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Effects of predation-risk on habitat use by Himalayan Snowcocks

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Summary. When given a choice, animals often prefer foraging habitats where predation risk is low, even if such habitats provide reduced foraging opportunities. We evaluated foraging rates of tame but free-ranging Himalayan Snowcocks (*Tetraogallus himalayensis*) in 16 types of alpine habitats. Foraging rate was highest on level or slightly-sloping terrain and where grasses were relatively abundant. We also observed 102 wild snowcocks and found they were most nervous about raptorial predators when on level or slightly-sloping terrain and in small coveys. Snowcocks face a dilemma: they are most vulnerable to raptors in areas where they can forage most efficiently. During summer snowcocks trade off higher foraging efficiency on level terrain for lower predation risk on steeper terrain. During winter, when raptor numbers are lower, snowcocks apparently revert to using level or slightly-sloping, high-efficiency foraging habitats. Risk of predation plays an important role in habitat selection and resource utilization by snowcocks.

Key words: Himalayan Snowcock – Predation risk – Habitat selection – Vigilance

Experimental studies have demonstrated that when animals are given a choice, they tend to prefer circumstances or habitats in which predation risk is low, even if foraging opportunities are reduced there (e.g., Fraser and Cerri 1982; Edwards 1983; Werner et al. 1983; Power 1984; Lima et al. 1985). The threat of predation may, therefore, contribute significantly to the characteristic patterns of habitat utilization observed in prey species.

Relatively few studies have examined the energy-gain versus predation risk dilemma directly. Most have involved animals exposed to unnatural environments and unnatural foraging or predation situations; few have focused on birds (e.g., Caraco et al. 1980; Grubb and Greenwood 1982; Lima 1985). In this study we investigate habitat selection in snowcocks by evaluating forage value and escape potential of a variety of foraging sites. We provide evidence that snowcocks avoid some high quality foraging habitats because the topography there imposes a high risk of predation. We first show how snowcock foraging efficiency varies between different types of foraging habitats. We then show that predation-risk is greater in certain topographic settings, regardless of the type of foraging habitat there. Finally, we show that snowcocks forage most frequently in terrain where predation-risk is low, even though habitat analysis indicates foraging efficiency is lower there than in high-risk areas.

Himalayan Snowcocks are native to Central Asia. The species was introduced to Nevada in 1963 (Bland and Temple 1990). A self-sustaining wild population of 250–500 is now established (Stiver 1985). Snowcocks remain above treeline throughout the year, and forage primarily on the leaves and seed stalks of grasses, forbs, and sedges (Mayers 1985). They are gregarious, and forage in coveys averaging 8 individuals (Dement'ev and Gladkov 1952, Bland 1982). Their main predators are raptors, and in open alpine habitat their only escape from attack is a swift, plummetting dive down steep slopes to cliffs or boulder fields that offer protective cover.

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Study area

Our study area was a 1.3-km^2 area centered around Thomas Peak (3449 m) in the Ruby-East Humboldt Mountains, Humboldt National Forest, northeast Nevada (115°24′N, 40°38′W, T32N, R58E, Sect. 25). At the lower limit of our study area, sheer valley walls yielded to scree slopes below, generally at about 3100 m. Snowcocks have rarely been observed at lower elevations in Nevada. Vegetation was dominated by coarse sedges, grasses, and forbs, with occasional moist forbs, wildflowers, and woody shrubs. Loope (1969) described two alpine meadow communities in the Ruby Mountains: xeric "alpine tundra," and mesic "alpine turf." The overall plant species composition of these two communities was actually quite similar; Whittaker's (1970) Coefficient of Community was 77%. Alpine tundra predominated on drier, less developed substrates, characteristic of high plateaus and ridges, and on south-facing slopes. Alpine turf was associated with deeper, moisture-retaining soils within cirques and valleys, particularly on shaded north and northeast slopes.

