SIGNS AT THE TOP: HABITAT FEATURES INFLUENCING SNOW LEOPARD *UNCIA UNCIA* ACTIVITY IN SAGARMATHA NATIONAL PARK, NEPAL

Mosheh Wolf* and Som Ale

Department of Biological Sciences (M/C 066), University of Illinois at Chicago, 845 West Taylor Street, 3352 SES, Chicago, IL 60607-7060, USA

We used logistic regression to examine factors that affected the spatial distribution of sign (scrapes, feces, footprints, spray or scent marks, and rubbing sites) in a newly reestablished population of snow leopards (*Uncia uncia*) in Sagarmatha (Mount Everest) National Park, Nepal. Our results indicate that terrain and human activity were the most important factors determining the spatial distribution of leopard activity, whereas presence of their major prey species (Himalayan tahr [*Hemitragus jemlahicus*]) had only a moderate effect. This suggests that localities at which these animals are active represent a trade-off between suitable habitat and avoidance of potential risk from anthropogenic origins. However, the influence of prey presence was likely underestimated because of the methodology used, and likely weighed in the trade-off as well.

Key words: activity patterns, human activity, Nepal, predator–prey, sign data, *Uncia uncia*

A central theme in ecology is the study of the interactions that determine spatial distribution and abundance of organisms (Krebs 2002). Multiple studies have demonstrated the role of predation risk in determining patterns of habitat use (Brown 1999; Creel et al. 2005; Fischhoff et al. 2007; Heithaus and Dill 2002; Lima and Dill 1990; Morris 2003), whereas others have demonstrated the effects of resource use (Boyce 2006; Jones 2001; Lyons et al. 2003; Marzluff et al. 2004; McLoughlin et al. 2002; Strickland and McDonald 2006). Because both foraging for resources and avoiding predation make demands on an individual's energy budget—usually simultaneously—animals must compromise between these demands when determining patterns of spatial activity (Heithaus and Dill 2002; Lima and Dill 1990; Verdolin 2006; Werner and Hall 1988).

Various aspects of the trade-off between predation risk and resource use have been studied by a number of researchers (Brown 1988; Heithaus and Dill 2002; Kotler et al. 1991; Martin 1995; Schmitz et al. 2004; Verdolin 2006; Werner and Hall 1988). The majority of research on risk avoidance, including comparisons of the relative effects of risk and resource availability on habitat use, has been limited to species at lower trophic levels such as prey or game species (Altendorf

et al. 2001; Cooper 2000; Cowlishaw 1997; Festa Bianchet 1988; Hebblewhite et al. 2005; Mysterud and Ims 1998; Svardson 1949; Witham 1978). In comparison, few studies have explored how mammalian predators balance risk and foraging, especially with regard to habitat selection. Studies of habitat use by mammalian carnivores have generally focused on effects of prey abundance (Carbone and Gittleman 2002; Fuller and Sievert 2001; Karanth et al. 2004; Litvaitis et al. 1986; McCarthy 2000; McCarthy et al. 2005; Oli 1994), effects of risk associated with interguild predation (Fedriani et al. 1999, 2000), and aggressive encounters with competing predators (Durant 2000), although a recent study by Thompson and Gese (2007) examined the trade-off between predation risk and food availability for small predators.

An additional factor affecting habitat selection by predators is human activity (Carroll and Miquelle 2006; Ciarniello et al. 2007; Gavashelishvili and Lukarevskiy 2008; Johnson et al. 2006; Linkie et al. 2006; Whittington et al. 2005). It is well established that humans and their activities affect ecological systems at all scales (Frid and Dill 2002; Hill et al 1997; Smith and Wishnie 2000; Tuyttens et al. 2001). Because humans commonly hunt large carnivores (Treves and Karanth 2003), these species should respond to human presence as to a risk factor, as well as responding to effects of habitat modification and prey depletion by humans. A number of studies have demonstrated that large predators such as grizzly bears (*Ursus arctos*—Ciarniello et al. 2007), wolves (*Canis lupus*—Whittington et al. 2005), leopards (*Panthera pardus*—

* Correspondent: mhwolf@uic.edu

Gavashelishvili and Lukarevskiy 2008), and tigers (*Panthera tigris*—Carroll and Miquelle 2006; Johnson et al. 2006; Linkie et al. 2006) demonstrate significant spatial response to human activity. Humans may therefore be perceived as predators of large mammalian carnivores and should be included in that capacity in habitat studies of such carnivores.

