

## Consumption of Wasps and Bees by Yellowstone Grizzly Bears

### Abstract

I investigated the consumption of wasps and bees by grizzly bears in the Yellowstone region, 1977–1992, using data collected during a study of radio-marked bears. Although wasps and bees were not a major source of energy, Yellowstone grizzly bears are among only a few populations of their species in North America known to consume these insects in sometimes noteworthy amounts. Consumption of wasps and bees was greatest during the driest months of the study and during years when abundant ungulate carrion and few whitebark pine seeds were available. Peak consumption during dry years probably reflected increases in wasp and bee populations, whereas little consumption during years when pine seeds were abundant probably reflected a relative preference for pine seeds. The odds that bears would consume wasps and bees were greatest when they were in forest stands with abundant coarse woody debris and considerable live basal area. Excavation of ground nests also was most extensive in dense forest stands. All detected exploitation involved excavation of nests, almost all of which were located in or under logs and stumps or in duff near the base of trees. It is not clear if this pattern of exploitation reflected the distribution of wasps and bees, and, if so, why wasps and bees were concentrated in dense forests with abundant coarse woody debris. In short, Yellowstone grizzly bears apparently consumed wasps and bees most often when and where these insects were most abundant as well as when known high-quality bear foods were scarce.

### Introduction

Consumption of wasps and bees (Hymenoptera: Vespidae and Apidae) by bears has hitherto received little scientific attention. However, even a casual survey of published research reveals that wasps and bees are part of the diets of black bears (*Ursus americanus* or *U. thibetanus*) and brown bears (*U. arctos*) throughout the northern hemisphere. In North America, consumption of wasps and bees by brown bears is relatively uncommon compared to consumption of these insects by black bears. Consumption was detected in only 6 of 21 brown bear diet studies versus 20 of 24 black bear diet studies compiled by Mattson (1998). Even so, consumption of wasps and bees by brown bears has been observed throughout brown bear range, including studies as far north as the southern Yukon (Pearson 1975) and central Alaska (Murie 1981) and as far south as central Montana (Aune and Kasworm 1989) and northwestern Wyoming (Craighead et al. 1995).

Details in the scientific literature about consumption of wasps and bees by bears are limited to anecdote and entries in tables summarizing bear diets. It is unclear whether wasps and bees are ever an important bear food and, if so, under what circumstances. Where feeding behaviors associ-

ated with consumption of native wasps and bees have been described, bears excavated these insects from subterranean nests (Sharafutdinov and Korotkov 1976, Slobodyan 1976, Lloyd 1979, Russell et al. 1979, Murie 1981, Servheen 1983, Cincjak et al. 1987). In places like the Yellowstone region, at the current southern limit of North American brown bear range, most social ground-nesting species are wasps of the genus *Vespula*, most commonly *V. acadica*, *V. pensylvanica*, *V. vulgaris*, and *V. consobrina* (Evans 1970, Evans and Eberhard 1970, Akre et al. 1981). Unfortunately, little is known about ecological relations of these ground-nesting wasps, especially in boreal or high-elevation forested environments (Bohart and Bechtal 1957, Evans 1970, Evans and Eberhard 1970, Spradbery 1973, Akre et al. 1981).

Grizzly bears (*U. a. horribilis*) in the Yellowstone region are among the North American brown bears known to consume wasps and bees (Craighead et al. 1995). Yellowstone grizzly bears obtain most of their energy from whitebark pine (*Pinus albicaulis*) seeds and tissue from elk (*Cervus elaphus*) and bison (*Bos bison*) (Mattson et al. 1991). Most ungulate tissue is consumed by bears during April–May as carrion from animals that died of natural causes during the previous three months (Mattson 1997a). Whitebark pine seeds are consumed by bears primarily during September–October, from cones in ground-level caches

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made by red squirrels (*Tamiasciurus hudsonicus*) (Mattson et al. 2001). When pine seeds are abundant, the bears eat little else besides them (Mattson et al. 2001). During years when pine seeds and carrion are scarce, grizzly bears in this region eat diverse other foods, including insects such as ants (Mattson 2001).

In this paper I describe foraging on wasps and bees by grizzly bears in the Yellowstone region using data collected during a study of radio-marked bears from 1977–1992. My analysis was exploratory and designed to address the following questions: (1) How did the likelihood and level of consumption of wasps and bees by grizzly bears vary with season and monthly weather? (2) How did the likelihood of consumption vary with availability of known high-quality bears foods, specifically ungulate carrion and whitebark pine seeds? (3) How did likelihood and levels of consumption vary with site and vegetation features?