The study was conducted from 15 June to 22 August, 1985; 18 June to 20 September, 1986; and 22 June to 24 August, 1987.

Methods

Description of foraging habitats

We evaluated foraging performance of snowcocks in 16 different alpine habitat types in prime snowcock range.

These habitats were described on the basis of 4 food-related characteristics, where each characteristic was categorized as being of either low or high value: low vegetative cover (<50%, range 8–49.5%) or high vegetative cover (>50%, range 50.5–96%), low relative density of grasses (<25%, range 0–25%) or high relative density of grasses (>25%, range 25.5–76%), low relative density of sedges (<17%, range 0–17%), or high relative density of sedges (>17%, range 17.5–48%), low relative density of forbs (<24%, range 0–24%) or high relative density of forbs (>24%, range 24.5–67%). Each habitat type was a different combination of these 4 two-state variables (i.e., $2^4 = 16$). Combinations of variables that did not occur naturally on the study area (e.g., low vegetative cover and high relative density of sedges) were fabricated by transplanting or removing plants just prior to foraging trials.

Six 0.07-ha plots were established in each type of foraging habitat, resulting in 96 foraging-performance plots. Vegetation variables on each plot were measured by point frequency. Two 80-cm cords, marked at 10-cm intervals, were stretched into an "X" over the center of the plot. Vegetative cover was defined as the percentage of 10-cm marks that rested on plants; relative abundance of grasses, sedges, or forbs was the percentage of marks that rested on plants of those types.

Estimation of foraging potential

We measured foraging rates of 3 sub-adult, tame, snowcocks (1 male, 2 females) to determine the value of each of 16 foraging habitats as a feeding site. Foraging rate was assumed to be a valid indicator of a habitat's foraging potential. Snowcocks were hatched in captivity and purposely imprinted on human handlers using procedures described by Kimmel and Healy (1987). Tame birds allowed us to observe their foraging behaviors closely without introducing a strong observer influence (Bland and Temple 1987). Wild snowcocks, on the other hand, are extremely wary and would have flushed from us at great distances (>200 m). Our tame birds were held in outdoor pens on the study area and periodically transported to preselected plots in foraging habitats. All three birds were tested on each of the 16 habitat types described above.

Prior to foraging trials, all tame birds were given an opportunity (>10 hrs) to develop foraging experience in each of the available habitats (i.e., a range of slope, vegetation cover, etc.). We were confident that the birds developed "normal" foraging behavior quite rapidly because the variety of potential forage plants was quite limited in the study area; most were of grass or herb lifeforms. To verify that our tame birds foraged as efficiently as wild individuals in equivalent situations, we compared foraging efficiency (time to consume 400 pecks of food) of tame birds on the same patches of habitat where we had measured foraging efficiency of wild birds. There was no significant difference in a paired-sample comparison of the mean rates at which wild and tame birds fed ($t = 0.30$, df $= 16$, $P > 0.50$).

At each foraging plot we released a tame snowcock and recorded the time for it to consume 400 pecks of food. If a bird engaged in non-foraging behaviors (e.g., it dustbathed, laid down, or became distracted by an outside influence) for more than 15 sec, we stopped recording until foraging resumed. We attempted to standardize motivation for foraging by fasting the birds overnight and for at least 45 min between foraging trials. Because these birds had never been attacked by predators and because we (their "surrogate parents") never reinforced fright behavior (Thaler 1986), it is unlikely they acquired any habitat-related insecurities about predators.

We used fcatorial analysis of variance to determine whether or not foraging efficiency (sec/400 pecks) was dependent on any of the 4 vegetation characteristics we measured.

Estimation of predation-risk

We assumed that the level of vigilance among wild snowcocks was directly related to the perceived risk of predation in a given location, this being a result of past learning experience as well as selective pressure. In order to determine whether snowcocks were more or less vulnerable to and, hence, nervous about raptorial predators in different situations, we observed the vigilance behavior of wild snowcocks from blinds located at least 300 m away.

