

Predation risk and foraging behavior of the hoary marmot in Alaska

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Summary. I observed hoary marmots for three field seasons to determine how the distribution of food and the risk of predation influenced marmots' foraging behavior. I quantified the amount of time *Marmota caligata* foraged in different patches of alpine meadows and assessed the distribution and abundance of vegetation eaten by marmots in these meadows. Because marmots dig burrows and run to them when attacked by predators, marmot-to-burrow distance provided an index of predation risk that could be specified for different meadow patches.

Patch use correlated positively with food abundance and negatively with predation risk. However, these significant relationships disappeared when partial correlations were calculated because food abundance and risk were intercorrelated. Using multiple regression, 77.0% of the variance in patch use was explained by a combination of food abundance, refuge burrow density, and a patch's distance from the talus where sleeping burrows were located. Variations in vigilance behavior (look-ups to search for predators while feeding) according to marmots' ages, the presence of other conspecifics, and animals' proximity to their sleeping burrows all indicated that predation risk influenced foraging.

In a forage-manipulation experiment, the use of forage-enhanced patches increased six-fold, verifying directly the role of food availability on patch used. Concomitant with increased feeding, however, was the intense construction of refuge burrows in experimental patches that presumably reduced the risk of feeding. Thus, I suggest that food and predation risk jointly influence patch use by hoary marmots and that both factors must be considered when modeling the foraging behavior of species that can be predator and prey simultaneously.

Introduction

Optimal foraging models are mathematical statements of how organisms should feed so as to maximize their fitness. Models have been developed to predict several aspects of foraging, including diet composition, patch choice, time spent in and use of a patch, and movements between patches (reviewed in Pyke et al. 1977; Krebs 1978; Kamil and Sargent 1981).

A central problem faced by modelers of foraging behavior is to identify the proper "currency" for their calculations (Schoener 1971). In most models, it is energy per unit time. An optimal forager is thus defined as one that maximizes its net rate of energy gained when feeding. Whereas these "energy" models have been supported in some cases (Werner and Hall 1974; Goss-Custard 1977; Pyke 1981), investigators have noted that energy may not always be the appropriate currency (Westoby 1974), that more than one currency may be important (Covich 1976; Belovsky 1978), and that the choice of currencies other than energy might lead to predictions similar to those of an energy-based model. Charnov (1976), for instance, showed that an energy efficiency model correctly predicted the foraging behavior of captive mantids (*Hierodula crassa*). However, he also noted that foraging risks (tumbling from the bush, capture by a predator) might also account for mantids' feeding behavior.

Energy maximization alone may not account for all foraging decisions when a foraging animal is also vulnerable to predators. For example, sticklebacks (*Gasterosteus aculeatus*; Milinski and Heller 1978), juvenile backswimmers (*Notonecta hoffmanni*; Sih 1980, 1982), bluegill sunfish (*Lepomis microchirus*; Werner et al. 1983), and cyprinid minnows (*Rhinichthys atratulus*; Cerri and Fraser 1983) all exhibit changes in foraging behavior when predation risk is varied experimentally.

In this report, I describe the feeding behavior of hoary marmots (*Marmota caligata*) in southcentral Alaska and examine how the risk of predation influenced their foraging. *M. caligata* is an herbivore that feeds in open meadows and evades predators by running to burrows. Like *M. monax* (Grizzell 1955), *M. flaviventris* (Armitage 1982), *M. olympus* and *M. marmota* (Barash 1975), *M. caligata* is preyed on by terrestrial (e.g., *Canis latrans*, *Lynx canadensis*) and avian (e.g., *Aquila chrysaetos*) predators (Barash 1975; Olendorff 1976; Noyes and Holmes 1979). In general, marmots' vulnerability is probably greater when they forage away from their protective burrows rather than close to them. However, because marmots feed selectively among plant species (Barash 1973; Hansen 1975; Andersen et al. 1976; Armitage 1979), because they crop vegetation faster than it regenerates (Wood 1973; Holmes 1979), and because weight gained by feeding is important to surviving hibernation (Armitage and Downhower 1974; Armitage et al. 1976) and to females' reproductive success (Andersen et al. 1976), marmots cannot simply confine all feeding to small areas near burrows or rock slides. They must move away from these "safe" areas and consequently become more vulnerable to predators (Anthony 1962; Armitage 1962; Barash 1973; Johns and Armitage 1979).

