

Myrmecophagy by Yellowstone grizzly bears

David J. Mattson

Abstract: I used data collected during a study of radio-marked grizzly bears (*Ursus arctos horribilis*) in the Yellowstone region from 1977 to 1992 to investigate myrmecophagy by this population. Although generally not an important source of energy for the bears (averaging <5% of fecal volume at peak consumption), ants may have been an important source of protein during midsummer and were heavily consumed during some years. Myrmecophagy was most common annually when known high-quality foods were scarce, as well as during the warmest months of the study, when regional average temperatures exceeded 12–15°C. Bears tended to select large ants (>8 mm long) nested in logs over small ants (≤6 mm long) nested under stones. Optimal conditions for consumption of ants occurred on the warmest sites with ample substrate suitable for ant nests. For ants in mounds, this occurred at low elevations at non-forested sites. For ants in logs, this occurred at low elevations or on southerly aspects where there was abundant, large-diameter, well-decomposed woody debris under an open forest canopy. Grizzly bears selected moderately decomposed logs 4–5 dm in diameter at midpoint. Ants will likely become a more important food for Yellowstone's grizzly bears as currently important foods decline, owing to disease and warming of the regional climate.

Résumé : Les données recueillies de 1977 à 1992 dans la région de Yellowstone au cours d'une étude de Grizzlis (*Ursus arctos horribilis*) porteurs d'émetteurs radio a permis d'étudier la myrmécophagie chez cette population. Bien qu'une source peu importante d'énergie pour les grizzlis (en moyenne, <5 % du volume fécal au moment de la consommation maximale), les fourmis peuvent constituer un apport important de protéines au milieu de l'été et elles sont consommées en abondance certaines années. La myrmécophagie est un phénomène commun les années où il y a pénurie d'aliments de haute qualité et aussi au cours des mois les plus chauds, quand les températures régionales moyennes dépassent 12–15°C. Les ours ont tendance à choisir les grosses fourmis (>8 mm) qui vivent dans les troncs tombés plutôt que les petites fourmis (≤6 mm) dissimulées sous les pierres. Les conditions optimales de consommation des fourmis se réalisent aux endroits les plus chauds où les fourmis trouvent une grande abondance de substrats pour faire leur nid. Chez les fourmis qui font des monticules, ces conditions se réalisent à des sites non boisés, à faible altitude. Chez les fourmis qui vivent dans les troncs morts, ces conditions prévalent dans les terres basses ou sur les adrets où elle trouvent en abondance des débris de bois bien décomposés de diamètre important en milieu forestier ouvert. Les Grizzlis choisissent de préférence les troncs moyennement décomposés de 4–5 dm de diamètre au milieu. Les fourmis risquent de devenir une nourriture plus abondante chez les Grizzlis de Yellowstone quand les sources de leurs aliments actuels seront épuisées, à cause de la maladie ou du réchauffement du climat local.

[Traduit par la Rédaction]

Introduction

Consumption of ants (Hymenoptera: Formicidae) by bears (Carnivora: Ursidae) occurs worldwide, although there is much variation in amounts consumed among and within ursine species. Sloth bears (*Melursus ursinus*) at times consume little else but termites and ants (Joshi et al. 1997), whereas polar bears (*Ursus maritimus*) apparently consume none (Mattson 1998). Among other bears of northern latitudes, Asiatic and American black bears (*Ursus thibetanus* and *Ursus americanus*, respectively) and European brown bears (*Ursus arctos arctos*) at latitudes above 55°N consume

the greatest volumes of ants (Elgmork and Kaasa 1992; Mattson 1998; Swenson et al. 1999). Brown or grizzly bears (*Ursus arctos horribilis*) in arctic and interior boreal regions of Asia and North America consume the fewest (Mattson 1998).

Grizzly bears in the interior Yellowstone region of the western United States of America (U.S.A.) sometimes consume substantial volumes of ants during hot dry years (Mattson et al. 1991). However, in contrast to northern Scandinavia (Elgmork and Kaasa 1992; Swenson et al. 1999) or Minnesota, U.S.A. (Noyce et al. 1997), it is unlikely that ants are a major source of energy. Whitebark pine (*Pinus albicaulis*) seeds and tissue from elk (*Cervus elaphus*) and bison (*Bos bison*) have been the sources of most energy and nutrients in recent decades (Mattson 1997a; Jacoby et al. 1999; Mattson et al. 2001). Even so, ants might augment diet protein at critical times (Eagle and Pelton 1981) and may become a more important source of energy to Yellowstone's grizzly bears as the global climate warms (Mattson 2000).

In this paper I present a detailed description of factors associated with consumption of ants by Yellowstone's grizzly bears. I aspire to explain important features of myrmeco-

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phagy by this population, thereby providing a sound basis for management of habitat features affecting grizzly bear consumption of ants. My analysis focuses on answering the following questions: (1) How important are ants as a source of energy and nutrients to grizzly bears in this region? (2) How is consumption of ants affected by weather and availability of known high-quality foods? (3) What types of ants and ant nests are selected? (4) What site and vegetation features are associated with greatest probabilities and intensities of ant consumption? (5) What kinds of mounds or coarse woody debris are associated with ant consumption?

In relation to this, I designed the analysis partly to test the following expectations derived from previous research: (i) Ants were consumed by Yellowstone's grizzly bears as a source of either energy or protein. Peak consumption of ants during midsummer, when pupae and alates were presumably most abundant in ant nests, would be consistent with orientation towards energy (Redford and Dorea 1984; Noyce et al. 1997), whereas peak consumption during the seasonal nadir of diet protein (Eagle and Pelton 1981; Swenson et al. 1999) or during years when other sources of protein were scarce would be consistent with orientation towards amino acids. (ii) Annually, consumption of ants was greatest following warm springs (Noyce et al. 1997). (iii) Larger ants either were (Ogborn 1990; Johnson 1996) or were not (Noyce et al. 1997; Swenson et al. 1999) preferentially selected. (iv) Ants in thatch mounds and coarse woody debris were consumed proportionally more often in spring and after midsummer, respectively (Elgmork et al. 1978; Swenson et al. 1999). (v) Large-diameter moderately decomposed coarse woody debris was selected by bears excavating ants (Johnson 1996).

I found no basis in previous research for expectations regarding the effects of site features and vegetation structure on consumption of ants by bears, although by first principles, the amount, size, and degree of decomposition of coarse woody debris, live and dead forest overstory basal area, and slope, aspect, and elevation all likely had an effect.

I used data collected during a field study of free-ranging radio-marked Yellowstone grizzly bears from 1977 to 1992 to address these questions and expectations. For some questions (2, 4, and 5) there were ample relevant data with bias subject to statistical control. For other questions (1 and 3) the data were weaker, typically because of uncontrollable bias. The design of this study was not adequate for testing formal hypotheses. However, it was adequate for determining patterns of use and whether these patterns were consistent with the results of previous research, thereby supporting or failing to support particular expectations.

Study area

The approximately 23 000-km² study area corresponded to the known range of Yellowstone's grizzly bear population, extending south–north from latitude 43°30' to 45°15'N and east–west from longitude 109°30' to 111°30'W. Most of the area occupied by grizzly bears was above 2100 m elevation and consisted of remote mountains and plateaus surrounded by valleys and plains more intensively settled or used by humans. Annual temperatures averaged

about 0°C. Precipitation varied in amount and timing with elevation and geographic location, being drier to the north and east and exhibiting an April–June peak to the north and an October–February peak to the south (Dirks and Martner 1982). Most precipitation fell as snow, with winter accumulations reaching 20–260 cm before it melted during March–June, depending primarily on elevation and latitude.

Most (~75%) of the study area was forested and most of this forest was dominated by lodgepole pine (*Pinus contorta*; Despain 1990). Whitebark pine was abundant only above 2500 m elevation. Alpine areas were most common in the eastern one-third of the study area, above 3050 m. Other non-forested areas consisted of wet meadows at mid-elevations and, particularly in the northern one-quarter of the study area, extensive grass- and shrub-lands characterized by Idaho fescue (*Festuca idahoensis*), mountain sagebrush (*Artemisia tridentata vaseyana*), and bluebunch wheatgrass (*Agropyron spicatum*) at low elevations (<2250 m). Forest structure varied considerably during the study, primarily because of tree mortality due to fire and epidemic populations of mountain pine beetle (*Dendroctonus ponderosae*; Despain 1990). The largest fire occurred in 1988 and burned approximately 560 000 ha.

Ungulates were abundant in most of the study area. There were about 45 000 elk and 2000 bison in or near Yellowstone National Park (Singer 1991). Major increases in elk and bison populations occurred during the study. Mule deer (*Odocoileus hemionus*) and moose (*Alces alces*) were also common at lower and higher elevations, respectively. Knight and Eberhardt (1985), Mattson et al. (1991), Blanchard and Knight (1991), and Craighead et al. (1995) described aspects of the study area in greater detail.

Methods

Grizzly bears were trapped, marked, and radio-relocated according to methods described by Knight and Eberhardt (1985) and Blanchard and Knight (1991). As in other studies of this nature, efforts were made to trap representatively (by area and less so by sex and age), but differences among animals in susceptibility to capture, together with administrative and logistical constraints on access, precluded a random sample. All radio-relocations used in this analysis were made from fixed-wing aircraft and recorded according to their universal transverse mercator (UTM) coordinates. Relocations were made at approximately 4-day intervals.