## Methods

The approximately 23,000 km<sup>2</sup> study area, from 43°30' to 45°15'N latitude and from 109°30' to 111°30'W longitude, corresponded to the known range of Yellowstone's grizzly bear population. Most of the area occupied by grizzly bears is >2100 m in elevation and consists of remote mountains and plateaus surrounded by valleys and plains more intensively settled or used by humans. Annual temperatures average about 0°C. Monthly averages during April through October range from –2°C to 13°C. Temperatures rarely exceed 27°C in most areas. Precipitation varies in amount and timing with elevation and region and falls mostly as snow that reaches accumulations of 20–260 cm, depending on location, before melting during March–June (Dirks and Martner 1982). About 75% of the study area was forested and most of this forest was dominated by lodgepole pine (*Pinus contorta*) (Despain 1990). Craighead et al. (1995) described the study area in detail.

Grizzly bears were trapped, marked, and radio-relocated according to methods described by Knight and Eberhardt (1985) and Blanchard and Knight (1991). A subset of radio-relocations was visited and described according to methods described by Mattson (1997b, 2000). Field crews also described sites where grizzly bear feeding or bedding sign was encountered en route to and from telemetry locations. At each location, field

crews established a variable-radius forest inventory plot (Avery and Burkhart 1994) at the center of grizzly bear activity. Trees were tallied, identified as live or dead, and the diameter of each was measured at 1.4 m aboveground. Additional information was collected within 10 m of plot center, including descriptions of coarse woody debris. These descriptions were indices of amount (1–7, none to heavy), size (1–7, small to large), and degree of decomposition (1–6, solid to well-decomposed). Based on double sampling, indices of size and amount were related to volume of woody debris, in kg m<sup>-2</sup>, as follow: total volume = –0.0008 + 0.764ln(amount x size);  $r^2 = 0.75$  (Mattson 1997b).

Field crews described all signs of feeding and collected all feces (scats) found at telemetry locations and elsewhere from 1977–1992. From 1986 to 1992, descriptions of feeding activity included measurements of excavations. For excavations of wasp and bee nests in duff or soil, length (*A*), width (*B*), and depth (*C*) were measured. Where a log or snag had been excavated, average diameter of the log where it was torn by the bear (*A*), total tear length (*B*), and average tear as a percent of total log circumference (*C*) were measured. Total excavated volume (in dm<sup>3</sup>) was calculated as the product of *A* x *B* x *C* for simple excavations and as  $\pi (A/2)^2 \times B \times C$  for logs and snags (Elgmork and Unander 1998, Mattson 2001).

The concurrent collection of scats and information on feeding activity maximized comparability of data from these two sources at broad scales. I did not ascribe scat contents to specific feeding sites because foods found in scats were often not consumed at the site of collection given the 7–13 hr transit time of digesta (Pritchard and Robbins 1990). Thus, I compared data from scats and feeding sites by month but not by specific 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, percent of total fecal volume, and mean percent for scats in which the item occurred.

I used logistic regression analysis (Demaris 1992) to specify the effects of explanatory variables on the likelihood that a bear had or had not excavated wasp or bee nests at a given location. Radio-telemetry locations or feeding sites were units of analysis. I specified two models: one using

only data from telemetry locations, including sites where no feeding sign had been found, and the other using only data from sites with feeding sign, but including plots not at telemetry locations. I gave priority to the first model and used the second to confirm patterns. When wasps or bees had been excavated, I used multiple linear regression (Weisberg 1985) to specify the effects of explanatory variables on the total volume of excavations. 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. I used change-in- $AIC_c$  ( $\Delta$ ) to quantify the relative effect of each variable in a given model (Burnham and Anderson 1998). Because the value of  $AIC_c$  is affected by sample size,  $\Delta$  is comparable within but not among models. I deemphasized statistical hypothesis testing for reasons well stated elsewhere (Johnson 1999) and I present  $P$ -values solely as confirmatory information.