To examine the potential influence of predation risk on hoary marmots' foraging, I tested three predictions: (1) Marmots spend more time feeding in low-risk patches than high-risk patches, other things (e.g., nutrient availability) being equal. (2) Marmots exhibit vigilance behavior (visual surveys to detect predators) that varies with risk: older marmots are less vigilant than younger age classes and vigilance varies with the proximity of conspecifics and the availability of protective burrows. (3) The time marmots spend foraging in various patches depends on both the food available in a patch and the predation risk to which a marmot is exposed when in the patch. Although other factors [e.g., ambient temperature (Armitage 1962; Holmes 1979), kinship and social relations (Johns and Armitage 1979; Holmes 1984)] also influence marmots' foraging, here I concentrate on food and the risk of predation.

Materials and methods

Study animal. Hoary marmots (hereafter "marmots") are large (3–8 kg adults), diurnal herbivores (family Sciuridae) that live colonially in open alpine and subalpine meadows in the northwestern United States, western Canada, and Alaska. At my Alaskan study site, marmots are active from early May through

late September, and they hibernate the remainder of the year. I classify marmots as juveniles, yearlings, 2-year-olds, or adults if they are active in their first, second, third, or fourth (or greater) summer; "young" refers collectively to nonadult age classes. A "colony" is an adult pair and their 2–5 young that live together in an area with boundaries that are relatively fixed between years. Residents of a colony associate year-round (except dispersing 2- or 3-year-olds) and overwinter together in the same hibernaculum. All colonies that I studied had at least one contiguous neighboring colony [Fig. 1, in Holmes (1984)]. See Barash (1974, 1980) and Holmes (1979, 1984) for details on the behavioral ecology of hoary marmots.

Study site. I observed marmots in the Independence Mine Valley of southcentral Alaska (65 km north of Anchorage and 8 km east of Grubstake Gulch) for three field seasons (early May to early September, 1974–1976), and made 2 week visits in May, 1977 and July, 1978. The 1.6 × 3.2 km valley (elev. 990 m, ca. 300 m above treeline) is surrounded by steep peaks on three sides, and has a relatively flat meadow covering its floor. This meadow is typical of slow-growing, high-latitude (61° N), short mesophytic grasslands (Bliss et al. 1973) that are rich in herbaceous plants and dwarf shrubs. At the height of plants' growing season (mid July), the mean live aboveground plant biomass was 117.6 ± 11.5 g/m² (±SE) and the mean height of the vegetation was 20.3 cm (range = 5–75 cm) in meadows where marmots foraged. Talus piles used by marmots as activity centers exist where steep peaks meet the flatter meadow.

Observational and assessment techniques. My assistants and I observed marmots (1,115 h, 1974–1976) with binoculars and a 60 × variable power spotting scope by sitting quietly in exposed locations on the edges of colonies. We identified 11 colonies and livetrapped and individually marked (ear tags, fur dye, and an 8 cm piece of colored construction flagging attached subcutaneously between the shoulders) all residents ($n = 29$) in five colonies. Because of unique characteristics (e.g., pelage patterns), eight animals that were never trapped were also recognizable. Because marmots were difficult to trap after they moved from their hibernacula (23 trapping h per individual), repeated captures of individuals during the summer was rarely possible.

I assessed: (1) the time marmots spent feeding in different parts of the meadow, (2) specific kinds of foraging behaviors, (3) the identity, distribution, and abundance of plant species eaten by marmots, and (4) the distribution of burrows available to marmots for predator escape. Scan samples (Altmann 1974) and grid systems were used to quantify the amount of time marmots foraged in different parts of the meadow. To choose an appropriate scan interval, 3 consecutive days were spent at each of four colonies (1–12 July, 1974), observing one colony at a time (5–7 marmots). The identity, behavior, and location of each resident was recorded at 1-, 3-, 5-, and 10-min intervals during the morning foraging bout (0730–1030 H). A marmot was foraging if it was ingesting vegetation with its head down, moving along (presumably) searching for vegetation with its head down, or chewing with its head up. The percentage of total time aboveground recorded as "foraging" (all age classes combined) was significantly ($P < 0.05$) lower for the 10-min versus 5-min scan interval, and thus I chose the 5-min interval to quantify foraging time and meadow use, given the lack of significant differences among the 1-, 3-, and 5-min intervals.

To quantify patterns of meadow use, marmots were located during scans with reference to a staked grid system (30 × 30 m quadrats, hereafter a "patch") overlaid on a colony or in relation to rocks, shrubs or burrows. To determine if my presence affected meadow use, I made limited observations on two colonies from behind a boulder. Neither the mean foraging distance

from the talus nor the mean frequency of foraging interruptions (looking up to survey the area) changed significantly (observer visible vs. observer not visible; $P > 0.1$).