Site visits and measurements

Field crews visited and described some of the aerial-telemetry locations. Selection of locations to visit was not random, primarily because of logistical constraints. Most of the study area was without roads, and use of helicopters was either administratively prohibited or prohibitively expensive. Ground sampling consequently emphasized equal representation of different areas and classes of bears as well as visits to as many telemetry locations as possible. Field crews also described every instance of grizzly bear feeding or bedding sign encountered en route to and from telemetry locations.

Feeding sign attributable to black bears by the presence of diagnostic hairs or tracks was either not described or was identified as such. Even so, the remainder of documented feeding sign not associated with telemetry locations of radio-marked grizzly bears probably included some that was attributable to black bears. We assumed that this fraction was small, based on analysis of hairs that were collected from 100 bear beds in 1979 under the sampling protocols used for documenting consumption of ants.² Of the collected hairs, 70% were from grizzly bears and 17% from black bears. The remainder were from non-ursid species.

²H.D. Picton and R.R. Knight. 1980. Obtaining biological information from grizzly bear (*Ursus arctos horribilis*) hair. Paper presented at the Northwest Section, Wildlife Society, April 8–10, 1980, Banff, Alberta.

Each telemetry location or feeding site was described according to protocols in Mattson (1991, 2000). Elevation (m), aspect (deg.), and slope (deg.) were recorded. Field crews also located variable-radius forest-inventory plots at the center of grizzly bear activity or, in the absence of bear sign, at a randomly selected distance (≤ 10 m) and direction from the recorded radiotelemetry UTM coordinate. All trees in the plot were identified to species, whether dead or alive, and the diameter of each was measured at 1.4 m above ground. Additional information on vegetation structure was recorded within about 10 m of plot center in a 314-m² area. This information included three indices and one measure of coarse woody debris (amount: 1–7 (none to heavy); size: 1–7 (small to large); decomposition: 1–6 (solid to well decomposed; Talbot 1934); and percent cover), Fischer's (1981) classification of size and volume of woody debris, and estimated percent cover of forbs, graminoids, shrubs, and overstory trees (>1.4 m tall). Based on double sampling, indices of size and amount were related to total volume of woody debris (kg·m⁻²) as follows: total volume = $-0.0008 + 0.7638 \ln(\text{amount} \times \text{size})$ (Mattson 1997b). I worked closely with all field personnel who used subjective descriptors between 1984 and 1992, and I was able to standardize their application (i.e., achieve consistent convergence of estimates) through regular field exercises.

Field crews described all grizzly bear sign found at or en route to or from telemetry locations. Sign that was spatially contiguous, often being part of what appeared to be a single foraging bout, was included in these descriptions and ascribed to a specific location if the sign was within about 200 m of the specified UTM coordinates. During 1986–1992, excavations for ants in logs and thatch or earthen mounds were measured. For logs, diameter at midpoint of the log, average diameter of the log where it was torn by the bear (A), total tear length (B), and average tear width as a percentage of total log circumference (C) were measured. For mounds, length (A_1) and width (A_2) of the base, estimated height before excavation (B), and estimated percentage of total mound volume excavated by the bear (C) were recorded. Total excavated volume was calculated as the product of $\pi(A/2)^2 \times B \times C$ for logs and $\frac{1}{3}\pi[(A_1 + A_2)/4]^2 \times B \times C$ for mounds (Elgmork and Unander 1998).

Field crews obtained additional measures at a subset of grizzly bear feeding sites between 1988 and 1992. At sites where a bear had excavated a log, midpoint diameter, species, and degree of decomposition of all unexcavated logs within 5 m were recorded. Where logs or mounds had been excavated, resistance to excavation was estimated by means of 2–10 applications of a clawometer to substrate deemed comparable to that used by the bear. The clawometer is a 5-tined potato fork shaped to resemble the claws of a grizzly bear. Field crews inserted the tines into a substrate and recorded the maximum resistance (kg) to disengagement on a gauge attached to a box-spring scale (Holcroft and Herrero 1984; Mattson 1997c). At feeding sites where grizzly bears had overturned rocks or woody debris in pursuit of ants, field crews estimated the mass (kg) of the overturned material.

Like Noyce et al. (1997), crews used a probabilistic field key to identify ants found in nests exploited by bears between 1986 and 1992. Total body length (mm), color of the head, thorax, and gaster, type of nest (in thatch or earthen mound, under rock, under woody debris, or in woody debris), elevation (m), and site were used to key specimens to leads that usually corresponded to more than one species. Species within these groups were further distinguished by notation indicating the commonness of each in the study area and their prior identification by ant taxonomists in feces (scats) and at feeding sites (see below).

Collections and identifications by the Wheelers

In 1979, under the auspices of this study, Drs. George and Jeanette Wheeler collected ants from 78 nests in the Yellowstone ecosystem. They noted the location and type of nest, identified the

species of ant, noted its length (mm) and other defining characteristics, and commented on the likely commonness of the species in the ecosystem, based on their experience and reference to other works (e.g., Gregg 1963; Wheeler and Wheeler 1963, 1982). The Wheelers also identified 81 specimens of ants collected by field crews from feeding sites as well as in 16 scats collected during 1979–1981. This information formed the basis of keys used for field identifications during 1986–1992.

Although the Wheelers collected ants in order to assemble a list of species for the region, I used their collection to identify tendencies in grizzly bears' selection of types of nests and sizes of ants. I did this by contrasting what the Wheelers had collected with what was found at grizzly bear feeding sites between 1986 and 1992. I took this approach in the absence of resources for more rigorously sampling the 23 000-km² ecosystem for availability of ants and their nests. I assumed that biases associated with estimating regional availability by extrapolation from small intensively sampled areas, as has been done elsewhere (cf. Ogborn 1990; Noyce et al. 1997; Swenson et al. 1999), were comparable in magnitude to those associated with using a regional survey to do the same.

Scat collection and composition

As with feeding sites, all scats thought or known to be from grizzly bears were collected by field crews at and en route to and from telemetry locations of radio-marked bears between 1977 and 1992. This concurrent collection maximized the comparability of information from scats and feeding sites. Scats were dried and analyzed for percent content according to methods described by Mattson et al. (1991). Results were reported by month and year as total frequency of occurrence in scats, percentage of total fecal volume, and mean percentage for scats in which the item occurred. Results are presented at the finest taxonomic resolution possible and summarized by broad taxonomic groupings that include mammals and fishes.

Data analysis

I used statistical regression models and information-based methods to specify vectors of covariates to explain grizzly bears' use of ants. Accordingly, I used maximum-likelihood methods for parameter estimation and the sample-size-adjusted version of Akaike's Information Criterion (AIC_c; Burnham and Anderson 1998) for model selection. Compared with unadjusted versions of AIC, AIC_c guards against overfitting models at small sample sizes. I used the change in AIC (Δ) associated with deleting independent variables, in turn, to judge the relative importance of each (Burnham and Anderson 1998). I also used Δ to represent the relative importance of variables grouped according to whether they were distal or proximal (see below) or represented different aggregate effects such as weather or vegetation structure. The Δ value obtained by deleting a group of variables is not equal to the sum of Δ values for individual constituent variables, in part because of covariances among them. I de-emphasized statistical hypothesis testing for reasons well stated elsewhere (e.g., Johnson 1999) and instead placed emphasis on developing models sufficient for statistical inference based on the assumption of conditional independence (Dawid 1979; Rosenbaum 1984; Holland 1986; Mattson 2000). I present P values solely as confirmatory information.

I used logistic regression analysis to specify the effects of independent variables based on the likelihood that a bear had or had not consumed ants at a given location. The units of analysis were radiotelemetry locations or feeding sites. For each activity (e.g., excavation of mounds or excavation of woody debris) I specified two models, one using only data from telemetry locations, including sites where no feeding sign was found, and the other using only data from sites with feeding sign but including plots not at telemetry locations. I gave priority to models of the first type and used models of the second type for confirming patterns. Given that

Table 1. Descriptions of habitat types and frequency of ant consumption by grizzly bears in each as a percentage of telemetry locations only, with or without feeding sign, and at sites with feeding sign only, Yellowstone region, 1977–1992.