A mature bird was chosen arbitrarily from a covey. We recorded the cumulative sec this focal bird was vigilant during a 3-min period, following the methods of Powell (1974). We initiated observations only after focal snowcocks engaged in active foraging, and never when we were aware of disturbances that might have influenced vigilance (e.g., human or raptor activity). Focal snowcocks were considered non-vigilant as long as their heads remained declined, thus non-vigilance encompassed an array of foraging and maintenance behaviors. If focal snowcocks lifted their heads to horizontal or beyond, and held them there momentarily or longer, they were considered vigilant.

We made 102 3-min vigilance observations from blinds overlooking both steeply-sloping (>40% slope) and level or slightly-sloping (<40% slope) terrain. Three observations were made in succession, whenever possible on 3 different focal birds from the same covey. Time of day, size of covey, wind speed, temperature, slope, and the estimated area within the bird's field of view were recorded for each observation set.

We used factorial analysis of variance to determine whether or not the vigilance of snowcocks (% of time vigilant) was dependent on any of several factors: time of day (0600–1000 h, 1000–1400 h, or 1400–1800 h), slope of terrain (either <40% or ≥40%), size of focal bird's covey, focal bird's field of view, wind speed, and temperature.

Estimation of habitat use

We estimated the use of steep terrain (>40% slope) versus level terrain (<40% slope) by wild snowcocks with two indexes: frequency with which coveys were observed in these respective terrains, and volume of accumulated fecal material/unit area. To compare frequency of use we recorded hrs spent searching for and the hrs spent observing snowcocks in the two types of terrains. To compare dropping accumulations we collected droppings from each of 232 16-m² plots, of which 4 were located in each 2-ha block of the study area. We also estimated percent vegetative cover (<10%, 10–25%, 25–50%, 50–75%, or >75%), and slope (%) at each plot. Droppings were later oven dried (105° C for 48 h) and ground to a powder sufficiently fine to pass through a 2-mm mesh screen. The volume (cm³) of powdered droppings was an index of cumulative use of a plot by snowcocks (Neff 1968; Bland 1982; Mayers 1985).

Raptor observations

We recorded the numbers of each species of raptor observed in the study area each hour. If an individual raptor returned to the study area after an absence of 5 or more min it was counted again because we were interested in frequency of raptor disturbance, not actual number of raptors.

We observed 20 raptor attacks on snowcocks. For each attack we recorded the behavior of snowcocks and attacking raptors and noted topography of the site.

Results

Foraging potential of habitats

Factorial analysis indicated relative abundance of grasses and the interaction between forb and sedge abundance had significant effects on the time it took birds to consume 400 pecks of food (Table 1). Mean foraging efficiency was better in habitats with high rather than low relative abundance of grasses (308.4 and 326.5 s/400 pecks, respectively). Mean foraging efficiency was also better in habitats where sedges predominated over forbs (300.6 s/400 pecks) than where forbs predominated over sedges (323.2 s/400 pecks).

Foraging efficiency was also affected by terrain, as was vegetation composition. Slope had a significant negative ($\beta = -10.26$) effect on foraging efficiency ($F = 8.358$, df = 2.76, $P = 0.004$), meaning snowcocks foraged more efficiently on level terrain. Slope also had a significant negative ($\beta = -14.54$) effect on relative abundance of forbs ($F = 6.320$, df = 2.76, $P = 0.013$), meaning relative abundance of forbs was greater on level terrain. Other vegetative characteristics, including the ones that affected foraging efficiency, were not affected by slope.

These findings indicate snowcocks forage best on level terrain and that this effect is due primarily to slope: preferred grasses were not more abundant on level terrain, and relative abundance of forbs, though higher on more level terrain, did not appear to influence foraging efficiency.