I recorded two interdependent foraging behaviors that were related to predator vigilance: The number of "look-ups" per minute and the amount of feeding time per minute (both behaviors recorded during the same 1-min intervals). That is, rather than feeding continuously with their heads down, marmots stopped frequently to look up (often standing bipedally) and survey the area by rotating their heads 30–45° in both directions (hereafter a "look-up"). A primary function of these look-ups is to search for predators (Barash 1973; Carey 1983). "Feeding time" refers to periods when marmots were stationary with their heads down ingesting vegetation or moving along slowly ingesting vegetation. If look-ups lasted longer than 10 s, they were omitted from analyses because they often indicated a change in activity (e.g., feeding to social). Thus, data on look-ups and feeding time portray concentrated rather than modal feeding.

Plant species eaten by marmots were identified by micro-histological analysis of fecal samples and an estimate was made of the percentage dry weight of each species in marmots' diets (Hansen and Flinders 1969; Hansen 1975). Despite the limitations of this method (reviewed in Holechek et al. 1982), it was used because the differential digestion of plant species seems more problematic for ruminants than non-ruminants like marmots (Holechek et al. 1982); feeding trials with yellow-bellied marmots revealed that digestibility correction factors were not needed for species of plants ingested most frequently by free-living animals (Carey 1983); and direct observation methods (e.g., bite-counts) were not possible due to marmot-observer distance, vegetation type and density, and marmots' selectivity in feeding (Bjurgstad et al. 1970). Fecal samples were collected four times during the summer (Table 1) in four colonies and were analyzed by a technician after field data were collected. "Selected plants" are defined arbitrarily as those species that together made up over 90% of marmots' diets by dry weight (Table 1).

To assess the distribution and abundance of all plant species in marmot colonies, I used a modified point-quadrat technique (Mueller-Dombois and Ellenberg 1974). At each of 441 points in a patch (picture the intersecting lines of a grid with 1.5 × 1.5 m squares overlaid on a 30 × 30 m patch, which gives 441 "points"), a rod (2 mm diameter) was lowered blindly by one person while another recorded the identity and number of times the rod touched different individuals of each species. The technique provides a reliable measure of species distribution and abundance (Holmes 1979), and it can be used to compare plant abundance (frequency) among patches (Mueller-Dombois and Ellenberg 1974).

The distribution and abundance of burrows in a colony was measured to provide an index of risk. Because marmots flee to burrows when attacked by predators, risk can be approximated by marmot-to-burrow distance, although other factors are also influential (e.g., type of predator, running speed of the marmot, degree of protection afforded by the burrow). Marmots ran to two kinds of burrows. First, sleeping burrows were located in talus piles or rock jumbles where residents spent the majority (>80%) of their nonfeeding time. Second, refuge burrows (refugia) were excavated by marmots and were found throughout meadows in which they foraged (range = 65–120 refugia per colony, $n = 6$ colonies). I assumed that sleeping burrows provided greater predator protection than refugia because of the formers' greater length (at least 3.5 m versus 1.5 m, approximately), multiple (three to five) rather than single entrances/exits, and less accessible nature due to surrounding boulders.

Table 1. Diets of Alaskan hoary marmots (percent dry weight of total diet) determined by microhistological analyses of feces

Plant species ^a	15 June	5 July	25 July	13 August
<i>Carex spp.</i>	83.0%	91.2%	78.0%	86.3%
<i>Arnica alpina</i>	0.4	2.8	6.9	4.0
<i>Festuca altaica</i>	6.7	0.9	0.9	2.8
<i>Valeriana sitchensis</i>	–	0.3	3.1	2.5
<i>Geum rossii</i>	1.8	1.1	3.3	2.1
<i>Epilobium angustifolium</i>	2.2	–	–	0.7
<i>Ranunculus acris</i>	2.6	0.9	1.9	–
<i>Viola epsipila</i>	–	0.6	1.2	–
<i>Achillea millefolium</i>	–	0.3	0.3	–
<i>Lupinus arcticus</i>	–	–	0.3	–
<i>Petasites sagittatus</i>	0.4	0.3	–	0.3
<i>Deschampsia atropurpurea</i>	–	–	0.3	–
<i>Phleum alpina</i>	0.4	–	–	–
<i>Salix spp.</i>	0.7	0.3	0.3	–
Lichens	0.7	–	–	0.7
Moss	0.4	–	0.3	0.3
Other ^b	0.7	1.0	3.2	0.3

^a Species above the line are 'selected plants' – those that collectively made up more than 90% of marmots' diets by dry weight

^b "Other" includes at least eight species, none of which represents more than 0.1% of diets

To quantify patch risk, I measured the distance from the center of a patch to the nearest sleeping burrow in the talus and assumed that as this distance increased risk also increased. For refugia, I determined their density in a patch and reasoned that after burrows were dug risk and density were negatively related. I also systematically located 49 points in a patch (picture the intersecting lines of a grid with 5 × 5 m squares overlaid on a 30 × 30 m patch, which gives 49 "points") and measured the distance from each point to the nearest refugium in the patch. I assumed that risk was negatively related to a patch's mean refuge burrow distance.