		Frequency of ant consumption			
		No. of telemetry locations		No. of feeding sites	
Habitat type	Description	In or under logs	Mounds	In or under logs	Mounds
Nonforest types					
DRYMD	Dry meadows and grasslands; typified by <i>Agropyron spicatum</i>	1	3	5	11
LITHC	Rocky convex ridges; tundra; typified by <i>Festuca idahoensis</i> and <i>Poa alpina</i>	0	1	0	1
MESMD	Mesic meadows and grasslands; typified by <i>Geranium viscosissimum</i> , <i>Phleum alpinum</i> , and <i>Agropyron caninum</i>	6	7	6	10
WETMD	Marshes, fens, and wet meadows; typified by <i>Carex</i> spp., <i>Deschampsia cespitosa</i> , and <i>Calamagrostis canadensis</i>	3	0	5	6
Forest types					
DOPEN	Dry sites recently deforested by timber harvest or fire	8	1	18	6
HABLA	High-elevation subalpine fir (<i>Abies bifolia</i>) climax sites; typified by <i>Arnica</i> spp. and <i>Juniperus communis</i>	10	2	32	2
HPIAL	High-elevation forested sites with mature whitebark pine	8	0	13	1
HPSME	High-elevation Douglas-fir (<i>Pseudotsuga menziesii</i>) climax sites; typified by <i>Arnica cordifolia</i> , <i>Berberis repens</i> , <i>J. communis</i> , and <i>Symphoricarpos oreophilus</i>	11	3	28	10
HVASC	High-elevation sites with the ground layer dominated by grouse whortleberry (<i>Vaccinium scoparium</i>)	10	1	37	2
LPICO	Low-elevation lodgepole pine-dominated sites; typified by <i>Carex geyeri</i> , <i>Carex rossii</i> , <i>Calamagrostis rubescens</i> , and <i>Purshia tridentata</i>	13	0	28	8
MOPEN	Mesic–wet sites recently deforested by timber harvest or fire	9	2	17	6
LPIEN	Low-elevation Engelmann spruce (<i>Picea engelmannii</i>)-dominated sites; typified by <i>C. canadensis</i> , <i>Equisetum arvense</i> , and <i>Galium trifolium</i>	13	0	42	1
MABLA	Mesic–wet subalpine fir climax sites; typified by <i>Thalictrum occidentale</i> and <i>Osmorhiza chilensis</i>	13	1	37	2
MPSME	Mesic Douglas-fir climax sites; typified by <i>Symphoricarpos albus</i> , <i>Spirea betulifolia</i> , and <i>C. rubescens</i>	35	1	49	6

a specific type of activity had occurred, I used multiple linear regression to specify the effects of independent variables on the level of that activity (e.g., total volume of excavated material). In this way I analyzed the effects of various factors on grizzly bear activities at two hierarchical levels: (1) the likelihood that an activity would occur and (2), given that it had occurred, its level. This implied a hierarchy of choice by bears regarding whether or not they would engage in an activity and, if they did, how intensively and for how long.

I specified models using explanatory factors likely to be operational at broad temporal and spatial scales (distal factors) and at the scale of the immediate site (314 m²; proximal factors). Some level of choice by bears likely occurred at broad scales, i.e., a bear may have chosen to be at specific place at a specific time, engendering certain feeding opportunities because of coarse vegetation and weather patterns. Conversely, a bear may have chosen to engage in an activity solely on the basis of proximal conditions. The presence of distal factors in a best model therefore implied choice by bears sensitive to broad-scale features of their environment. The presence of proximal factors implied choice that was sensitive to more immediate features. This approach approximates Johnson's (1980) concept of hierarchical habitat selection and follows Salmon's (1970) philosophy of statistical explanation and relevance.

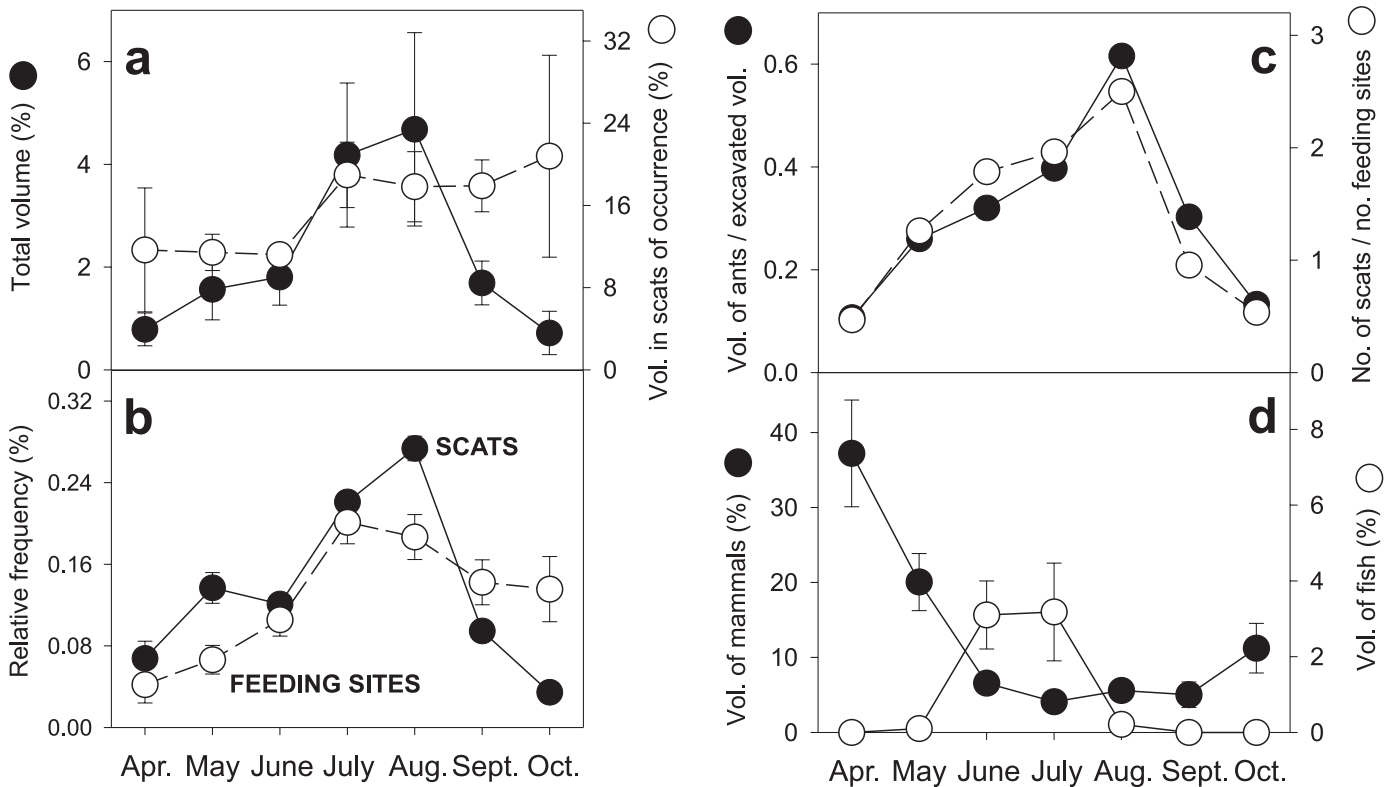
Proximal factors were measured, as described above, at sites with bear sign or where a bear had otherwise been located by radio-

telemetry. Distal factors were enumerated from other sources. Numbers of bison and elk were taken from annual counts in the ecosystem; numbers of whitebark pine cones were averaged from annual counts at fixed transects throughout the study area; and monthly temperatures (°C) and precipitation (cm) were taken from regional summaries published by the U.S. National Oceanic and Atmospheric Administration. Mattson (2000) provided a more detailed description of these distal factors and their sources.

Broad habitat conditions, as well as sites analyzed for bear activity, were described in terms of 14 habitat types (Table 1). These types were aggregations of fine-resolution syntaxonomic units described by Mueggler and Stewart (1980) and Steele et al. (1983) for the study area. Aggregation was by clustering on the basis of similarities in documented bear activity and by similarities of site and vegetation conditions. Mattson et al. (1999) described these habitat types and their derivation in greater detail.

The extent of habitat types (HTs) in each bear management unit (BMU) was obtained by GIS analysis of regionwide HT maps. I emphasized several HTs in the analysis: mesic non-forest (MESIC) and mesic Douglas-fir (*Pseudotsuga menziesii*) climax (MSPME) because of the concentration of ant feeding activity within them (Table 1); the dry, recently burned or harvested forest (DOPEN) because of its identification with the effects of extensive wildfires during 1988; and bison winter range (BIS) and habitats containing mature whitebark pine (HPIAL) because of their identification with

Fig. 1. Monthly diet and activity related to myrmecophagy by Yellowstone grizzly bears in 1977–1992. (a) Content of ants as a percentage (mean \pm 1 SE) of total fecal volume and as an average percentage of individual scats in which ants were detected. (b) Relative frequency of ants in scats and at all sites with feeding sign. (c) Ratio of total volume of ants in scats to total volumes excavated by bears in pursuit of ants and ratio of the total number of scats containing ants to the total number of feeding sites where ants were pursued. (d) Volume of mammals and fish as an average percentage of total fecal volume.



availability of alternative high-quality foods. I used BMUs to frame the effects of regional availability of HTs because of their correspondence in size to female grizzly bears' life ranges and because of the fidelity of most females to individual BMUs (Mattson 1997c; Mattson 2000).

Results

Grizzly bear activity and vegetation and site conditions were documented at 1853 telemetry locations attributable to 140 radio-marked bears between 1977 and 1992. The median number of locations per bear was 8 and the upper and lower limits of the 1st and 3rd quartiles were 3 and 19 locations, respectively. The total number of sites with feeding sign was 2769, including 1744 sites not associated with telemetry locations. A total of 6662 feces were collected and analyzed during the same period. Fewer observations were used to derive models (see below) because data for some independent variables were missing.