Seasonal occurrence of raptors

The occurrence of raptorial predators in the study area and, hence, the predation pressure on snowcocks, fluctuates seasonally. Red-tailed Hawks and Golden Eagles, the 2 greatest threats to snowcocks, were the most frequently observed raptor species in the study area during summer (54.6% and 30.4% of raptor sightings, respectively, $n = 877$). By November eagles and hawks that visited the study area during summer either migrated southward or ceased to visit higher elevations. Raptors probably do not return to alpine areas of Humboldt National Forest until March or April (R. Oakley, pers. comm., Smith and Murphy 1973). Raptorial predators are, therefore, primarily a threat to snowcocks during summer months (April–October).

Table 1. Analysis of variance for the influence of habitat characteristics on foraging efficiency (time required to consume 400 pecks of food) of snowcocks

Source of variation	*F*-ratio	*df*	*P*
% vegetative cover[a] (factor (A)	0.234	1	0.629
relative % grasses[a] (factor B)	4.596	1	0.033
relative % forbs[a] (factor C)	2.879	1	0.091
relative % sedges[a] (factor D)	0.368	1	0.545
Two-way interaction (A × B)	0.524	1	0.470
Two-way interaction (A × C)	3.098	1	0.080
Two-way interaction (A × D)	3.318	1	0.070
Two-way interaction (B × C)	0.039	1	0.844
Two-way interaction (B × D)	2.596	1	0.108
Two-way interaction (C × D)	6.643	1	0.010
Four-way interaction (A × B × C × D)	3.393	1	0.067

[a] All proportional data were arcsine transformed for analysis

Terrain and predation risk

Vigilance behavior of snowcocks typically consisted of many 1- to 3-sec bouts of vigilance and a few longer bouts. Factorial analysis indicated that only slope and the focal bird's covey size significantly affected vigilance ($F = 5.378$, df = 1, $P = 0.023$ and $F = 4.506$, df = 1, $P = 0.036$, respectively). Vigilance was negatively correlated with both slope ($r = -0.192$, $n = 102$, $P = 0.025$), and covey size ($r = -0.191$, $n = 102$, $P = 0.025$).

None of the 20 raptor attacks we observed was successful. However, we found 2 dead snowcocks; at least one clearly killed by a raptor. The raptor-killed bird was found near the edge of a large level plateau. Feathers leading from the bird toward the center of the plateau indicated it had been struck in flight by a raptor and left a trail of feathers to where it struck ground.

Fourteen (70%) of the 20 raptor attacks occurred on meadows, 3 (15%) on rocky outcrops, and 2 (20%) on cliffs. Twelve (60%) involved Golden Eagles, 6 (30%) involved Red-tailed Hawks, and 1 each involved a Prairie Falcon and a Cooper's Hawk. Fourteen attacks (70%) were initiated by raptors flying at low altitudes, 6 (30%) at high altitudes. Seventeen (85%) involved snowcocks on steep terrain, 3 (15%) on level terrain. In response to attacks by Golden Eagles, snowcocks always took flight, and eagles usually pursued them for at least a short distance. Snowcocks generally only took flight from Red-tailed Hawks when they appeared overhead with no advance warning, but these hawks seldom pursued snowcocks in flight. Most raptor attacks (74%) involved coveys smaller than the mean covey size of 8.

Habitat utilization patterns

During 138 h of search for snowcocks on steep terrain, we observed birds for 24 h (17.4% of time). During 210 h of searching on level terrain, we observed snowcocks for only 20 h (9.5% of time searching). The frequency with which wild snowcocks frequented steep versus level terrain during our summertime studies was significant ($x^2 = 3.98$, $df = 1$, $P = 0.05$).

Dropping accumulations on plots throughout the study area were not dependent on percent vegetative cover ($F = 0.141$, $df = 1$, $P = 0.708$) or slope ($F = 0.003$, $df = 1$, $P = 0.956$). The cumulative use of broad habitat types over the period of a year or more that droppings persist seemed to be similar. Droppings collected on level terrain were, however, noticeably older and drier, on average, than those collected on steep terrain, suggesting most droppings on level terrain had accumulated in winter or early spring, prior to our field season.