Finally, to examine experimentally the relationship between patch use and forage abundance, I spread 75 kg/ha of ammonium nitrate on two patches in each of two colonies in 1 year (early August) to determine if fertilized patches would be used more than unfertilized patches the following year (Willhite et al. 1955). Fertilized and unfertilized patches were matched for the frequency of selected plants, distance from the talus, and refuge burrow density, and there was no significant difference in foraging time on fertilized and unfertilized patches prior to experimentation ($P > 0.1$).

Statistics and sampling. Parametric (oneway ANOVA, Scheffé's contrasts, and t -tests) and nonparametric (χ^2 and Mann-Whitney U) tests were used to analyze data (Blalock 1972). The relationship of patch use to forage availability and risk was examined with linear regression (zero-order, partial, and multiple regression). Means \pm SE are reported.

Statistical analyses on look-ups and feeding time are based on data from individually recognizable marmots that lived in five neighboring colonies [see Fig. 1 in Holmes (1984), the five most northeastern colonies]. These animals included 5 adult males, 5 adult females, 12 2-year-olds, and 15 yearlings (data on juveniles are not reported here). Because only 3 marmots

(yearlings) from these colonies disappeared during the study, statistical comparisons are based largely on data from the same individuals between years.

Analyses of look-ups and feeding time are based on a computer-selected random sample because individuals were sometimes observed repeatedly during a 2–3 h foraging period. The random sample was stratified by age class, the proximity of other foraging animals, and marmots' distances from the talus, all of which influence feeding (details below). Statistical comparisons within and between strata are balanced for variations in the other strata. For instance, if look-ups by adults and yearlings are compared, the proximity of other marmots and the distance from the home talus are balanced for both age classes.

Regression analyses are based on data from 12 marmots that lived in the two colonies whose composition (1 adult male, 1 adult female, and 4 2-year-olds in each colony) and foraging area (size, vegetation biomass and composition, and burrow density) were most similar to those of the nine other colonies (Holmes 1979). To assess patch use, numbered stakes (2 m tall) were placed in both colonies, dividing each into about 90 patches (e.g., Fig. 1). For each colony, I calculated (based on scan samples) the total amount of feeding time and the percentage of the total feeding time that marmots foraged in each patch (data from all residents in a colony combined). Data were collected from mid June to mid August, 1976 (320 h of observation) when fecal-sample and plant-distribution data were also collected.

Results

Use of foraging areas

The foraging area of a colony (the polygon enclosing 80% of all feeding observations for residents of a colony recorded during scan samples, mid June to mid August, 1975–1976) averaged 9.2 ha (range = 8.9–10.0 ha, $n=6$ colonies), and residents had access to all parts of their own colony's foraging area (see also Barash 1974). That is, marmots did not defend parts of their colony's foraging area against other residents (only 10 intracolony agonistic encounters were observed during two seasons in three intensively studied colonies), although yearlings and 2-year-olds tended to move short distances (5–10 m) from a feeding location when approached by the resident adult male (67% of 52 approaches). Marmots from one colony rarely strayed into another colony's foraging area, despite the fact that all 11 colonies abutted one and usually two other colonies. In 24 of 30 instances when an intruder spent ≥ 5 min in the foraging area of a neighboring colony, the intruder departed when approached by either of the resident adults (Holmes 1984).

I examined residents' use of their colony's foraging area in two ways. First, 21 of 91 patches (23.1%) accounted for 68.8% of all foraging time in 1975 and 73.4% of all foraging time in 1976 at the most intensively studied colony (Fig. 1).