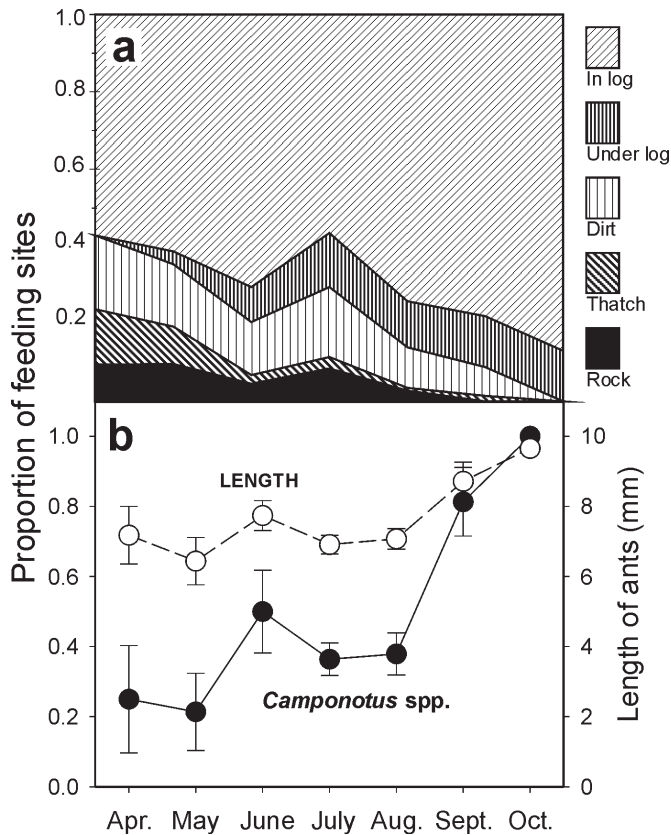
Seasonal patterns of use

Peak consumption of ants by Yellowstone's grizzly bears coincided monthly with maximum reward for effort expended and with least relative volumes of mammals and fish in scats. Averaging data for 1977–1992, ants constituted peak fractions of fecal material and occurred most often in scats during July and August (4.2 and 4.7% and 22 and 27%, respectively; Figs. 1a and 1b). During one singular year (1977) ants comprised 28 and 35% of total fecal vol-

umes during July and August, respectively. Ant consumption peaked in frequency at feeding sites during July–October, and composed 14–20% of all detected activity during this period (Fig. 1b). Considering only scats where ant remains were detected, volumes also peaked (18–21%) during July–October (Fig. 1a). I calculated the ratio of the total volume of ants in fecal material to the total volume of nest material excavated by bears, and the ratio of the total number of scats with ants in them to the total number of feeding sites where consumption of ants was detected, to indicate the monthly level of reward obtained by bears from foraging on ants. By this reckoning, reward was the amount of ants obtained relative to the amount of effort expended as indicated by the volume of excavated material or the number of searches. Both indices strongly peaked in August and were comparatively high during June and July (Fig. 1c). Relative volumes of proteinaceous foods (mammals and fish) in grizzly bear scats were lowest during August and September in areas where fish were available, and during June–September elsewhere (Fig. 1d).

The type of ant nest exploited by bears varied by month ($n = 530$, goodness of fit, $G^2 = 0.00$, $df = 6$, $P = 1.00$; Fig. 2a). Use of nests under rocks and in thatch and earthen mounds peaked in April, reached a secondary peak in July, and declined to none by October, commensurate with a steady monthly increase in exploitation of nests in and under logs. Use of the typically log-dwelling genus *Camponotus* correspondingly increased ($n = 231$, goodness of fit, $G^2 = 0.00$, $df = 1$, $P = 0.98$), along with minor increases in overall

Fig. 2. (a) Proportions of different types of ant nests exploited. (b) Lengths of ants (mean \pm 1 SE) consumed by Yellowstone grizzly bears and proportion of feeding sites where ants of the genus *Camponotus* were found, by month, in 1986–1992.



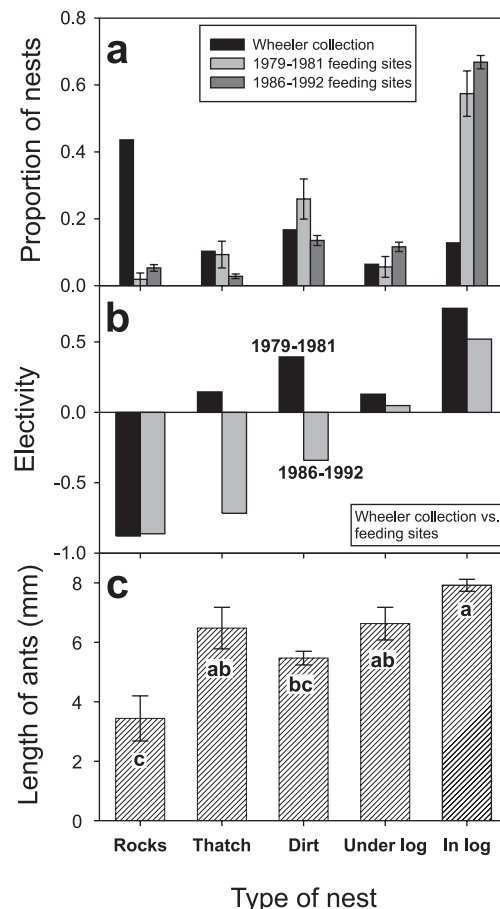
length of exploited ants ($n = 232$, $r^2 = 0.052$, $F_{[6,225]} = 2.1$, $P = 0.059$), especially during September and October (Fig. 2b).

Selection of nests, ant size, and use of ant taxa

In contrast to the Wheelers' findings, during 1986–1992 Yellowstone's grizzly bears exploited nests in logs much more often than nests under rocks and in thatch mounds (67 vs. 13% and 8 vs. 54% of observed nests, respectively; Figs. 3a and 3b). They also exploited ants >8 mm long much more often (46 vs. 8% of collections) and exploited ants ≤ 6 mm long much less often (37 vs. 73% of collections). Patterns of nest use by bears during 1986–1992 did not differ appreciably from patterns of use during 1979–1981 (Fig. 3a), when the Wheelers identified ant species collected in scats and at feeding sites. Lengths of ants collected at grizzly bear feeding sites differed substantially among nest types ($n = 232$, $r^2 = 0.22$, $F_{[4,227]} = 16.2$, $P < 0.001$). Ants in logs and thatch mounds were longest, whereas ants under rocks were shortest (Fig. 3c). Conversely, there was little difference in resistance to excavation (kg) among nest types ($n = 73$, $r^2 = 0.068$, $F_{[3,69]} = 1.7$, $P = 0.178$). Overall, thatch mounds excavated by bears were larger than excavated earthen mounds (MANOVA Wilks' $\lambda = 0.95$, $df = 2,200$, $P = 0.004$). The base of each type was 7.8 ± 1.4 (mean \pm 1 SE) and 5.2 ± 0.2 dm, respectively, and the height of each was 1.8 ± 0.2 and 1.4 ± 0.04 dm, respectively.

Most of the ants identified during 1979–1981 and 1986–1992 belonged to 8 of a total 24 species groups. The most

Fig. 3. Features of nests from which ants were collected during 1979 and exploited by Yellowstone grizzly bears in 1979–1992. (a) Proportional distribution of collections by G. and J. Wheeler and of feeding by bears during 1979–1981 and 1986–1992 among nest types. (b) Electivity of use (Vanderploeg and Scavia 1979), comparing the Wheeler collections from 1979 with grizzly bear exploitation in 1979–1981 and 1986–1992. (c) Lengths of ants (mean \pm 1 SE) collected from nests exploited by grizzly bears. Means with the same letters do not differ significantly by the Tukey–Kramer multiple-comparisons test at $\alpha = 0.05$.



commonly identified group during both periods was *Camponotus modoc/herculeanus* (30 and 37% of the total of 81 and 224 identifications for 1979–1981 and 1986–1992, respectively). This group, together with *Formica occulta/argentea* (12 and 13%), *F. oreas/subnuda* (10 and 12%), *F. neorufibarbis* (15 and 9%), *F. subsericea/densiventris* (5 and 8%), *Lasius sitkaensis/F. densiventris* (3 and 5%), *F. haemorrhoidalis* (3 and 3%), and *F. altipetens* (5 and 2%), composed 81 and 92% of all identifications for 1979–1981 and 1986–1992, respectively. Among nest types, *F. haemorrhoidalis* and *F. oreas/subnuda* together accounted for 67% of all ants identified in exploited thatch mounds; *F. occulta/argentea* for 58% of all ants identified in earthen mounds; *C. modoc/herculeanus* for 56% of all ants identified in logs; *F. subsericea/densiventris* and *F. oreas/subnuda* together for 57% of all ants identified under logs; and *Tapinoma sessile* for 50% of all ants identified under rocks.

Effects on probability of ant consumption

The probability that Yellowstone grizzly bears consumed

Table 2. Logistic regression models of the logit-transformed probability that ants nesting in or under woody debris were consumed by Yellowstone grizzly bears between 1977 and 1992 for telemetry locations only, with or without feeding sign, and at sites with feeding sign only.