We explored the effects of resource availability and human presence on the spatial distribution of activity by the snow leopard (*Uncia uncia*), a large carnivore that has recently reestablished itself in the Mount Everest region of Nepal. Snow leopards disappeared from the Everest region in the 1960s. In 1976, this region (an area of 1,148 km^2) was designated as the Sagarmatha (Mount Everest) National Park. Snow leopards have recently reinhabited the park, apparently following the recovery of populations of Himalayan tahr (*Hemitragus jemlahicus*), the snow leopard's main prey (Ale et al. 2007). Prey may influence habitat selection in this carnivore species: distribution of the prey may explain much variation in habitat use of snow leopards in Mongolia (McCarthy 2000; McCarthy et al. 2005) and density of prey may be a factor determining predator home range sizes (Litvaitis et al. 1986). Human activity also is thought to affect leopard presence and activity (Jackson and Wangchuck 2001; McCarthy 2000). Based on this information, we predicted that snow leopards would focus their activity in the areas where prey is abundant and would reduce activity near areas with intense human presence. To test these predictions, we used logistic regression to identify factors associated with the spatial distribution of sign (e.g., scrapes, feces, and footprints) left by snow leopards in Sagarmatha. Our results yield important new insights into the factors affecting the spatial distribution of leopard activity, including the role of humans in shaping the activity patterns of these animals.

MATERIALS AND METHODS

Sagarmatha National Park (27°46′19″–27°6′45″N, 86°30′53″–86°99′08″E) lies in the Solu-Khumbu District of the northeastern region of Nepal. Elevations in the park range from the highest mountain peaks in the world (Everest, Lhotse, and Cho-oyu) to valleys that are located <3,000 m above sea level. We sampled 4 major valleys in Sagarmatha: Namche, Phortse, Gokyo, and Thame. The main study area lay between the villages of Namche and Phortse and Gokyo Lake. This area encompassed the upper catchment of the Dudh Kosi River (Bothe Kosi and Imja Khola streams), as well as the lower part of the Cho-Oyu Valley. The vegetation of the study area consisted primarily of scrubland and forest habitats. Open forest at 3,000–4,000 m is dominated by *Pinus wallichiana*, *Abies*, and *Betula utilis*. As elevation increases, patches of open forest grade into subalpine grassland and scrubland zones (4,000–5,000 m) characterized by thick mats of *Juniperus* and *Rhododendron* (see Buffa et al. [1998] for details about vegetation).

Wildlife occurring in the park includes game birds (e.g., Impeyan pheasant [*Lophophorus impejanus*], Tibetan snow-cock [*Tetraogallus tibetanus*], and blood pheasant [*Ithaginis cruentus*]) and several small mammalian herbivores (e.g., the Himalayan pika [*Ochotona himalayana*]). Several carnivores also occur in the park, such as the Himalayan weasel (*Mustela sibirica*), the hill fox (*Vulpes vulpes*), the golden jackal (*Canis aureus*), and the snow leopard (Lovari et al. 2005). Ungulates in the region include Himalayan tahr, the rare Himalayan serow (*Capricornis sumatraensis*), and the musk deer (*Moschus chrysogaster*—Lovari 1992). In addition, the area supports several thousand domestic yak (*Bos grunniens*) and yak–zebu cattle (*Bos taurus*) hybrids. During the daytime, these animals are often allowed to graze unguarded above the treeline, returning at night to rudimentary sheds in areas of human habitation. Snow leopards were the only large predators known to be present within the study area during our study period (Ale 2007; Ale et al. 2007).

We used leopard sign—feces, footprints, scrapes, scent marks, and sites where the animals had rubbed against rock—to determine sites where snow leopards were active. This is a method commonly used for monitoring large predators, which is low cost and has minimal impact on the species being studies (Wilson and Delahay 2001). To detect snow leopard sign, we trekked the region extensively, visiting all locations where we judged snow leopards and tahr to occur, employing the techniques of the Snow Leopard Information Management System (Jackson and Hunter 1996), a standardized approach widely used in snow leopard research. Sampling was conducted during the autumns of 2004 (October–November, 58 days) and 2005 (August–November, 111 days) and in the summer of 2006 (May and June, 32 days); 2 persons worked continuously from 0600 to 1600 h on each sampling day, for a total sampling effort of 4,020 person-hours over the course of the study. For each sign encountered, we recorded the date and location; the latter was determined using Garmin eTrex Venture global positioning system receivers (20-m accuracy; Garmin International Inc., Olathe, Kansas). To avoid spatial autocorrelation and pseudoreplication, we considered signs found within 50 m of each other during the same year to represent a single site.

Habitat characterization.—To determine the characteristics of the habitat available for use by snow leopards, random sites were selected from areas that had been surveyed for snow leopards but at which no snow leopard sign was found (≥50 m from the nearest snow leopard sign). For an adequate representation of the habitat in the study region, we selected 5 times as many of these "available" sites as the number of sites at which activity was detected. Hawth's Tools for ArcGIS 9.x (www.spatialecology.com) was used for random selection of sites. Available (randomly selected) and use (snow leopard sign was detected) sites were characterized with respect to a number of habitat and anthropogenic variables, as well as presence of prey. We plotted all variables at a 50 × 50-m cell resolution as layer files in ArcGIS 9.1. We used Hawth's Tools for ArcGIS 9.x (www.spatialecology.com) to quantify habitat variables for all sites.