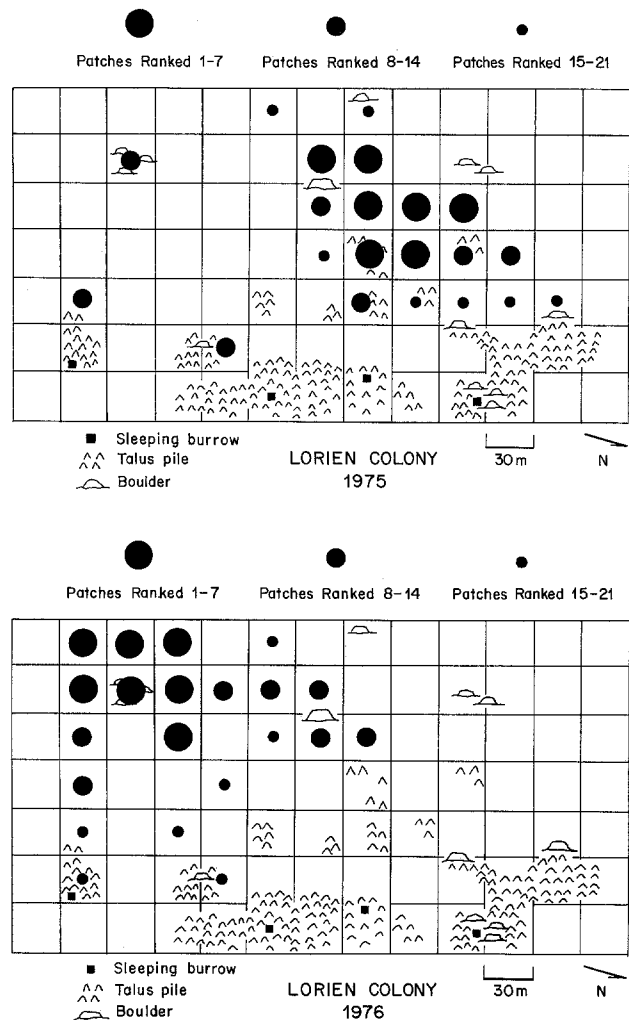


Fig. 1. The 21 patches (30 × 30 m quadrats) used most often for foraging by five hoary marmots resident at one colony in 1975 and 1976 (data collected mid June to mid August in both years). The three sizes of circles indicate the first, second, and third most intensively used groups of seven patches (arbitrarily, seven patches per group – see text)

(The number 21 was picked arbitrarily after noting that the 22nd patch accounted for <2% of all foraging time). At the next most intensively studied colony, the top 21 patches accounted for 70.5% (1975) and 77.1% (1976) of the total foraging time. Examining the 21 most frequently used patches more closely, the percentage of foraging time among the top seven-ranked patches did not differ significantly at either colony in 1975 or 1976 ($P > 0.1$ for all tests). However, the percentage of foraging time among the top 14-ranked patches did differ significantly at each colony in both years ($P < 0.01$ all tests).

Second, residents' mean foraging distance from their home talus was 49.9 ± 5.6 m. The mean dis-

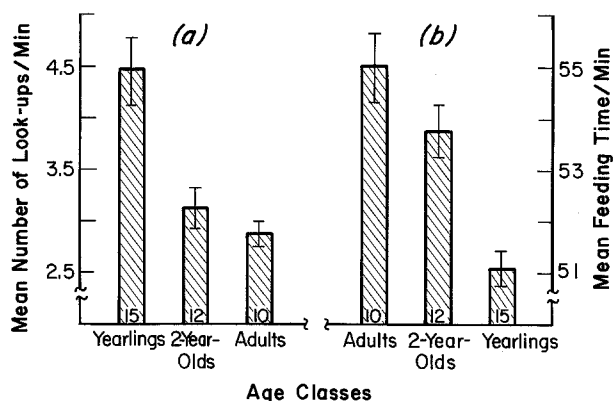


Fig. 2. **a** The mean (\pm SE) number of times per minute that marmots in different age classes looked up when foraging, and **b** the mean (\pm SE) amount of time per minute (s) that marmots in different age classes spent feeding with their heads down. The primary purpose of look-ups was presumably to search for predators (see text). Data were collected from mid-June to mid-August in 1975 and 1976 on individually marked marmots that lived in five colonies (number of animals shown inside bars)

tances increased significantly ($P < 0.001$) with marmots' ages; adults foraged significantly ($P < 0.05$) farther from the talus ($\bar{x} = 52.1 \pm 3.8$ m) than 2-year-olds ($\bar{x} = 43.4 \pm 2.5$ m), who foraged significantly ($P < 0.05$) farther from the talus than yearlings ($\bar{x} = 32.2 \pm 2.9$ m).