Independent variable	Telemetry locations only			Feeding sites only		
	β	SE	Δ	β	SE	Δ
Constant	17.7	8.9		8.5	3.7	
Proximal factors						
Amount of woody debris (index)	4.7 ^a	1.5	11	1.5 ^b	0.3	23
Amount of woody debris (index)	-2.9	1.0	10	-0.031 ^c	0.010	7
Size of woody debris (index)	0.20	0.06	9	0.028 ^c	0.008	18
Decomposition of woody debris (index)	0.33 ^b	0.14	4	0.44 ^b	0.14	8
Total basal area (m ² ·ha ⁻¹)	0.85 ^b	0.29	7	0.89 ^b	0.24	11
Total basal area (m ² ·ha ⁻¹)	-0.25 ^a	0.07	10	-0.031 ^a	0.010	20
Elevation (m)	-3.8 ^b	1.1	10	-0.0027	0.0004	43
Aspect (deg. from N)	0.0060	0.0017	12	0.000016 ^c	0.000008	3
Slope (deg.)				-0.073	0.022	9
Slope (deg.)				0.93 ^b	0.24	15
Distal factors						
No. of whitebark pine cones						
Previous year	-0.00085 ^c	0.00019	24	-0.00057 ^c	0.00015	16
Current year	-0.26 ^b	0.10	5			
Number of bison	-0.00081	0.00021	14	-1.9 ^b	0.4	20
Avg. monthly temperature (°C)	0.0060 ^c	0.0011	29	0.0055 ^c	0.0010	33
Julian date	2.0 ^b	0.4	25	1.4 ^b	0.4	14
MESIC HT (% of BMU)	-0.0023 ^c	0.0011	3			
LPICO HT (% of BMU)	0.0023 ^c	0.0012	2	0.24 ^b	0.09	4
DOPEN HT (% of BMU)				-0.036	0.010	11
Statistics						
G^2 (df)	861 (1 × 10 ³)			1079 (2 × 10 ³)		
P	1.00			1.00		
R^2_L	0.58			0.58		
n	1496			1877		

Note: β is an estimated parameter and Δ is the change in AIC with deletion of the corresponding variable. Several variables appear twice in models as polynomials. Transformations of second terms in these polynomials are indicated. HT, habitat type.

^aCoefficient is for data transformed by $\ln(x + 1)^2$.

^bCoefficient is for data transformed by $\ln(x + 1)$.

^cCoefficient is for data transformed by $(x + 0.5)^2$.

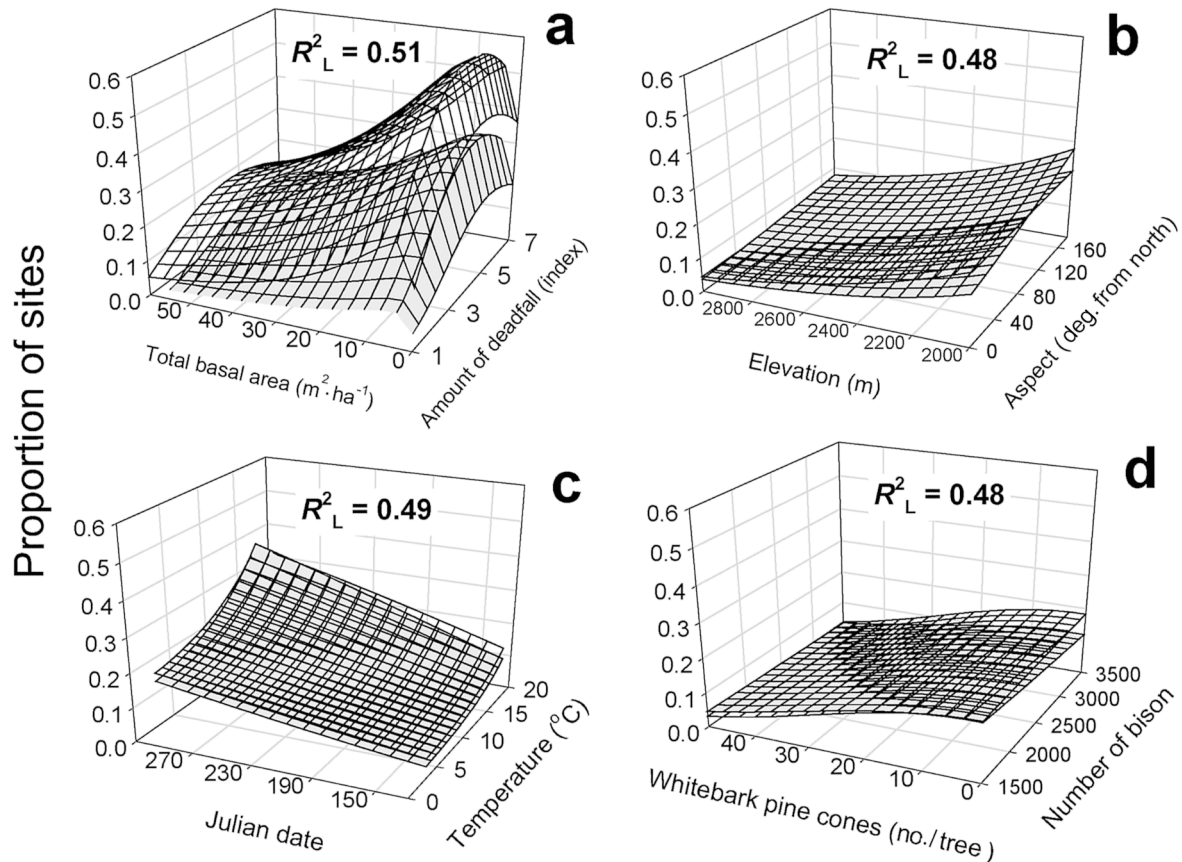
ants from nests in and under logs was affected by 13 factors considered in this analysis (Table 2). Overall, distal and proximal factors were of about equal importance for the model, based on telemetry locations only ($\Delta = 116$ vs. $\Delta = 119$). Factors representing vegetation structure (total basal area (a polynomial) and size, decomposition, and amount (a polynomial) of woody debris) had the greatest effect ($\Delta = 92$), factors representing average monthly temperature and Julian date had the second greatest effect ($\Delta = 63$), factors representing annual abundance of high-quality foods (numbers of bison and whitebark pine seeds during the current and previous years) had the third greatest effect ($\Delta = 35$), and factors representing the extent of habitat types (MESIC and LPICO) had the least effect ($\Delta = 21$).

The probability that bears consumed ants from logs peaked where there was minimal forest overstory (<10 m²·ha⁻¹) and yet substantial amounts of deadfall (Fig. 4a). Odds in favor of ant consumption also increased with size and decomposition of woody debris (Table 2). Probability of use increased on south-facing sites and at lower elevations (Fig. 4b), as well as during the warmest months (average >15°C) of the

study and late in the bears' non-denning season (Fig. 4c). Consumption of ants in or under logs was least likely during years when the bison population was largest and (or) during and following years when large pine-seed crops were available and being exploited by bears (Table 2, Fig. 4d).

The probability that bears consumed ants from nests in thatch and earthen mounds combined at a telemetry location was affected by 6 factors considered in this analysis (Table 3). Proximal factors had more effect than distal ones ($\Delta = 41$ vs. $\Delta = 32$). Of the factors, those associated with abundance of high-quality foods (extent of bison winter range and HPIAL) had the greatest effect ($\Delta = 21$), vegetation structure (i.e., overstory basal area) had the second greatest effect ($\Delta = 17$), physical site features (elevation and aspect) had the third greatest effect ($\Delta = 14$), and average monthly temperature had the least effect ($\Delta = 12$). Probability of consumption was highest where there was no forest cover, and was quite low elsewhere (Fig. 5c). As with logs, use of ants from mounds was more likely at lower elevations and during the warmest months of the study, when average temperatures exceeded 12°C (Figs. 5a and 5b).

Fig. 4. Probability that ants from woody debris were exploited at a site by Yellowstone grizzly bears in 1977–1992 relative to the total basal area of the forest overstory and amount of coarse woody debris (*a*), elevation and aspect, translated into number of degrees from north (*b*), regional average monthly temperature and Julian date (*c*), and annual numbers of bison in the region and cones produced on whitebark pine transects the previous year (*d*). Shaded mesh surfaces show relationships using only telemetry locations of radio-marked bears. Open mesh surfaces show relationships using only sites with feeding sign, including sites not associated with radio-marked bears. Statistics are given for the relationships based on telemetry locations only.



Effects on intensity of exploitation at a feeding site

Among exploited logs, total volume of excavations at a feeding site ($TVOL_L$ in dm^3) was primarily positively related to the average size of coarse woody debris (SZWD; $\Delta = 2.9$) and secondarily related to a polynomial of average monthly temperature (TEMP in $^{\circ}C$; $\Delta = 1.1$):

$$(TVOL_L + 0.5)^{0.5} = 13.3 + 0.100SZWD - 1.63TEMP + 0.079TEMP^2 \quad (n = 277, R^2 = 0.074, F_{[3,273]} = 7.3, P < 0.000)$$

The total number of logs excavated or rolled at a feeding site ($TNUM_L$) was primarily positively related to percent cover of coarse woody debris (PWD; $\Delta = 2.5$) and secondarily related to total amount of winter (November–March) precipitation (WPPT in cm; $\Delta = 0.2$):

$$\ln(TNUM_L + 1) = -0.155 + 0.120\ln(PWD + 1) + 0.245\ln(PWD + 1) \quad (n = 281, R^2 = 0.058, F_{[2,278]} = 8.5, P = 0.000)$$

Among mounds, the total volume of excavations at a feeding site ($TVOL_M$ in dm^3) was related to a polynomial of elevation (ELEV in m; $\Delta = 1.3$), peaking at low and high elevations:

$$TVOL_M = 5577 - 1.52ELEV + 0.00010ELEV^2 \quad (n = 76, R^2 = 0.156, F_{[2,73]} = 6.8, P = 0.002)$$