For each site (use and available), the habitat variables recorded were elevation, annual precipitation, and distance

from the nearest river. Elevation was derived from a digital elevation model mapped at a 50×50-m resolution. From this model, we also calculated slope and aspect for each sampling site using ArcGIS 9.1. Rivers were mapped as ArcGIS line-feature map layers, and annual precipitation was mapped as a 50×50-m–resolution ArcGIS raster layer. Distances from rivers were calculated in increments of 100 m using the ''Buffer'' function in ArcGIS 9.1, and were mapped on a 50×50-m–resolution ArcGIS raster layer. To quantify human presence, we followed the procedures used for rivers to map the distance of sites from trails and settlements; these measurements also were calculated in 100-m increments and mapped as geographic information system layers.

To quantify the presence of prey, we used counts of tahr from the study site. During 2004 and 2006, we counted tahr in all 4 valleys within the study area. We located tahr from a number of suitable vantage points during periods of good visibility by scanning opposite slopes of the mountain using 8×21 binoculars (Schaller 1977). Once tahr were located, we used Nikon $15\times$–$60\times$ spotting scopes (Nikon Inc., El Segundo, California) to determine the number of calves, yearlings, adult females, and adult males in the herd. For each herd or group (a small subset of animals from a herd—Ale 2007) encountered, we recorded the location as a global positioning system fix and noted habitat and terrain type within a radius of 20 m. From these group locations, we used the adaptive kernel method (Worton 1989) to create utilization distribution layers for tahr, with data from 2004 and 2006 pooled for analysis. Prey presence layers were created using Hawth's Tools for ArcGIS 9.x.

Statistical analysis.—To compare available and use sites with regard to the effects of physical habitat, prey abundance, and human presence on the spatial distribution of leopard sign, we developed logistic regression models similar to resource selection functions, following a used-versus-available habitat sampling protocol (Manly et al. 2002). This is a commonly used method for deriving habitat-use patterns from radiotelemetry locations (Boyce et al. 2002; Manly et al. 2002). Because we assumed that each site at which sign was detected represented a record of leopard activity at that location, we considered this method generally appropriate for detecting activity (but see the caveats below). We employed a use–available rather than a use–nonuse model because, in our study, lack of a sign was not an indication of lack of use. All locations at which snow leopard sign was detected were designated as ''use sites,'' whereas the randomly selected sites described above were used as ''available sites.''

Using a binary logistic regression model, we calculated the probability of the ith unit being used and selected, versus available and selected, as:

$$\tau(x_i) = \frac{e^{\ln\left[\frac{(1 - P_a)P_u}{P_a}\right] + \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \ldots + \beta_p x_{ip}}}{1 + \sum_{k=1}^{n_i} e^{\ln\left[\frac{(1 - P_a)P_u}{P_a}\right] + \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \ldots + \beta_p x_{ip}}},$$

with P_a being the probability of an available unit being sampled and P_u being the probability of a used location being

sampled. The selection probability model was:

$$w(x_i) = e^{\beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \ldots + \beta_p x_{ip}}.$$

The selection function was, therefore:

$$w(x_i) = e^{\beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \ldots + \beta_p x_{ip}}.$$

The maximum likelihood of the model was:

$$\ln\left[L(\beta_0, \beta_1, \beta_2, \ldots, \beta_p)\right] =$$
$$\sum_{i=1}^{n} \left\{ y_i \ln[\tau(x_i)] + (1 - y_i)\ln[1 - \tau(x_i)] \right\}.$$

We chose the best-performing model from among an a priori model set with all possible variables included using Akaike's information criterion (AIC—Burnham and Anderson 1998). To validate the model, we used the k-fold validation method (Boyce et al. 2002), which determines whether a model generated from a partial data set (the full data set with a subset of points removed) predicts the frequency distribution of values in the remaining data set (only use sites). Specifically, we assigned habitat-selection values to the study area based on the selection function presented above (with coefficients derived from the logistic model of the partial data set). We then tested whether sites in the remaining portion of the data set had higher habitat selection values by running a Spearman rank correlation between the frequencies of the habitat selection values for these sites (within binned habitat value categories of equal size following Boyce et al. [2002]) and the binned habitat selection values. Although most habitat selection studies divide their data into $k = 5$ subsets, because we had a relatively small data set we divided it into only $k = 4$ subsets. We also tested the explained variance of the selection model derived from the entire data set by generating a receiver operating characteristic curve and measuring the area under the curve (Boyce et al. 2002; Cumming 2000). Logistic regression models and areas under the curve were calculated using SPSS version 13.0 (SPSS Inc., Chicago, Illinois). All data collection was done in accordance to the animal care and use guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