Look-ups per minute and feeding time per minute

The mean number of look-ups per minute and the mean feeding time per minute varied significantly across age classes (Fig. 2, $P < 0.001$ for both behaviors). Adults and 2-year-olds did not differ significantly from each other in frequencies of look-ups ($P > 0.05$), but both classes looked up significantly less often than yearlings ($P < 0.01$). Adults fed significantly longer than 2-year-olds who, in turn, fed significantly longer than yearlings ($P < 0.05$ for all tests).

Look-ups per minute and feeding time per minute were also analyzed with respect to (1) a marmot's proximity to conspecifics and (2) its distance from the talus. Marmots feeding near a conspecific (≥ 1 marmot within 10 m) looked up significantly less often ($\bar{x} = 2.3 \pm 0.2$, $n = 79$ look-ups among 15 animals) than those feeding alone (no animal within 15 m, $\bar{x} = 3.3 \pm 0.1$, $n = 182$ look-ups among 24 animals, $P < 0.001$). Using data from the same 1-min intervals, marmots foraging near a conspecific fed significantly longer ($\bar{x} = 55.0 \pm 0.5$ s) than ones that fed alone ($\bar{x} = 53.5 \pm 0.3$ s, $P < 0.01$).

Marmots foraging near (< 50 m) the talus looked up significantly less often ($\bar{x} = 2.6 \pm 0.3$, $n =$

93 look-ups among 18 marmots) than those that fed away (> 50 m) from the talus ($\bar{x} = 3.1 \pm 0.1$, $n = 63$ look-ups among 13 marmots, $P < 0.01$). Based on the same intervals, animals near the talus fed significantly longer ($\bar{x} = 54.0 \pm 0.5$ s) than those that fed away from the talus ($\bar{x} = 52.1 \pm 0.6$ s, $P < 0.01$). (The 50 m distance was used because it approximated marmots' mean foraging distance – see above).

Predators and risk

Potential predators (*Canis latrans*; *Lynx canadensis*; *Gulo gulo*; *Aquila chrysaetos*) were sighted in the valley on 82.5% of all days, but successful predation by a natural predator was not seen. When young marmots and adults were feeding together (< 10 m apart) and a predator (*C. latrans*) appeared, adults ran to and reached the talus ($\bar{x} = 11.5 \pm 2.09$ sec, $n = 5$ adults) significantly ($P < 0.01$) sooner than young marmots ($\bar{x} = 19.8 \pm 3.4$ s, $n = 8$ young). When I surreptitiously approached a foraging animal from behind a boulder, adults responded (started to run) significantly ($P < 0.01$) sooner ($\bar{x} = 2.3 \pm 0.6$ s) than young marmots ($\bar{x} = 4.1 \pm 1.5$ s).

Regression analyses: patch use, forage, and risk

In 1976, I selected 20 patches (10 each in two colonies) marked with stakes to examine the relationship of patch use to a forage factor and a risk factor by linear regression. Forage factor refers collectively to (1) the frequency of all plant species in a patch, (2) the frequency of selected plants in a patch, and (3) the percentage of all plants in a patch that were selected plants. Risk factor refers collectively to (1) the number of refugia in a patch, (2) the mean distance to a refuge burrow in a patch, and (3) the distance from a patch to a sleeping burrow in the talus. For regression analyses, I ranked each colony's 90–100 patches according to their relative percentage use (use by all residents combined) and divided them into groups of 10 (i.e., ranks 1–10, ranks 11–20, etc.). Then I chose (randomly) one patch from each group of 10 for the regression analyses. I combined the data from the two colonies because their age and sex composition, the identity and abundance of selected plants, and foraging behaviors (look-ups and feeding time) were similar (Holmes 1979).

Correlations between patch use and each of the three forage and three risk variables were all significant ($P < 0.05$, Table 2), indicating that patch use could be predicted by each of the six variables.

Table 2. Pearson correlations between patch use (percent of total foraging time spent in a given patch) and the three forage factor variables and the three risk (of predation) factor variables

Forage variables	Frequency of all plant species	Frequency of selected plant spp ^a	Percent of selected plant spp ^b
Percent of patch use	$r=0.72$ $P<0.01$	$r=0.68$ $P<0.01$	$r=0.67$ $P<0.02$
Risk variables	Number of burrows	Mean distance to burrow	Distance to talus
Percent of patch use	$r=0.65$ $P<0.02$	$r=-0.55$ $P<0.05$	$r=-0.80$ $P<0.01$

^a See Table 1 for definition of "selected plants"

^b Percent of all plants in a patch that were "selected plants"

Because the forage and risk variables were often intercorrelated, partial correlations were computed. First, however, I determined which of the three forage and three risk variables were the best predictors of patch use. I arbitrarily designated the frequency of selected plants to represent the forage factor because correlations between each of the three forage variables and patch use were nearly identical (Table 2). For the risk factor, I used both the number of refugia per patch and the patch's distance from the talus because they were more highly correlated with patch use than was the mean distance to a refuge burrow (Table 2).