I considered both proximal and distal effects in the analysis (Mattson 2000, Mattson 2001). Distal effects were those operational at broad temporal and spatial scales while proximal effects were operational at the scale of the immediate site. Proximal effects were represented by measures taken at telemetry locations or other sites of grizzly bear activity. Distal effects were enumerated from other sources, as follow. Numbers of ungulate carcasses on elk and bison winter ranges during spring and numbers of cones on whitebark pine trees were taken from counts at fixed transects. Monthly temperatures and precipitation were taken from regional summaries published by the U.S. National Oceanic and Atmospheric Administration (NOAA). I also used a running two-month sum of growing season (i.e., April–October) precipitation in the analysis. Mattson (2000) provided a more detailed description of these distal factors and their sources.

## Results

During this study, 6662 scats were collected and 1853 telemetry locations of radio-marked bears were investigated to determine activity of the associated animal. Feeding sign was found at a total of 2769 sites, including sites not associated with a telemetry location. Remains of adult wasps or bees were found in 33 scats whereas sign of foraging for wasps or bees was found at 35 sites.

No identifiable remains of wasp or bee larvae or pupae were detected in scats.

Grizzly bears consumed few wasps and bees in the Yellowstone region, generally <1% total scat volume (Figures 1a and 1b). However, use was greater during some years, as during 1988 when remains of wasps and bees accounted for 3% and 6% of total fecal volume during August and September. On average, levels of consumption and related foraging peaked during these two months (Figures 1a and 1b). I calculated the ratio of total volume of wasp or bee remains in fecal material to total volume of nest material exca-

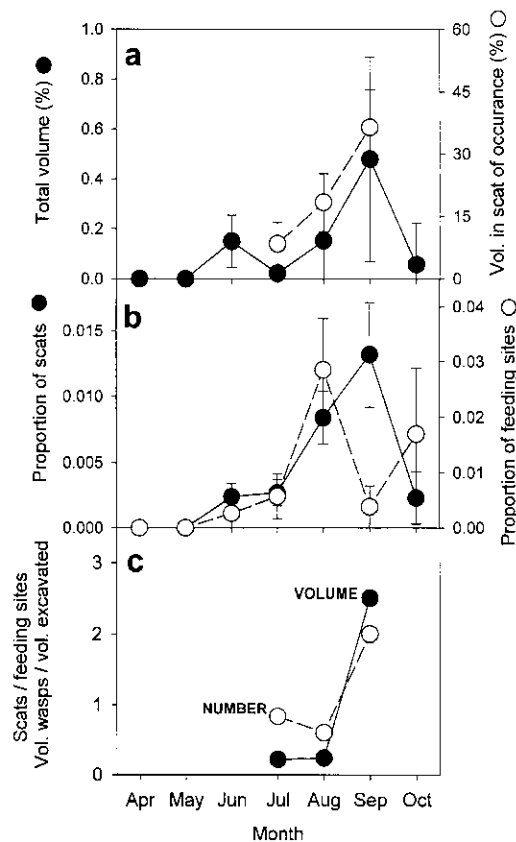


Figure 1. Monthly patterns associated with consumption of wasps and bees by Yellowstone grizzly bears, 1977–1992: (a) remains of wasps and bees as a percent of total fecal volume, averaged among years ( $\pm 1$  SE), and as a percent of scats in which they were found, averaged among scats; (b) proportion of scats and feeding sites where the remains of wasps and bees or associated feeding sign were found; and (c) indices of reward obtained by consuming wasps or bees.

TABLE 1. Regression models for relations between either the logit-transformed probability that wasps or bees had been consumed, or the natural-log transformed volume of total excavations, and distal and proximal factors, for Yellowstone grizzly bears, 1977–1992.  $\beta$  is a parameter estimate and  $\Delta$  is change in  $AIC_c$  with deletion of the corresponding variable from the model. Statistics for logistic regression models are for goodness-of-fit tests.