RESULTS

During 2004–2006, 223 locations with snow leopard sign were found within the study area. The majority of sign consisted of scrapes ($n = 131$ total), with feces being the 2nd most common type of leopard sign detected ($n = 55$); pugmarks were not as common, with most encountered in 2005 (15 of 23; Table 1). Only a small number of spray-scent marks and rubbing sites were detected ($n = 7$ each; Table 1). There were no significant differences between logistic models (with all variables included) when data were separated by year or sign type (Wald tests for multiple variables, $P > 0.2$). We therefore pooled data across sign types and years. After combining all signs that were located within the same year and ≤ 50 m from one another, we were left with 177 sign locations, or use sites, for our analysis.

TABLE 1.—Summary of snow leopard (*Uncia uncia*) sign encountered in Sagarmatha National Park, Nepal, by year and sign type.

	Year			
Sign type	2004	2005	2006	Total
Feces	18	16	21	55
Rubbing site	—	—	7	7
Pugmark	2	15	6	23
Scrape	33	68	30	131
Spray–scent	—	3	4	7
Total	53	102	68	223

The top-performing model for the complete data set included all the variables tested, so we present this model only (the partial data sets are for verification purposes, so we focus on top-performing models for these, as well). In our models (both complete and partial), presence of sign had a significant negative relationship with both elevation and snow depth in winter (Tables 2 and 3). This suggests a preference for both low elevation and areas with less snowfall. There was only a weak correlation between snowfall and elevation within the study area ($r = -0.34$, $r^2 = 0.116$), suggesting that the effects of these variables on snow leopard activity were likely independent of one another. A negative relationship with slope also was detected (Tables 2 and 3), suggesting that snow leopard sign was less common in steep areas, although this relationship was not as strong as the relationship between leopard sign and the 3 physical habitat variables already mentioned. Finally, a significant positive relationship was detected between leopard sign and distance from rivers (Tables 2 and 3), indicating a preference for proximity to rivers or to valleys (most with rivers flowing in them).

With regard to human activity, the presence of snow leopard sign was positively related to distance from trails and settlements, indicating decreased activity in the proximity of human activity. Although the relationship with distance from trails was significant, the relationship with distance from settlements, although it was included in the top-performing model (based on AIC), was not significant (Tables 2 and 3).

Finally, with regard to prey, the presence of snow leopard sign was positively related to density of tahr herds (Tables 2 and 3). The *k*-fold verification data sets revealed Pearson correlation coefficients ranging from 0.72 to more than 0.95, indicating a fair degree of consistency within the data, and a good performance in predicting habitat use (Table 2). The top-performing model based on the entire data set performed well, as evident from the values for McFadden's ρ^2 and Nagelkerke pseudo-r^2 values, as well as the high area under the receiver operating characteristic curve (AUC in Table 3).

DISCUSSION

The rarity of sightings of snow leopards in the wild suggests that these animals tend to avoid humans (Jackson 1996; Schaller 1977). This would match the recorded effects of human activity on habitat use by other large predators such as grizzly bears, wolves, and tigers (Ciarniello et al. 2007; Johnson et al. 2006; Linkie et al. 2006; Whittington et al 2005). Locations of snow leopard sign indicated that the animals on our study site reduced their activity around areas of human presence, especially trails. Generally, predators avoid large or frequented roads and trails, especially in areas where hunting or harassment is common (James and Stuart-Smith 2000; Kaartinen et al. 2005; Linkie et al. 2006; Whittington et al. 2005). Although hunting is not common in our study area, most trails are frequented by tourists, guides, and porters and their yak caravans, which may create a significant amount of disturbance and harassment to the secretive cats. Thus, humans may be a substantial determinant of where snow leopards are active.

Perhaps not surprisingly, the presence of tahr had a significant positive relationship with the presence of snow leopard sign. However, the presence of tahr did not have as strong an effect as several aspects of the physical habitat, including elevation, snow depth, and distance from rivers. It was unexpected to find that elevation was negatively related to snow leopard activity, because snow leopards are generally thought to prefer higher elevations (Fox 1994; Jackson 1996;

TABLE 2.—The coefficients of the variables included in the top-performing models (using Akaike's information criterion) for each of the 4 sets from the *k*-fold verification. At the bottom are the Spearman rank correlations (r_ss) between the frequency (adjusted) of sites within each value bin and the rank of that bin. The value of the each site in a subset was calculated using coefficients derived from models developed from the data set with that subset removed. Superscripts are the significance levels of the of the model coefficients (Wald tests) and Spearman rank correlations: * $P < 0.05$; ** $P < 0.005$; *** $P < 0.0005$.