The total number of excavated mounds ($TNUM_M$) exhibited a similar relationship to elevation ($\Delta = 4.1$) and was greatest on sites without forest cover (i.e., overstory basal area, TBA in $m^2 \cdot ha^{-1}$; $\Delta = 0.2$):

$$TNUM_M = 365 - 0.777\ln(TBA + 1) - 0.098ELEV + 0.0000066ELEV^2 \quad (n = 83, R^2 = 0.240, F_{[3,79]} = 8.3, P < 0.000)$$

Effects on use of individual logs and mounds

Among logs selected for use by bears and all other logs within a 5 m radius, the logs most likely to be excavated by bears ($p_{\text{excavated}}$) were intermediate in diameter at midpoint (DIAMD, as a polynomial, in dm; $\Delta = 14.6$) and decomposition was generally advanced but not complete (DCMP, as a polynomial; $\Delta = 101$):

$$\text{logit}(p_{\text{excavated}}) = -15.8 + 7.17\ln(\text{DIAMD} + 1) - 2.29[\ln(\text{DIAMD} + 1)]^2 + 12.5\ln(\text{DCMP} + 1) - 3.33[\ln(\text{DCMP} + 1)]^2 \quad (n = 462, R_L^2 = 0.25, \text{goodness of fit}, G^2 = 211, \text{df} = 185, P = 1.00)$$

The first derivative with respect to midpoint diameter equaled 0 at 3.8 dm (Fig. 6a), corresponding to the diameter at which the odds in favor of use peaked.

When the diameters of excavated logs at their midpoint and at the point of excavation were compared (DIAEX in dm), the difference between the two measures (DIF) was related to a polynomial of midpoint diameter:

$$\text{DIF} = -1.70 + 1.36\text{DIAMD} - 0.197\text{DIAMD}^2 \quad (n = 109, R^2 = 0.61, F_{[2,106]} = 84, P < 0.000)$$

In other words, bears selected areas near the midpoint of small logs, areas increasingly farther towards the butt (large) end of midsized logs, and areas increasingly farther towards the small end of the largest logs they used. The first derivative with respect to midpoint diameter equaled 0 at 4.1 dm, corresponding to the size of log at which the greatest positive differential between selected and midpoint diameters occurred. DIF itself equaled 0 at 1.6 and 5.3 dm.

Volume excavated from individual logs (VOL_L in dm^3) was most strongly related to diameter of the log at the point of excavation ($\Delta = 31.5$) and secondarily positively related to the degree of decomposition ($\Delta = 1.4$):

$$\text{VOL}_L = -10.4 + 2.84\text{DIAEX}^2 + 0.991\text{DCMP}^2 \quad (n = 200, R^2 = 0.35, F_{[2,197]} = 53, P < 0.000)$$

Resistance to excavation (RESIST in kg) in excavated logs was negatively related to the degree of decomposition:

$$\ln(\text{RESIST} + 1) = 3.90 - 0.434\text{DCMP} \quad (n = 14, r^2 = 0.44, F_{[1,12]} = 9.7, P = 0.009)$$

When logs that were rolled by bears were compared with those that were excavated, the logs most likely to be rolled were smaller in diameter at midpoint ($\Delta = 224$) and located in areas where the overstory basal area was smaller ($\Delta = 12.5$) (Fig. 6b):

$$\text{logit}(p_{\text{rolled}}) = 7.26 - 6.27\ln(\text{DIAMD} + 1) + 0.00003\text{TBA}^2 - 0.452\ln(\text{TBA} + 1) \quad (n = 362, R_L^2 = 0.52, \text{goodness of fit}, G^2 = 150, \text{df} = 214, P = 1.00)$$

Volume excavated from a single mound (VOL_M) was most strongly related to height (HGT in dm) and length of the base (BASE in dm) ($\Delta = 10.4$ and $\Delta = 41.0$, respectively). Excavated volume was secondarily positively related to amount of forest overstory basal area ($\Delta = 6.0$):

$$\ln(\text{VOL}_M + 1) = -1.40 + 1.26\ln(\text{BASE} + 1) + 0.446\text{HGT} + 0.113\ln(\text{TBA} + 1) \quad (n = 202, R^2 = 0.69, F_{[3,198]} = 145, P < 0.000)$$

The size of mounds used by bears (SZMD) was positively related to total overstory basal area ($\Delta = 9.7$), orientation of the site towards the south (SOUTH in degrees from north; $\Delta = 1.9$), and a polynomial of elevation ($\Delta = 5.8$):

$$\ln(\text{SZMD} + 1) = -594 + 0.0136\text{TBA} + 0.210\ln(\text{SOUTH} + 1) - 0.0382\text{ELEV} + 88.3\ln(\text{ELEV} + 1) \quad (n = 177, R^2 = 0.24, F_{[4,172]} = 14.2, P < 0.000)$$

In other words, mounds selected for use by bears were largest under forest cover, on southerly aspects, and at low and high elevations.

Discussion

How important are ants to Yellowstone's grizzly bears?

Ants are potentially a major source of energy and protein for bears (Noyce et al. 1997; Swenson et al. 1999). Subtracting the N bound in chitin, there is about 34–54 and 27–56% crude protein and about 21 and 18 $\text{kJ}\cdot\text{g}^{-1}$ digestible energy in ants of the genera *Camponotus* and *Formica*, respectively (Ogborn 1990; Noyce et al. 1997; Swenson et al. 1999). Among common bear foods this protein and digestible energy content is consistently surpassed only by fish and some tissues of ungulates (Pritchard and Robbins 1990). Moreover, given average dry masses of *Camponotus* and

Formica spp. (6.7 and 1.3 mg, respectively; Brian 1978), average numbers of each type found in some bear scats (544 and 2008, respectively; Ogborn 1990) and likely daily defecation rates of bears during periods of peak ant consumption (4–7; Roth 1980), ants could provide 300–500 $\text{kJ}\cdot\text{d}^{-1}$ to a bear feeding exclusively on them. Based on figures in Swenson et al. (1999), even a single large mound could provide about 230 kJ of digested energy. These values represent a large fraction of daily maintenance costs (about 700 kJ) for a 70-kg bear whose diet contains 35% crude protein (Rode and Robbins 2000). This could be an optimistic appraisal, given that the digestive efficiency of bears may be impaired by the formic acid common in formicine ants.

Table 3. Logistic regression models of the logit-transformed probability that ants nesting in mounds were consumed by Yellowstone grizzly bears in 1977–1992 for telemetry locations only, with or without feeding sign, and at sites with feeding sign only.

Independent variable	Telemetry locations only			Feeding sites only		
	β	SE	Δ	β	SE	Δ
Constant	-2.3	1.7		-2.8	0.8	
Proximal factors						
Total basal area ($\text{m}^2 \cdot \text{ha}^{-1}$)	-0.16 ^a	0.04	17	-0.10 ^a	0.07	18
Elevation (m)	-0.0020	0.0007	6	-4.7 ^c $\times 10^{-7}$	1.1 $\times 10^{-7}$	45
Slope (deg.)	-0.41 ^b	0.19	3			
Distance to forest/non-forest edge (m)				-0.16 ^b	0.07	3
Abundance of elk thistle (<i>Cirsium scariosum</i>) (index)				0.84	0.38	2
Distal factors						
Avg. monthly temperature ($^{\circ}\text{C}$)	0.0073 ^c	0.0021	12	0.0045 ^c	0.0013	41
HPIAL (% of BMU)	1.1 ^b	0.4	7	0.75 ^b	0.21	11
Bison winter range (% of BMU)	0.10	0.04	5	0.36 ^b	0.12	9
Statistics						
G^2 (df)	283 (2×10^3)			701 (2×10^3)		
P	1.00			1.00		
R^2_L	0.87			0.77		
n	1586			2168		

Note: β is an estimated parameter and Δ is the change in AIC with deletion of the corresponding variable.

^aCoefficient is for data transformed by $\ln(x + 1)^2$.

^bCoefficient is for data transformed by $\ln(x + 1)$.

^cCoefficient is for data transformed by $(x + 0.5)^2$.

However, formic acid constitutes only 2–9% of formicine ants (Swenson et al. 1999) and the extent of this effect, if any, is unknown.

Although Yellowstone's grizzly bears frequently consumed ants during July and August, ants were almost certainly a minor source of energy compared with ungulate tissue and whitebark pine seeds. Ants were a substantially smaller fraction of the diet of Yellowstone's grizzly bears than of the diets of brown bears in northern Europe or black bears worldwide. Ants accounted for 20% of the annual intake of digested energy by brown bears in central Scandinavia, where they composed 12–16% of fecal volumes during spring and summer (Swenson et al. 1999). This compares with average fecal fractions of 4–5% during peak consumption by Yellowstone's bears.