All significant correlations of patch use with the original forage and risk variables (Table 2) disappeared when partial correlations were calculated between patch use and the number of refugia per patch, the patch's distance from the talus, and the frequency of selected plants in a patch (Table 3). For example, the initial correlation between patch use and the frequency of selected plants ($r=0.68$, $P<0.01$, Table 2) was no longer significant ($r=0.06$, $P>0.1$, Table 3) after the effect of distance to the talus was removed. Overall, partialing out the risk effect had a greater impact on the patch use-forage abundance correlation than removing the forage effect had on the patch use-risk correlation (Table 3).

Finally, I used multiple regression to examine both the individual and combined effects on patch use of (1) the frequency of selected plants per patch (the forage factor), (2) the number of refugia per patch, and (3) the patch-talus distance (the latter two variables making up the risk factor). The linear combination of these variables was significantly related to patch use and accounted for 77.0% of

Table 3. Partial correlations between patch use^a by foraging marmots and selected variables^b that made up the forage (*above line*) and risk (*below line*) factors

Dependent variable	Independent variable	Control variable	r	$P<$
Percent use	Frequency of selected plants ^c	Distance to talus	0.06	0.42
Percent use	Frequency of selected plants	Number of burrows	0.54	0.07
Percent use	Frequency of selected plants	Distance to talus and no. of burrows	-0.20	0.31
Percent use	Distance to talus	Frequency of selected plants	-0.56	0.06
Percent use	Number of burrows	Frequency of selected plants	0.44	0.12

^a Percent total foraging time spent on a given patch

^b Choice of variables for partial correlations explained in text

^c See Table 1 for definition of "selected plants"

Table 4. Multiple regression analysis of patch use^a by foraging marmots (dependent variable) with the forage factor (frequency of 'selected plants'^b in a patch) and the risk factor (number of refuge burrows in a patch and patch's distance from the talus containing sleeping burrows)

Overall multiple regression results					
	Analysis of variance	df	F	P	
Multiple R	0.88				
Multiple R^2	0.77	Regression	3	6.83	<0.03
Multiple R^2	0.66	Residual	6		
Independent variables					
	r	r^2	F	P	
Frequency of selected plants	0.20	0.04	0.26	>0.1	
Number of refuge burrows	0.42	0.176	3.25	>0.1	
Distance to the talus	-0.79	0.624	4.82	<0.1	

^a Percent total foraging time spent in a given patch

^b See Table 1 for definition

its variance ($P<0.03$, Table 4). No single independent variable correlated significantly with patch use ($P>0.1$), although "distance to the talus" approached significance ($P<0.1$, Table 4; P values for each independent variable are based on regression coefficients computed *after* the effect of each of the other independent variables has been removed.) The squared coefficients (r^2 in Table 4) for each independent variable show that the risk factor accounted for more of the variance in patch use than the forage factor, and that "distance to the talus" outweighed the "number of refuge burrows" as an indicator of risk.

Forage manipulation experiment

Two things occurred in the experimental patches the year after fertilizer was applied. First, their use (percentage total foraging time) was 625% greater than it was prior to fertilizer application ($P < 0.001$). This six-fold increase was associated with an 11.0% increase in crude protein content in selected plants (all species combined), as revealed by a proximate analysis of plant nutrients (Goering and von Soest 1970). In contrast, there was no significant change between years in the use of non-experimental patches ($P > 0.1$). Second, marmots excavated 13 new refugia the year after fertilizer was applied, 11 of which were in experimental patches. Thus, 84.6% of all new refugia were dug in 11 of 180 (6.1%) available patches so that increased foraging after fertilizer was applied coincided with increased digging (decreased risk) in a patch.

Discussion

I conclude that the feeding behavior of Alaskan hoary marmots was influenced by both the availability of forage and the risk of predation. These influences were indicated by patterns of patch use (Fig. 1), by variations in predator vigilance as a function of risk (Fig. 2), and by correlations between patch use and various forage and risk factor variables (Table 2, 3, and 4).