Discussion

Snowcocks face a dilemma: they forage most efficiently on level or slightly-sloping habitats, but they are subjected to higher predation-risk in these habitats. Foraging efficiency is probably greater on level habitats because of the relative ease of locomotion there. Despite this increased foraging efficiency, level terrain is underutilized during summer because snowcocks are exposed to an unacceptably high risk of predation there; they can not escape raptor attacks on level ground as well as on steep slopes. As a result, snowcocks tend to forage on or close to steep slopes and cliffs. They appear to be trading-off higher foraging efficiency on level terrain for lower predation risk on steeper terrain.

Snowcocks that forage in steep habitats must expend more energy to move around than they would in more level habitats. However, for snowcocks foraging under the threat of raptor predation (i.e., in summer), net energy gains would be reduced in level habitats as well, because snowcocks must sacrifice potential foraging time for increased predator-searching. Predators also inflict energy costs when they force snowcocks into escape flights. Escape flights result in a loss of elevation that must be regained by walking uphill. Also, the further downslope snowcocks are forced, the more vulnerable they become to subsequent predation because slopes level out at lower elevations.

The patterns of vigilance we observed among snowcocks are typical of those observed among other gregarious species: vigilance behavior of individuals increased as the perceived threat of predation increased (Cerri and Fraser 1983; Lendrem 1983), and decreased as group size increased (Powell 1974; Lazarus 1979). Our observation that most attacks were on groups smaller than average size contradicts studies of some other species (e.g., Bertram 1978; Ives and Dobson 1987).

Since snowcocks choose to avoid topographic settings associated with higher predation-risk, predictable patterns of habitat-use have emerged. The ratio of level-to-steep habitats in an area has a profound influence on how intensely snowcocks use the area. In the most general way, this accounts for the tendency for snowcocks to frequent higher elevations of a given range. Higher elevations provide increasingly steep slopes, more extensive cliffs, and more potential for plummeting escape flights. Mayers (1985) found increasing accumulations of snowcock droppings with increasing elevation and attempted to attribute this to vegetation differences. Unfortunately, his rank-correlation analyses did not separate the confounding effect of elevation itself, which we believe may have been the principal effect.

Population density and seasonal distribution of snowcocks are probably affected by the proportions of level and steep habitats in a given area. Our findings suggest the greatest summertime densities of snowcocks should be found where alpine meadows are located on steep slopes, or abutting steep cliffs. In the Ruby-East Humboldt Range, such areas are most abundant in Townships 32N 58E and 31N 58E, which is, indeed, where we have found the greatest numbers of snowcocks in summer (Bland, unpublished data).

Snowcocks remain in alpine areas over the winter, but in winter their patterns of habitat use apparently changes. Deep accumulations of snow can preclude foraging in most areas except wind-blown ridges or plateaus. Raptors rarely visit alpine areas during winter, so snowcocks are free to forage on wind-blown plateaus from which the risk of predation excludes them in summer. During winter, snowcock droppings accumulate on level ground rather than on steep ground, resulting in similar annual accumulations of droppings in both steep and level habitats.

Selective pressures of raptorial predators have played an important role in the evolution of several snowcock behaviors. Under predatory pressure exerted primarily by *Aquila* eagles, snowcocks have evolved several escape strategies in response to aerial predators, and have based their summertime habitat selection on predation-risk.

Studies of habitat-selection patterns of gallinaceous birds have typically consisted of assessing relative availability of habitat types and determining how frequently birds use them. The behaviors which link structure and composition of habitat types with a species' use of habitats have seldom been quantified. In this study, in addition to describing a range of foraging habitats and comparing them on the basis of snowcock use, we have proposed a mechanism underlying these observed patterns.

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