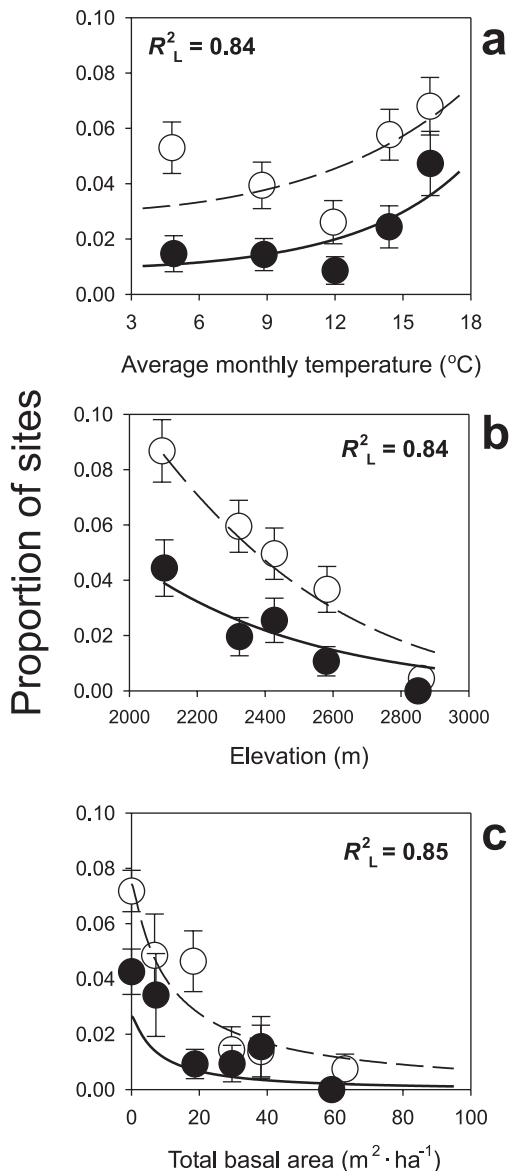
Even so, like many foods eaten by Yellowstone's grizzly bears, ants were probably an important source of energy for certain bears at certain times (Mattson et al. 1991) and an important seasonal source of protein during times of regionwide protein scarcity. Ants were a major source of energy for the population during midsummer in 1977, when ants composed >25% of total fecal volume. In addition, consumption of ants was negatively correlated seasonally with consumption of mammals and peaked when consumption of mammals and fish was at its annual nadir. Energy metabolism for maintenance increases sharply if the bears' diets contain <12–35% crude protein (Rode and Robbins 2000). Without ants, the late-summer diet of Yellowstone's grizzly bears would very likely have been at or below this level. If so, ants likely contributed to lowering the costs of maintenance for bears in this ecosystem by providing protein at a time of year when this nutrient was inherently scarce. Con-

versely, ants were almost certainly not a major source of early-season amino acids for lean growth, in contrast to what was probably the case for brown bears in Scandinavia and black bears in northern Minnesota (Noyce et al. 1997).

Although Yellowstone's ants may have provided much-needed protein, their consumption by grizzly bears in this region is also consistent with selection based on energy. The volumes of ants consumed relative to excavated volumes of material peaked during June–August. This general result was consistent with increases in the percent volume of ants in individual scats in July–October. Yellowstone's grizzly bears were apparently more successful at consuming ants from June onwards, especially during August, than in earlier months of the year. This suggests that the midsummer peak in ant consumption was accompanied, if not motivated, by greater energetic rewards. In any case, these results are consistent with a general midsummer peak in availability of vulnerable pupae and alates among most ant species in most types of nests (Scherba 1961; Sanders 1972; Noyce et al. 1997; Swenson et al. 1999).

However, few pupae or alates were recorded in feces collected during this study. This was probably not an artifact of more digestion of pre-adult than of adult ants. Swenson et al. (1999) provide evidence that digestibility differs little and digestible energy hardly at all between adults and pupae. It may be that pre-adult ants were difficult to distinguish. It also may be that, in agreement with observations by Onoyama (1988), Noyce et al. (1997), and Swenson et al. (1999), bears indeed ate few pre-adult forms of ants during most of this study. Nevertheless, conclusions regarding timing of peak consumption of ants by bears would not be contradicted. Even if undetected consumption of pupae and

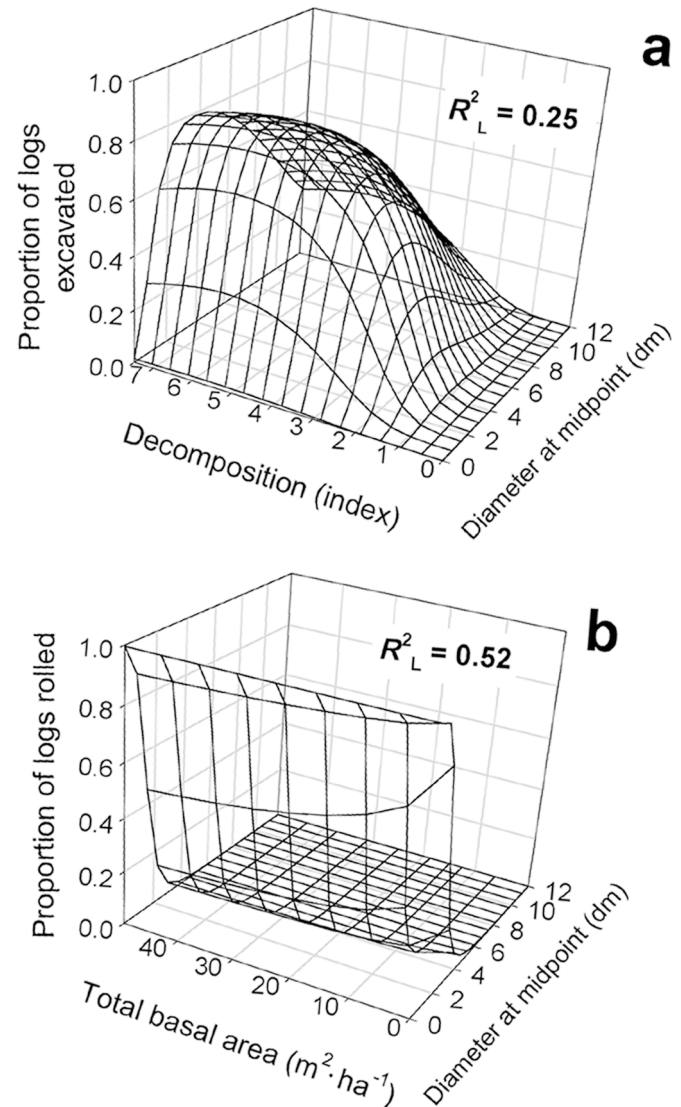
Fig. 5. Probability that ants from mounds were exploited at a site by Yellowstone grizzly bears in 1977–1992 relative to average regional monthly temperature (a), elevation (b), and total basal area of the forest overstory (c). Data are shown as the means and SE, based on quintiles or septiles of the data and are shown to illustrate goodness of fit. Solid lines and solid circles show relationships using only telemetry locations of radio-marked bears. Broken lines and open circles show relationships using only sites with feeding sign, including sites not associated with radio-marked bears. Statistics are given for the relationships based on telemetry locations only.



alates escalated during July and August, this would constitute even stronger evidence for a peak in energetic benefits of consuming ants during midsummer.

Regardless of the nutritional benefits, consumption of ants was important to Yellowstone's grizzly bears because of the frequency with which it occurred and the related indirect enhancement of fitness, especially among females. During certain times of year ants were consumed at about one-fifth of

Fig. 6. (a) Probability that among all options within a 5 m radius, a log was excavated by a bear relative to midpoint diameter and degree of decomposition of the log. (b) Probability that a log was rolled by a bear, as opposed to only excavated, considering logs exploited at all feeding sites, for Yellowstone grizzly bears in 1977–1992.



all sites where feeding sign was found. This high frequency of consumption was confirmed by the results of fecal analysis. Moreover, female grizzly bears that frequently consumed ants were more successful than other females at keeping cubs alive until the age of weaning, especially compared with females that consumed concentrated high-quality foods such as fish or ungulate carrion (Mattson 2000). This can be attributed to the dispersed nature of myrmecophagy and the associated lower likelihood of encountering adult bears that posed a lethal threat to cubs (Mattson 2000).

How do weather and other foods affect consumption of ants?

Ants were consumed less often when or where either whitebark pine seeds or bison were more abundant, which

suggests that ants were consumed by Yellowstone's grizzly bears partly to compensate for the reduced availability of high-quality foods. During and following years when large whitebark pine seed crops were produced and bears fed on little else (Mattson et al. 1991, 2001), they less often consumed ants that nested in and under woody debris. Similarly, ants from mounds were consumed less frequently in areas with the greatest numbers of mature whitebark pine trees. I offer no defensible speculation concerning why consumption of ants from mounds and woody debris was differentially sensitive to the spatial and temporal abundance of pine seeds, respectively.

Declines in consumption of ants in and under woody debris during increases in the bison population are consistent with bears eating ants for both protein and energy. Bison are an important source of both (Green et al. 1997; Mattson 1997a), and plausibly supplanted ants in the bears' diet as their numbers increased. However, grizzly bears were more likely to consume ants from mounds in areas where bison winter range was more, rather than less, extensive. It is not clear why consumption of ants from mounds was positively associated with bison range. Bison range did not mask the effects of other habitat features, such as the extent of various non-forested habitats, nor is there a documented positive connection between bison and ant abundances.