	Data subset			
Variables	1	2	3	4
Elevation	−0.004***	−0.003***	−0.003***	−0.004***
Slope	−0.031*	−0.045**	—	—
Snow depth	−0.012***	−0.002**	−0.016***	−0.016***
Distance from river	0.011***	0.011***	0.011***	0.009***
Distance from settlement	—	—	—	0.0005*
Distance from trail	0.007***	0.008***	0.008***	0.007***
Tahr groups	33.32***	25.49***	17.67***	—
Constant	13.87	10.09	15.01	27.55
r_s	0.717*	0.786*	0.903**	0.952**

TABLE 3.—Top-performing model derived from all data, along with Wald tests for the coefficients of variables included. McFadden's ρ^2 and the Nagelkerke pseudo-r^2 demonstrate the improvement of the explanatory power of best model, and area under the curve (AUC) indicates explanatory power (the first 2 coefficients have values between 0 and 1, whereas AUC has values of 0.5–1). Superscripts represent levels of significance of the Wald tests: no superscript $P > 0.05$; * $P < 0.05$; ** $P < 0.005$; *** $P < 0.0005$.

Variables	Coefficients	Wald test
Elevation	−0.003	72.21***
Slope	−0.018	3.12**
Snow depth	−0.011	39.49***
Distance from river	0.001	72.93***
Distance from settlement	0.0002	2.59
Distance from trail	0.007	128.37***
Tahr groups	17.73	16.36***
Constant	20.03	
Log-likelihood of model	473.79***	
McFadden's ρ^2	0.495	
Nagelkerke pseudo-r^2	0.606	
AUC	0.934	

McCarthy and Chapron 2003; Schaller 1998). In our study population, the tendency for sign to be more prevalent at lower elevations suggests that snow leopards were more active in the areas that were most likely to lead to exposure to humans. Snow depth also may have contributed to this outcome, although winter snow depth was not significantly related to elevation (see ''Results''). Nevertheless, our findings suggest a potential trade-off between avoiding more severe environmental conditions and avoiding extensive contact with humans. Although snow leopards are known to be excellent climbers and prefer rocky outcrops as resting locations (Ahlborn and Jackson 1988; Chundawat 1990; Fox et al. 1991; Jackson 1996; McCarthy et al. 2005; Schaller 1977), our results suggest that they avoid steep slopes. However, in our analysis the slope variable was the average slope of the entire 50×50-m cell around the sign location, so this result may simply be the artifact of the resolution of our sampling method.

In our analyses, we used logistic regression models to identify factors influencing the spatial distribution of snow leopard activity. We considered a greater prevalence of sign as evidence of greater activity by snow leopards. In general, snow leopard sign such as spray sites or scrapes are used as territorial markings and are therefore likely placed within a short distance of evidence of conspecifics, such as near the edges of a territory. Thus, despite the fact that we considered closely placed sign (≤ 50 m apart) to be a single sample, it is likely that not all of our samples were truly independent, potentially leading to overestimation of the importance of some of the habitat variables quantified. However, the strength of our best-fit model suggests that our findings are robust.

It is important to note that our analyses examined where snow leopards were likely to leave sign, rather than habitat selection per se. Nonetheless, areas that are highly attractive to these animals are likely to accumulate more sign and hence

relationships between the prevalence of sign and the habitat variables included in our models should reflect a real tendency for the animals to use the environments identified by our analyses. Because it is not known exactly how many snow leopards were represented in our sample, it is possible that our results reflect habitat use by only a small subset of the population. However, analysis of the footprints encountered during the study suggests a minimum sample size of 10 different individuals (Ale 2007), indicating that our findings reflect the habitat preferences of a reasonable subset of individuals. Finally, it is possible that the nature of the sign examined provides a biased perspective on habitat use, particularly with regard to prey abundance. For example, sign such as scrapes or feces may reveal the presence of leopards to their prey, with the result that snow leopards may reduce use of these signs in areas where prey are common. Although we cannot discount this possibility, the occurrence of sign was positively related to prey abundance, indicating that leopards were active in areas where tahr were present.

Snow leopard sign is undoubtedly a less-accurate method for examining habitat use than actual sightings or radiotelemetry 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 solitary felids such as tigers and snow leopards is notoriously difficult to study (Karanth and Nichols 1998). Surveys based on sign (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 to criticisms about their accuracy (Bailey 1993; McCarthy 2000; Norton 1990). However, previous research (Ahlborn and Jackson 1988) has revealed that snow leopard scrapes predicted 87% of habitat use by these animals, suggesting that, for this species, sign can be a reliable indicator of leopard presence. 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 logistic modeling techniques, sign surveys also promise to reveal important ecological patterns. For example, Mortelliti and Boitani (2008) used logistic modeling of sign data to investigate the effects food resources as well as patch-, neighborhood-, and landscape-scale variables on the distribution of carnivores. In comparison, techniques such as mark–recapture or monitoring individuals with radiocollars, although more rigorous, are expensive, labor-intensive, and time-consuming. Thus, despite its limitations, use of sign represents a valuable method for assessing carnivore presence when other, more costly, options of animal monitoring are not feasible.