Selective use of a colony's foraging area (Fig. 1) suggests that marmots were sensitive to variations in habitat "quality" when feeding. One aspect of "quality" appeared to be the quantity of forage available, because marmots concentrated their foraging in patches with the greatest abundance of selected plants (Table 2), as predicted by energy-based optimal foraging models (see Pyke et al. 1977). In addition, the reduced availability of plants caused by foraging (Wood 1973; Holmes 1979) and the slow regeneration time of Arctic plants (Bliss et al. 1973) may explain why marmots shifted their feeding between years to different areas within their colony's boundaries (Fig. 1). On the other hand, when food was about equally available (i.e., controlled statistically), marmots spent more time feeding in low-risk patches than high-risk patches (Table 2). Thus, patch "quality" was also influenced by risk, and the prediction that marmots would feed more in low-risk than high-risk patches when food was about equally available is supported.

Forage "quality" may also have influenced patch use. To examine this, a proximate analysis

(Goering and van Soest 1970) was performed to quantify plant nutrients (crude protein, fat, cellulose and hemicellulose, lignin, and total mineral content) but no clear correlations emerged between nutrient content and the use of selected plants, (Table 13, Holmes 1979; but see Carey 1983). Secondary compounds in plants affect their acceptability to *M. flaviventris* (Armitage 1979), but I did not analyze plants at my study site for the presence of any toxins.

The distance marmots foraged from the talus was inversely related to age. If the risk of predation were negatively related to marmots' ages and positively related to mean foraging distance from the talus, then the age-foraging distance pattern further indicates that risk affected patch quality. Young marmots did appear more vulnerable to predators than adults, since young were slower to detect (start running) a potential threat and took longer to reach the safety of the talus once they detected the predator. Because foraging can reduce food availability (Wood 1973), adults may also have fed farther from the talus than young to reduce forage competition with their offspring. For instance, female *M. caligata* in Washington State foraged less within 5 m of the burrows that contained their young than females without infants, despite the maternal females spending twice as much nonforaging time near their burrows (Barash 1980).

Consistent with my second prediction, vigilance behavior increased as (presumed) risk increased (see also Carey 1983). That is, marmots exposed to higher risk (younger animals, animals feeding alone, and animals feeding far from the talus) looked up more often and spent less time feeding than marmots exposed to lower risk (older animals, animals feeding near another conspecific, and animals feeding close to the talus). Note, however, that because look-ups and feeding time are interdependent, they appropriately represent a single behavioral measure. In addition, although vigilance and risk were related statistically, differences were small (Fig. 2) and their biological significance is unknown.

Having discussed how risk might be related to age and distance from the talus, I note only that greater vigilance by younger marmots and marmots feeding away from the talus again documents the risk-sensitive nature of feeding by *M. caligata*. Among the ground-dwelling sciurids, solitary individuals or those at the periphery of a group are more vigilant than those surrounded by conspecifics (Armitage 1962; Barash 1973; Svendsen 1974; Hoogland 1979, 1981; Carey 1983). That Alaskan

marmots foraging alone were more vigilant than those foraging near conspecifics further suggests that risk influenced foraging.

The final prediction that patch use would depend on both forage and risk was supported by results from the multiple regression analysis (Table 4). Neither the forage factor nor the risk factor alone were significantly related to patch use, but together they accounted for 77.0% of the variance in patch use. Reminiscent of Charnov's (1976) suggestion for mantids, analysis of marmots' patch-use patterns based solely on a forage factor would have produced results consistent with energy-based optimal foraging models (Pyke et al. 1977). That food abundance and predation risk were intercorrelated (Table 3) accounts for the spurious support given to energy-based models.

In an independent study of yellow-bellied marmots, Carey (1983) presents results that mirror in several ways those reported here. The use of foraging areas by *M. flaviventris* correlates positively with food availability and negatively with habitat characteristics (e.g., refuge burrow density, vegetation density that interferes with visual searches for predators) that increase the risk of predation. Moreover, young yellow-bellied marmots are more vigilant than adults and vigilance (time spent looking for predators) decreases as foraging group size increases (Carey 1983). Thus predators have influenced the feeding behavior of *M. flaviventris* and *M. caligata*, and both species have adopted some similar behaviors to reduce risk.

In conclusion, my observations on hoary marmots do not reveal whether risk or food was the primary determinant of patch use in the study population. Such an either-or approach, however, may not be productive because risk and food availability seemed interrelated, as suggested by the experimental addition of fertilizer to foraging areas. That is, a six-fold increase in feeding time on forage-enhanced patches indicated that patch use was influenced by forage availability. Simultaneously, though, the increase in feeding time was matched by intense construction of refuge burrows that reduced the vulnerability of animals feeding in the enriched patches. Thus, the inter-relation between food and risk on patch use is apparent and suggests that both factors must be considered when modeling the foraging behavior of organisms that are predators and prey simultaneously.

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