (number of signs = 85). Snow leopards used cliffs disproportionately more than their availability ($\chi^2 = 16.3$, *d.f.* = 2, $p = 0.001$; adjusted for overall transect length).

among four valleys in Sagarmatha did not fit clearly with the pattern of tahr vigilance, but it nevertheless revealed the valley (Namche) with the most leopard signs.

Our focus on the vigilance behaviors of tahr resulted in a high number of sightings of rare snow leopards. We spotted snow leopards three times in 2004 (Namche), twice in 2005 (Phortse), and once in 2006 (Thame). On 14 October, 2005 (4:35–6:15 pm), we observed two adult snow leopards feeding together from the same yak carcass in Phortse. In the same area, complete genotype analysis established a minimum population of four snow leopards (two males and two females) from 2004-2006 (Lovari et al., 2009a). The repeated sightings in multiple years indicate that snow leopards have permanently returned to Sagarmatha. The tahr have responded accordingly, as indicated by their vigilance behavior in risk-prone areas (Fig. 1a, Table 2). Such risky areas, i.e., cliffs and patches of open forest, are the areas frequented by snow leopards (Fig. 1b, Table 2). The findings on snow leopard distribution and habitat use that involved radio-tagged snow leopards [Manang (Oli, 1994) and Dolpo in Nepal (Jackson and Ahlborn, 1989; Jackson, 1996); Ladakh in India (Chundawat, 1990); and Gobi in Mongolia (McCarthy et al., 2005)], are in line with our findings on snow leopard habitat use.

We associate snow leopard signs in a locality with snow leopard activity: the more signs, the more activity. Predator signs are undoubtedly a less accurate method for examining habitat use than actual sightings or radio-telemetry data. However, virtually all the world's large carnivores, particularly large felids, are rare, live in low densities, and occupy large home ranges (Sunquist and Sunquist, 2002). As a result, habitat use by large solitary felids is notoriously difficult to study (e.g., Karanth and Nichols, 1998). Surveys based on signs (Fox et al., 1991; Jackson and Hunter, 1996; see Wilson and Delahay, 2001 for review), albeit easy to execute and less expensive, have been subject

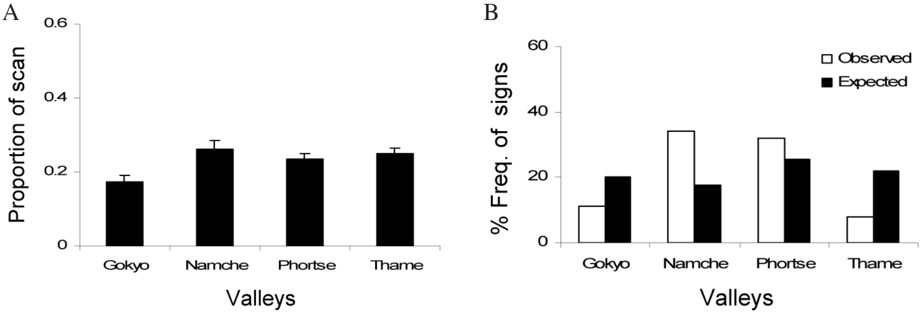

Fig. 2. A—Proportions (mean ± SE) of time spent scanning by tahr in different valleys during 20 min foraging bouts (number of foraging bouts=296). Tahr were most vigilant in Namche ($p = 0.003$). Tahr-vigilance both in Namche (0.26) and Thame (0.25) was significantly higher than that in Gokyo (0.17), $p = 0.002$. Comparisons between the vigilance in Phortse (0.23) and that in other three valleys were not statistically significant at $p < .05$. B—Percentage frequency of snow leopard signs in four valleys (number of signs, n=155). Namche revealed most snow leopard signs per transect length compared to other three valleys ($\chi^2 = 19.5$, $d.f. = 3$, $p = 0.001$, adjusted for the overall transect length).

to criticisms about their accuracy (Bailey, 1993; Norton, 1990; McCarthy, 2000). Previous research (Ahlborn and Jackson, 1988) has, however, revealed that snow leopard scrapes predicted 87% of habitat use by these animals, suggesting that, for this species, signs can be a reliable indicator of its presence, distribution, and habitat use. In general, sign data have been recommended for surveying carnivores at large spatial scales (Barea-Azcon et al., 2007), particularly for monitoring programs, because sign data may provide better indices for monitoring pronounced changes in population status (Choate et al., 2006). With advances in logistical modeling techniques, sign surveys also promise to reveal important ecological patterns (e.g., Mortelliti and Boitani, 2008; Wolf and Ale, 2009). In comparison, techniques such as mark–recapture or monitoring individuals with radio collars, although more rigorous, are expensive, labor-intensive, and time-consuming. Thus, despite its limitations, use of signs represents a valuable method for assessing carnivore presence and habitat use, when other more costly options of animal monitoring are not feasible.

Among valleys, the vigilance of tahr (Fig. 2a) only slightly corresponded with the distribution of snow leopard signs gleaned from transects (Fig. 2b)—the fit was not decisive. Given the rarity of signs, and the low density of snow leopards, transects are generally placed along landforms where snow leopards are considered most likely to travel. When comparing different areas (four valleys in our case), the selection of sign transects, and corresponding signs per unit of transect length, may have biased our perceptions of snow leopard distribution and abundance, as compared with what has been reported from snow leopard studies in Ladakh, India (Fox et al., 1991; Mallon, 1991) and in Qinghai, China (Schaller et al., 1988). For example, in Qinghai, China, cats marked the bases of hills flanking broad valleys in certain survey blocks, whereas, in contrast, the cats' travel routes were less well defined in other survey blocks, making it difficult to locate spoors along transects (Schaller et al., 1988). The general pattern, in our study, is, however, clear: the valley with the most leopard signs was the one with most alert tahr.