There was strong evidence that the likelihood of ant-eating by Yellowstone's grizzly bears peaked during the warmest months of this study, but no evidence that the likelihood of consumption was affected by precipitation level or spring temperatures. Likelihood of use escalated most noticeably when average regional temperatures exceeded 12–15°C. This is consistent with the production ecology of ants in temperate and boreal regions. At high latitudes the proliferation and maturation of ant populations are quite temperature-sensitive, increasing with ambient and nest temperatures (Brian 1978; Hölldobler and Wilson 1990). In general, the threshold of activity for boreal *Camponotus* species occurs at 7–10°C (litter temperature; Sanders 1972), whereas for temperate-zone *Myrmica* species, optimal nest temperatures are about 15–25°C (Elmes and Wardlaw 1983). Consistent with monthly trends, peak consumption of ants by Yellowstone's grizzly bears during the warmest months was probably caused by peak availability of ant biomass, especially in the form of pupae and alates.

What types of ants and nests are selected?

Yellowstone's grizzly bears seemed to prefer large ants and to eschew small ants that lived in small colonies. Compared with collections by taxonomists assembling a species list, Yellowstone's grizzly bears consumed large ants >8 mm in length much more often. Most of these large ants were of the genus *Camponotus*. Grizzly bears also consumed ants from within logs much more often and consumed ants from under stones much less often. The large number of samples collected from under stones by the Wheelers is consistent with general observations that most ant colonies, in fact, occur there (Hölldobler and Wilson 1990). The selection of nests by bears is also consistent with the association of the largest ants with logs and the smallest ants with stones. Moreover, populations found under stones tend to be

the smallest of any type of nest, especially in contrast to sizes of colonies found in thatch mounds (Brian 1978).

Because most of the largest ants consumed by Yellowstone's grizzly bears were of the genus *Camponotus*, it is possible that the apparent selection for large size was an artifact of selection for other characteristics typical of this genus. In fact, ants of the genus *Camponotus* probably contained more fat and less formic acid and fiber than ants of other genera common to the study area (Swenson et al. 1999). On the other hand, *Camponotus* spp. are generally fast-moving and aggressive (Johnson 1996) and tend to form smaller colonies than mound-dwelling species (Noyce et al. 1997). If Yellowstone's grizzly bears were, in fact, selecting *Camponotus* spp., then large individual size and high concentrations of digestible energy outweighed the disadvantages of small colony size and complicating behavioral responses.

The chronology of exploitation of nest types by Yellowstone's grizzly bears was consistent with that observed for bears elsewhere. Compared with ants in and under logs, ants in mounds and under stones were consumed proportionately more often earlier in the year, with consumption peaking during April and May. This held especially for ants in thatch mounds. Comparatively early use of mounds and stones was probably due to an earlier onset of ant activity in these nests and related earlier development and maturation of broods. Such accelerated phenology would have arisen from more favorable thermal characteristics of mounds and stones and the related ability of many mound-dwelling species to raise nest temperatures with metabolic heat, especially in contrast to log-dwelling *Camponotus* spp. (Brandt 1980; Coenen-Staß et al. 1980; Hölldobler and Wilson 1990). The strong early-season orientation towards thatch mounds might also have arisen partly from the fact that these mounds were the largest exploited by bears and, compared with ants in earthen mounds, were probably typified by a more pronounced migration of workers and brood from the periphery to the core as the summer progressed (Coenen-Staß et al. 1980; Elgmork and Unander 1998; Swenson et al. 1999).

What site and vegetation features are associated with myrmecophagy?

Yellowstone's grizzly bears selectively consumed ants from in and under logs where there was abundant substrate suitable for nests of log-dwelling ants, together with site and vegetation features that promoted nest warmth. Selection of sites with suitable nest substrate was evident in the association of ant consumption with abundant, large-diameter, well-decomposed woody debris. All of these features promote abundance of log-dwelling ants (Brian 1978; Harmon et al. 1986; Torgersen and Bull 1995). Selection of sites that promoted nest warmth was evident in the association of ant use with generally warmer ambient conditions (i.e., lower elevations) and (or) greater exposure of nests to incident radiation (i.e., southerly exposure and minimal forest overstory).

The extent of excavations by bears for wood-dwelling ants was more sensitive to the characteristics of woody debris than to site and overstory features. As might be expected, the total volume of excavations was related to the average size of woody debris, which is consistent with selection of larger logs by bears (see below), whereas the total number of

excavated logs was related to the total cover of debris. In summary, sites where advanced stand age, low-intensity crown fires, or high levels of insect-caused mortality led to the accumulation of abundant large-diameter decomposed woody debris under an open forest canopy were optimal for consumption of ants by bears, presumably because wood-dwelling ants were most abundant under these conditions.

Like ants in logs, ants in mounds were most likely consumed by Yellowstone's grizzly bears at warm, unshaded sites. In common with excavation of logs, this was indicated by an increasing likelihood of use with decreasing forest overstory or descending elevation. Unlike excavation of logs, the disassociation between forest cover and excavation of mounds by bears was probably due to the lack of dependence on input of coarse woody debris for nest material by mound-dwelling ants. I did not directly measure the abundance of ant mounds at all sites used by bears, but, in agreement with Gregg (1963), my general observation is that ant mounds were concentrated and otherwise most abundant in non-forested areas.

Like probability of use, the total extent and number of excavations in mounds at a site tended to be greatest in the open at low elevations. However, there was an exception to this general pattern: total volumes of excavations secondarily increased with elevation. This is plausibly explained by the fact that the volume excavated from a single mound was a function of the mound's original size, and mounds excavated by bears were largest at high and low, rather than intermediate, elevations in the study area. The reasons for this nonlinear elevational gradient in either size or size-related selection by bears are not known. Interestingly, bears excavated larger mounds in forests than in non-forested areas, partly because thatch mounds were used more commonly than earthen mounds in forests and thatch mounds were generally larger than earthen mounds (see above).

What type of log is selected for excavation?

When excavating for log-dwelling ants, Yellowstone's grizzly bears selected logs that were about 4–5 dm in diameter at midpoint and in which decay was at an advanced stage but not complete. The selection of partially decomposed logs is readily explained by the greater ease of digging in such a substrate than in logs that were completely sound or had a hard rind. The comparative avoidance of the most decomposed logs may have been due to the orientation of bears towards *Camponotus* spp., and the related greater concentration of this genus in sound or moderately decomposed logs than in logs in advanced stages of decay (Talbot 1934; Torgersen and Bull 1995).

Although logs 4–5 dm in diameter are large, they were not the largest available to foraging bears. These results thus temporize previous observations that ant-eating bears select the largest woody debris (Johnson 1996). It is unclear why Yellowstone's grizzly bears selected larger logs only up to a point. The explanation may, in part, be the same as that for early-season use of large thatched mounds. Log-dwelling ants and their brood are known to migrate from the periphery to the core of logs on a daily and seasonal basis in response to changes in temperature (Roces and Núñez 1995). With progression of the season and warming of log nests, ants may spend more of their time nearer the core or even

underground (Sanders 1970). Under these conditions, ants in the largest logs may be relatively unavailable to bears. The implicit benefit of larger colonies would be negated by greater difficulty of access to them. A possibly similar pattern was observed among grizzly bears scavenging on bison. Bears were most likely to scavenge mid-sized female bison rather than the largest males, probably because of greater difficulties in accessing and manipulating carcasses of the much larger and thicker hided bulls (Green et al. 1997).

Implications

Chronologically, optimal conditions for ant consumption by Yellowstone's bears from woody debris probably occur around 70–80 years after a major episode of tree mortality, reach a nadir around 100–150 years afterwards, and then become more common again. This is based on results presented here and common rates of snagfall (90% within 12–18 years; Lyon 1984; Harvey 1986; Mitchell and Preisler 1998), log decomposition (half-decomposed after about 60 years; Harmon et al. 1986), and accumulation of coarse woody debris (Romme 1982) in lodgepole pine forests. By this reasoning, conditions in the extensive forest areas burned during 1988 will not be optimal for consumption of ants by grizzly bears for another 60–70 years. Lodgepole pine stands that suffered major mortality from mountain pine beetles during the 1960s through mid-1980s should reach optimal conditions within 30–50 years.

These results suggest that harvesting forest stands will create optimal conditions for consumption of log-dwelling ants by grizzly bears within the subsequent 50–100 years only if large numbers of stems around 4–5 dm in diameter are left on the ground or left standing to fall on their own. In the nearer term, consumption of ants by bears may also be favored if the harvested stand contains large volumes of large-diameter woody debris ($>1.25 \text{ kg}\cdot\text{m}^{-2}$; Romme 1982; Mattson 1997b) that is left mostly intact during logging operations. Harvests and site treatments that remove all merchantable timber and break up and burn slash and preexisting woody debris threaten to reduce the prospects for consumption of ants by bears.

Ants are likely to become a more important source of energy and nutrients for Yellowstone's grizzly bears, with or without warming of the global climate. There are strong indications from this study that ant abundance and related consumption by bears increase with ambient temperature. Moreover, consumption of ants increases when few pine seeds are available. Whether or not climate warming directly forces an increase in consumption of ants, the likely loss of most whitebark pine in the region to the pathogen white pine blister rust (*Cronartium ribicola*; Mattson et al. 2001) alone will probably promote reliance on ants. Details concerning how the extent and structure of forests might change with climate warming are complex. However, even if forest cover declines, associated declines in log-dwelling ants are likely to be offset by increases in abundance and related use by bears of the mound-dwelling ants typical of grasslands and meadows. Regardless of our current prognoses, these results provide a basis for evaluating the effects of climate change on use of ants by Yellowstone's grizzly bears as regional projections of climate and forest conditions become more refined and defensible.

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