Independent variables	Probability of consumption: Telemetry locations only			Probability of consumption: Feeding sites only			Volume of excavations (dm <sup>3</sup> ) <sup>a</sup>		
	$\beta$	SE	$\Delta$	$\beta$	SE	$\Delta$	$\beta$	SE	$\Delta$
Constant	-10.3	4.7		-9.8	3.4		2.5	0.58	
Distal factors									
Cumulative precipitation (cm)	-4.8 <sup>a</sup>	1.2	39	-5.8 <sup>a</sup>	1.1	88			
Number of ungulate carcasses	3.3 <sup>a</sup>	1.6	9	3.7 <sup>a</sup>	1.2	20			
Number of whitebark pine cones (n tree <sup>-1</sup> )	-2.1 <sup>a</sup>	0.9	8	-2.0 <sup>a</sup>	0.7	11			
Proximal factors									
Total live forest basal area (m <sup>2</sup> ha <sup>-1</sup> )	1.02 <sup>a</sup>	0.39	10	0.86 <sup>a</sup>	0.24	16	0.067 <sup>c</sup>	0.028	3.6
Amount of coarse woody debris (index)	0.038 <sup>b</sup>	0.016	4	0.035 <sup>b</sup>	0.013	5	-0.034 <sup>b</sup>	0.011	0.1
Statistics									
$G^2$ or $F$ (df)		76 (879)			117 (937)			6.4 (2 / 26)	
$P$		1.00			1.00			0.005	
$R_t^2$ or $R^2$		0.96			0.95			0.33	
$n^d$		1556			2149			29	

<sup>a</sup>Coefficient was estimated for data transformed by:  $\ln(x + 1)$ .

<sup>b</sup>Coefficient was estimated for data transformed by:  $x^2$ .

<sup>c</sup>Coefficient was estimated for data transformed by:  $(\ln[x + 1])^2$ .

<sup>d</sup>Sample sizes used for modeling were less than total sample sizes because of missing values.

vated by bears, and the ratio of total number of scats with remains of these insects in them to total number of feeding sites where consumption was detected, to indicate the monthly level of energetic reward obtained by bears. Both indices peaked in September (Figure 1c), coincident with peak fractions of wasp and bee remains in scats where they were detected (Figure 1a). I did not calculate these indices for April–June or October because of few samples of scats ( $n \leq 3$ ) and feeding sites ( $n \leq 2$ ). There were 5, 12, and 12 feces containing the remains of wasps or bees collected during July, August, and September and 6, 20, and 6 sites with sign of feeding on these insects found during the same three months.

The probability that Yellowstone grizzly bears had consumed wasps or bees at a site, versus engaging in any other activity, was related to five factors considered in this analysis. Probability of consumption was more strongly related to proximal factors describing vegetation structure ( $\Delta = 37$ ) than to distal factors related to weather and availability of known high quality foods ( $\Delta = 20$ ). Of single factors, consumption was most strongly related to the sum of precipitation during the cur-

rent and previous month, number of ungulate carcasses available on ungulate winter ranges during spring, and amount of live overstory basal area at the site (Table 1). The negative relation to precipitation was acute (Figure 2a); probability of consumption dropped sharply with increased moisture. Proximally, probability of consumption increased with increasing amounts of both coarse woody debris (deadfall) and live basal area (Figure 2b). When wasps or bees had been consumed, total volumes excavated by bears to reach nests also increased with increasing live basal area but declined with increasing amounts of woody debris (Table 1).

The gray remains of paper nests were observed at the center of grizzly bear excavations at 33 sites where consumption of wasps or bees was documented. Diameters of 14 nests sufficiently intact to measure averaged  $1.1 \pm 0.4$  dm. Wasps, sometimes numerous, were observed in 30% of the 49 individual excavated nests. Of these nests, 26% were located partially in the base of stumps and snags, 22% were under logs, 17% were in logs, 17% were in forest duff <3 dm from the base of a tree, and 4% were in soil in the open.