We conclude that vigilance behavior of tahr indicates predation risk associated with snow leopard distribution and habitat use within valleys, but not necessarily snow leopard distribution across different valleys.

Although tahr were more vigilant in open forest (than in scrubland habitat) and on cliffs (than in broken and rolling terrain), where snow leopards left signs disproportionately, there was the alternative possibility that both habitats naturally may have evoked more alert behaviors than the others. It is possible that open forest habitat may require more vigilance in general, simply to stay in contact with disconnected members of the group, and that habitats with boulders or cliffs may simply require attention while moving about, so rapid "head-ups" and "head-turns" are likely to be frequent. If this is true, then tahr would also likely spend different amounts of time in feeding and moving on cliffs and in open forests than in other terrain. No significant differences occurred, however, between habitat types [$F_{(1,294)} = 1.44$, $p = 0.23$] and among terrain types ($F_{(2,293)} = 1.31$, $p = 0.27$] in time spent feeding and moving [between habitats: $F_{(1,294)} = 0.29$, $p = 0.39$, and among terrains: $F_{(2,293)} = 1.06$, $p = 0.35$] by tahr. Furthermore, among the valleys studied, tahr revealed no differences in time spent feeding ($F_{(3,292)} = 2.39$, $p = 0.07$), and moving ($F_{(3,292} = 0.008$, $p = 0.99$).

Over most of their range, snow leopards rely on blue sheep, *Pseudois nayaur*, or ibex, *Capra ibex*, as their principal prey (Schaller, 1998). Sagarmatha is unusual in that it lacks both, but supports tahr as the principal prey for snow leopards (Ale et al., 2007; Wolf and Ale, 2009; Lovari et al., 2009a,b). Studies indicate that predators can influence the size of prey populations through mortality, i.e., lethal effect (cf. Terborgh et al., 2001; Sinclair et al., 2003) and through non-lethal effects (Brown et. al., 1999; Ripple and Beschta, 2004). The non-lethal effects of predators include effects on habitat choice, group size, and activity pattern of prey. The return of snow leopards to Sagarmatha may be reflected in the tahr's degree of alertness towards predators. A wealth of empirical evidence suggests that predation risk is a primary reason for alertness in animals (Elgar, 1989; Caro, 2005).

The comeback of snow leopards in Sagarmatha may continue to impact on the ecology and behavior of tahr populations under natural conditions. The reintroduction of wolves caused rapid behavioral responses by elk, *Cervus elaphus* (Laundré et al., 2001), and moose, *Alces alces* (Berger et al., 2001), to the novel risk in Yellowstone. Predation risk by lions influenced the distribution of African herbivores in the landscape in Hwange National Park, Zimbabwe (Valeix et al., 2009). Roe deer, *Capreolus capreolus*, in hunted populations spent more time vigilant during the hunting season than outside it, in Aurignac, France (Benhaiem et al., 2008). Prey bias their feeding activity towards safer habitats, and while in risky habitats, they should increase their vigilance levels and group size in response to predation risk (Lima and Dill, 1990; McNamara and Houston, 1992; Sinclair and Arcese, 1995; Brown et al., 1999; Creel et al., 2005).

Although tahr elevated their vigilance in areas with greater snow leopard signs and thus in risky habitats and terrains in Sagarmatha, we detected no effect of group size on vigilance—a general and widespread effect (Elgar, 1989; Lima and Dill, 1990; Quenette, 1990; Roberts, 1996). Some studies on animal vigilance have found no effect or the opposite effect of group size on vigilance (Treves, 2000; Beauchamp, 2003). In Yellowstone National Park, USA, elk, *Cervus elaphus*, and bison, *Bison bison*, for instance, failed to show a group-size effect (Laundré et al., 2001). At present, we have no explanation for why tahr did not show any group-size effect on vigilance, but there may be a host of reasons that such a correlation does not emerge, and most have to deal with habitat complexity as a confounding factor. One reason may be that the group-size effect (via dilution and many-eyes effects) may have been masked by attraction effect, the idea that aggregations may attract predators (Parrish and Edelstein-Keshet, 1999). Ale and Brown (2007), using game theory models, suggest that in addition to the many-eyes effect and the dilution effect, group size may create an attraction effect, and all these effects may operate simultaneously to influence predation risk, the optimal level of vigilance, and optimal group size. The relation between vigilance and group size is contingent on the relative strengths of each and the interactions of these intertwining components of the group-size effect, indicating that vigilance within a group context is a game. The optimal vigilance of a forager depends on that of its group mates, and as a game of private costs and public benefits, the relationship between individual vigilance and group size is not straightforward (Ale and Brown, 2007).

We suggest that the presence of elusive predators may be detected, and their ecology revealed, by using a combination of standard wildlife techniques and the anti-predatory behavior of their main prey. Our findings and application of behavioral indicators may have conservation relevance, particularly in areas with limited resources and accessibility.

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