Most studies of habitat selection by large predators have tended to focus on the effects of either prey or human activity. However, our study suggests that carnivores may face important trade-offs between physical habitat features, human activity, and food availability. Because most large predators

are at risk, endangered, or on the brink of extinction, knowing how these factors influence habitat use is critical to the conservation of these species. To date, studies on wild populations of endangered snow leopards have focused on their conservation status, distribution, and patterns of movement (Fox et al. 1991; Jackson 1996; McCarthy et al. 2005; Schaller 1977, 1998). Studies of the abundance and distribution patterns of snowleopards in relation to their primary prey have been scarce, with the exceptions of a study in Mongolia (McCarthy 2000) and another in parts of China (Schaller 1998; Schaller et al. 1988). The population that we studied has recently reestablished itself and thus understanding habitat use by these animals vis-à-vis the physical environment, human activity, and prey distribution is an important step toward understanding factors that may facilitate the long-term survival of this species.

LITERATURE CITED

AHLBORN, G., AND R. M. JACKSON. 1988. Marking in free-ranging snow leopards in west Nepal: a preliminary assessment. Pp. 25–49 in Proceedings of the Fifth International Snow Leopard Symposium (H. Freeman, ed.). International Snow Leopard Trust, Seattle, Washington, and Wildlife Institute of India, Dehradun, India.

ALE, S. 2007. Ecology of the snow leopard and the Himalayan tahr in Sagarmatha (Mount Everest) National Park, Nepal. Ph.D. dissertation, University of Illinois at Chicago, Chicago.

ALE, S. B., P. YONZON, AND K. THAPA. 2007. Recovery of snow leopard Uncia uncia in Sagarmatha (Mount Everest) National Park, Nepal. Oryx 41:89–92.

ALTENDORF, K. B., J. W. LAUNDRE, C. A. L. GONZALEZ, AND J. S. BROWN. 2001. Assessing effects of predation risk on foraging behavior of mule deer. Journal of Mammalogy 82:430–439.

BAILEY, T. N. 1993. The African leopard: ecology and behaviour of a solitary felid. Columbia University Press, New York.

BAREA-AZCON, J. M., E. VIRGOS, E. BALLESTEROS-DUPERON, M. MOLEON, AND M. CHIROSA. 2007. Surveying carnivores at large spatial scales: a comparison of four broad-applied methods. Biodiversity and Conservation 16:1213–1230.

BOYCE, M. S. 2006. Scale for resource selection functions. Diversity and Distributions 12:269–276.

BOYCE, M. S., P. R. VERNIER, S. E. NIELSEN, AND F. K. A. SCHMIEGELOW. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

BROWN, J. S. 1988. Patch use as an indicator of habitat preference, risk of predation, competition. Behavioral Ecology and Sociobiology 22:37–47.

BROWN, J. S. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. Evolutionary Ecology Research 1:49–71.

BUFFA, G., C. FERRARI, AND S. LOVARI. 1998. The upper subalpine vegetation of Sagarmatha National Park (Khumbu Himal area, Nepal) and its relationship with Himalayan tahr, musk deeer and domestic yak. An outline. Pp. 167–175 in Top of the world environmental research: Mount Everest–Himalayan ecosystem (R. Baudo, G. Tartari, and M. Munawar, eds.). Ecovision World Monograph Series. Backhuys Publishers, Leiden, Netherlands.

BURNHAM, K. P., AND D. R. ANDERSON. 1998. Model selection and inference. Springer-Verlag, New York.

CARBONE, C., AND J. L. GITTLEMAN. 2002. A common rule for the scaling of carnivore density. Science 295:2273–2276.

CARROLL, C., AND D. G. MIQUELLE. 2006. Spatial viability analysis of Amur tiger Panthera tigris altaica in the Russian Far East: the role of protected areas and landscape matrix in population persistence. Journal of Applied Ecology 43:1056–1068.

CHOATE, D. M., M. L. WOLFE, AND D. C. STONER. 2006. Evaluation of cougar population estimators in Utah. Wildlife Society Bulletin 34:782–799.

CHUNDAWAT, R. S. 1990. Habitat selection by a snow leopard in Hemis National Park, India. International Pedigree Book of Snow Leopards 6:85–92.

CIARNIELLO, L. M., M. S. BOYCE, D. C. HEARD, AND D. R. SEIP. 2007. Components of grizzly bear habitat selection: density, habitats, roads, and mortality risk. Journal of Wildlife Management 71:1446–1457.