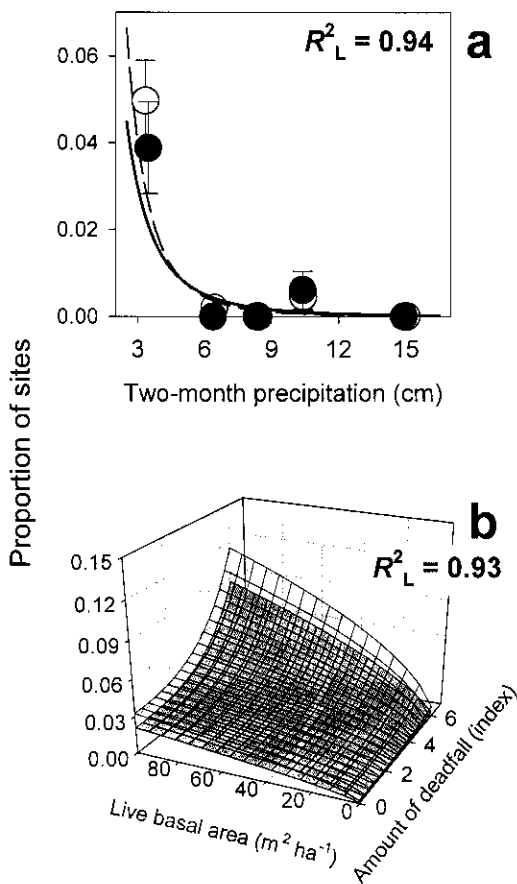


Figure 2. Relations between proportions of sites where wasps or bees had been consumed and (a) sum of precipitation during the current and previous month and (b) total live forest basal area and amount of coarse woody debris (deadfall). Filled circles and solid lines in (a) and the gray surface in (b) depict relations for telemetry locations only; open circles and dashed lines and the open mesh surface depict relations for all feeding sites. Circles denoting means and brackets denoting SEs are shown for quintiles of the data to illustrate goodness of fit;  $R^2$  values are for relations based on telemetry locations.

## Discussion

Peak consumption of wasps and bees by Yellowstone grizzly bears occurred late in the growing season, during August and September. This coincided with an apparent peak in the reward, or probable energetic benefit, of consuming these insects. A late season peak in relative abundance of wasps or bees, and related energetic benefit of use, is consistent with general trends

in seasonal population dynamics of social ground-nesting wasps. Single queens usually start a colony in spring with numbers of adults, pupae, and nest combs peaking by August (Evans and Eberhard 1970, Spradbery 1973). Comparatively high levels of consumption by bears in September may reflect delayed phenology of colonies in the Yellowstone study area because of a climate colder here than where most investigations of wasp population dynamics have occurred.

Yellowstone grizzly bears consumed the most wasps and bees during the driest months of the entire study. This agrees with observations by Sharafutdinov and Korotkov (1976) who noted heavy consumption of ground-dwelling wasps by brown bears in the Ural Mountains during a year when wasp populations proliferated because of hot dry weather. Although research done elsewhere is equivocal about relations between weather and wasp abundance, there are some indications that dry weather promotes the growth of wasp populations (Spradbery 1973). I speculate that bears consumed wasps and bees more often during the driest months of the driest years simply because wasps and bees were then more abundant.

Consumption also increased when whitebark pine cone crops were small and ungulate carrion was abundant earlier in the year. As with ants (Mattson 2001), Yellowstone's grizzly bears preferably consumed whitebark pine seeds in preference to wasps and bees. The positive association with availability of carrion during spring is not as easily explained. One speculative possibility is that growth of wasp populations was accelerated by availability and use of an energy-rich food (ungulate tissue) early in the growing season. Meat is readily consumed by wasps (Evans and Eberhard 1970, Spradbery 1973). Other explanations for this relation could involve changes in grizzly bear selection of foods like wasps and bees in response to availability of carrion and effects of weather correlated with over-winter mortality of ungulates.

The odds that Yellowstone grizzly bears consumed wasps and bees were greatest at sites with abundant deadfall and considerable basal area of live trees—conditions often associated with older forest stands (Romme 1982, Mattson 1997b). They also exploited more nests more thoroughly in dense forests, although not where deadfall was abundant. This association with live trees and woody debris is consistent with the frequent location of exploited wasp and bee nests in or under logs or

at the base of trees. Presumably, grizzly bears concentrated their foraging for wasps and bees in these kinds of sites because ground-nesting wasps were most abundant there. Even so, existing research gives no indication where wasps of boreal environments tend to nest, why this might be at sites where woody debris and live trees are more abundant, and, if so, how these stand features interact with effects of drought.

Although in North America wasps and bees are a common food of black bears, this is not the case for brown bears. Nowhere but in Yellowstone have North American brown bears been observed to consume wasps and bees more than a few times (Pearson 1975, Lloyd 1979, Russell et al. 1979, Murie 1981, Servheen 1983, Aune and Kasworm 1989). Yellowstone's grizzly bears are thus somewhat unusual among North American brown bears, not only in consuming these insects, but also by sometimes consuming noteworthy quantities of them. Even so, wasps and bees were not an important source of energy and nutrients for bears in this population during the study period, except during the extremely dry year of 1988 when regional precipitation during June–September was 39% of normal. As with many of Yellowstone's

grizzly bear foods (Mattson et al. 1991), wasps and bees are potentially important to some bears at some times. This may become more common if regional precipitation diminishes as the global climate changes.

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