COOPER, W. E. 2000. Tradeoffs between predation risk and feeding in a lizard, the broad-headed skink (Eumeces laticeps). Behaviour 137:1175–1189.

COWLISHAW, G. 1997. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. Animal Behaviour 53:667–686.

CREEL, S., J. WINNIE, B. MAXWELL, K. HAMLIN, AND M. CREEL. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86:3387–3397.

CUMMING, G. S. 2000. Using between-model comparisons to fine-tune linear models of species ranges. Journal of Biogeography 27:441–455.

DURANT, S. M. 2000. Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. Behavioral Ecology 11:624–632.

FEDRIANI, J. M., T. K. FULLER, R. M. SAUVAJOT, AND E. C. YORK. 2000. Competition and intraguild predation among three sympatric carnivores. Oecologia 125:258–270.

FEDRIANI, J. M., F. PALOMARES, AND M. DELIBES. 1999. Niche relations among three sympatric Mediterranean carnivores. Oecologia 121:138–148.

FESTA BIANCHET, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75:580–586.

FISCHHOFF, I. R., S. R. SUNDARESAN, J. E. CORDINGLEY, AND D. I. RUBENSTEIN. 2007. Habitat use and movements of plains zebra (Equus burchelli) in response to predation danger from lions. Behavioral Ecology 18:725–729.

Fox, J. L. 1994. Snow leopard conservation in the wild: a comprehensive perspective on a low density and highly fragmented population. Pp. 3–16 in Proceedings of the Seventh International Snow Leopard Symposium (J. L. Fox and D. Jizeng, eds.). International Snow Leopard Trust, Seattle, Washington.

Fox, J. L., S. P. Sinha, R. S. Chundawat, and P. K. Das. 1991. Status of the snow leopard *Panthera uncia* in north-west India. Biological Conservation 55:283–298.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:11–26.

Fuller, T. K., and P. R. Sievert. 2001. Carnivore demography and the consequences of changes in prey availability. Pp. 163–178 in Carnivore conservation (J. Gittleman, S. Funk, and D. Macdonald, eds.). Cambridge University Press, Cambridge, United Kingdom.

Gannon, W. L., R. S. Sikes, and the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809–823.

Gavashelishvili, A., and V. Lukarevskiy. 2008. Modeling the habitat requirements of leopard *Panthera pardus* in west and central Asia. Journal of Applied Ecology 45:579–588.

Hebblewhite, M., E. H. Merrill, and T. L. McDonald. 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf–elk predator–prey system. Oikos 111:101–111.

Heithaus, M. R., and L. M. Dill. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology 83:480–491.

Hill, K., et al. 1997. Impact of hunting on large vertebrates in the Mbaracayu Reserve, Paraguay. Conservation Biology 11:1339–1353.

Jackson, R. 1996. Home range, movements and habitat use of snow leopard in Nepal. Ph.D. dissertation, University of London, London, United Kingdom.

Jackson, R., and D. O. Hunter. 1996. Snow leopard survey and conservation handbook. International Snow Leopard Trust, Seattle, Washington.

Jackson, R., and R. Wangchuck. 2001. Linking snow leopard conservation and people–wildlife conflict resolution: grassroots measures to protect the endangered snow leopard from herder retribution. Endangered Species Update 18:138–141.

James, A. R. C., and A. K. Stuart-Smith. 2000. Distribution of caribou and wolves in relation to linear corridors. Journal of Wildlife Management 64:154–159.

Johnson, A., C. Vongkhamheng, M. Hedemark, and T. Saithongdam. 2006. Effects of human–carnivore conflict on tiger (*Panthera tigris*) and prey populations in Lao PDR. Animal Conservation 9:421–430.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. Auk 118:557–562.

Kaartinen, S., I. Kojola, and A. Colpaert. 2005. Finnish wolves avoid roads and settlements. Annales Zoologici Fennici 42:523–532.

Karanth, K. U., and J. D. Nichols. 1998. Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79:2852–2862.

Karanth, K. U., J. D. Nichols, N. S. Kumar, W. A. Link, and J. E. Hines. 2004. Tigers and their prey: predicting carnivore densities from prey abundance. Proceedings of the National Academy of Sciences 101:4854–4858.

Kotler, B. P., J. S. Brown, and O. Hasson. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. Ecology 72:2249–2260.

Krebs, C. J. 2002. Ecology: the experimental analysis of distribution and abundance. Prentice-Hall, Upper Saddle River, New Jersey.

Lima, S. L., and L. M. Dill. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Linkie, M., G. Chapron, D. J. Martyr, J. Holden, and N. Leader-Williams. 2006. Assessing the viability of tiger subpopulations in a fragmented landscape. Journal of Applied Ecology 43:576–586.

Litvaitis, J. A., J. A. Sherburne, and J. A. Bissonnette. 1986. Bobcat habitat use and home range size in relation to prey density. Journal of Wildlife Management 50:110–117.

Lovari, S. 1992. Observations on the Himalayan tahr and other ungulates of the Sagarmatha National Park, Khumbu Himal, Nepal. Oecologia Montana 1:51–52.

Lovari, S., S. B. Ale, and R. Boesi. 2005. Notes on the large mammal community of Sagarmatha National Park (Nepal). Proceedings of International Karakorum Conference. Islamabad, Pakistan.

Lyons, A. L., W. L. Gaines, and C. Servheen. 2003. Black bear resource selection in the northeast Cascades, Washington. Biological Conservation 113:55–62.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical analysis and design for field studies. 2nd ed. Kluwer Academic Publishers, Dordrecht, Netherlands.

Martin, T. E. 1995. Avian life-history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65:101–127.

Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. Ecology 85:1411–1427.

McCarthy, T. M. 2000. Ecology and conservation of snow leopards, Gobi brown bears, and wild Bactrian camels in Mongolia. Ph.D. Dissertation, University of Massachusetts, Amherst.

McCarthy, T. M., and G. Chapron. 2003. Snow leopard survival strategy. International Snow Leopard Trust and Snow Leopard Network, Seattle, Washington.

McCarthy, T. M., T. K. Fuller, and B. Munkhtsog. 2005. Movements and activities of snow leopards in southwestern Mongolia. Biological Conservation 124:527–537.

McLoughlin, P. D., R. L. Case, R. J. Gau, H. D. Cluff, R. Mulders, and F. Messier. 2002. Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic. Oecologia 132:102–108.

Morris, D. W. 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia 136:1–13.

Mortelliti, A., and L. Boitani. 2008. Interaction of food resources and landscape structure in determining the probability of patch use by carnivores in fragmented landscapes. Landscape Ecology 23:285–298.

Mysterud, A., and R. A. Ims. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. Ecology 79:1435–1441.

Norton, P. M. 1990. How many leopards? A criticism of Martin and de Meulenaer's population estimates for Africa. South African Journal of Science 86:218–220.

Oli, M. K. 1994. Snow leopards and blue sheep in Nepal: densities and predator : prey ratio. Journal of Mammalogy 75:998–1004.

Schaller, G. B. 1977. Mountain monarchs: wild sheep and goats of the Himalaya. University of Chicago Press, Chicago, Illinois.

Schaller, G. B. 1998. Wildlife of the Tibetan Steppe. University of Chicago Press, Chicago, Illinois.

Schaller, G. B., R. Jungrang, and Q. Mingjiang. 1988. Status of snow leopard *Panthera uncia* in Qinghai and Gansu provinces, China. Biological Conservation 45:179–194.

SCHMITZ, O. J., V. KRIVAN, AND O. OVADIA. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. Ecology Letters 7:153–163.

SMITH, E. A., AND M. WISHNIE. 2000. Conservation and subsistence in small-scale societies. Annual Review of Anthropology 29:493–524.

STRICKLAND, M. D., AND L. L. MCDONALD. 2006. Introduction to the Special Section on resource selection. Journal of Wildlife Management 70:321–322.

SUNQUIST, M. E., AND F. SUNQUIST. 2002. Wild cats of the world. University of Chicago Press, Chicago, Illinois.

SVARDSON, G. 1949. Competition and habitat selection in birds. Oikos 1:157–174.

THOMPSON, C. M., AND E. M. GESE. 2007. Food webs and intraguild predation: community interactions of a native mesocarnivores. Ecology 88:334–346.

TREVES, A., AND K. U. KARANTH. 2003. Human–carnivore conflict and perspectives on carnivore management worldwide. Conservation Biology 17:1491–1499.

TUYTTENS, F. A. M., N. STAPLEY, P. D. STEWART, AND D. W. MACDONALD. 2001. Vigilance in badgers *Meles meles*: the effects of group size and human persecution. Acta Theriologica 46:79–86.

VERDOLIN, J. L. 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. Behavioral Ecology and Sociobiology 60:457–464.

WERNER, E. J., AND D. J. HALL. 1988. Ontogenetic habitat shifts in bluegill—the foraging rate–predation risk trade-off. Ecology 69:1352–1366.

WHITTINGTON, J., C. C. ST. CLAIR, AND G. MERCER. 2005. Spatial responses of wolves to roads and trails in mountain valleys. Ecological Applications 15:543–553.

WILSON, G. J., AND R. J. DELAHAY. 2001. A review of the methods to estimate the abundance of terrestrial carnivores using field signs and observation. Wildlife Research 28:151–164.

WITHAM, P. G. 1978. Habitat selection by *Pemphigus* aphids in response to resource limitations and competition. Ecology 59:1164–1176.

WORTON, B. J. 1989. Kernel methods for estimating distribution in home-range studies. Ecology 70:164–168.