

Bear feeding activity at alpine insect aggregation sites in the Yellowstone ecosystem

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Bears (Ursidae) were observed from fixed-wing aircraft on or near alpine talus in the Shoshone National Forest between 15 June and 15 September in 1981–1989. Bears fed on insect aggregations at 6 known and 12 suspected alpine talus sites, disproportionately more at elevations >3350 m, on slopes >30°, and on south- and west-facing aspects. While at these sites, bears almost exclusively ate invertebrates, typically army cutworm moths (*Euxoa auxiliaris*). Subadult grizzly bears (*Ursus arctos horribilis*) appeared to be underrepresented at the sites, and proportionate representation of adult females with young appeared to decrease between 15 June and 15 September. Overall, observations of bears at these sites increased between 1981 and 1989. We suggest that alpine insect aggregations are an important food source for bears in the Shoshone National Forest, especially in the absence of high-quality foraging alternatives in July and August of most years.

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Des ours (Ursidae) ont été observés du haut d'un avion sur le talus alpin ou dans les environs, dans la forêt nationale de Shoshone, entre le 15 juin et le 15 septembre, de 1981 à 1989. Les ours se nourrissaient d'essaims d'insectes en 6 endroits connus et 12 endroits probables du talus alpin, plus particulièrement aux élévations >3350 m, sur les pentes de >30°, et sur les versants sud et ouest. À ces endroits, les ours mangeaient presque exclusivement des invertébrés, surtout des Légionnaires grises (*Euxoa auxiliaris*). Les Ours bruns (*Ursus arctos*) sub-adultes semblaient particulièrement sous-représentés à ces endroits, et la représentation des femelles adultes accompagnées de petits diminuait entre le 15 juin et le 15 septembre. De façon générale, le nombre d'ours observés à ces endroits a augmenté de 1981 à 1989. Nous croyons que les essaims d'insectes en zone alpine constituent une importante ressource alimentaire pour les ours de la forêt nationale de Shoshone, particulièrement en l'absence de brouet de haute qualité en juillet et en août la plupart des années.

[Traduit par la rédaction]

Introduction

Traditional bear feeding on major insect aggregations has been conclusively documented in only two areas: McDonald Peak in the Mission Mountains (Chapman et al. 1955; Servheen 1983; Klaver et al. 1986) and the Scapegoat Wilderness (Craighead et al. 1982; Keith Aune, Montana Department of Fish, Wildlife and Parks, Bozeman, personal communication), both in western Montana. Bears were known to eat army cutworm moths and ladybird beetles (*Coccinella* and *Hippodamia* spp.) in the Mission Mountains and army cutworm moths in the Scapegoat Wilderness, principally excavated from alpine talus. Bears' use of insect aggregations, either ladybird beetles or army cutworm moths, is also known in the mountains of the Rocky Mountain East Front (Keith Aune, personal communication) and Glacier National Park (Katherine Kendall, U.S. National Park Service, Glacier National Park, personal observation) in Montana. Elsewhere, bear feeding, sometimes intensive, on grasshopper (Orthoptera) aggregations melted out of glaciers (Gurney 1953) and caddis flies (Trichoptera) along the shores of Lake Baikal, USSR (Ustinov 1965) has been observed.

The Interagency Grizzly Bear Study Team (IGBST) first noticed radiotelemetered grizzly bears digging in alpine talus in 1986. These sites were visited by IGBST and Wyoming Game and Fish (WGF) personnel in 1987–1989. Other alpine talus feeding sites were identified during radiotelemetry and airborne observation of grizzly bears. The presence of scats and insects

and the behavior of bears at these sites indicated that the bears had excavated aggregations of army cutworm moths. In this paper, we summarize existing IGBST and WGF data concerning bears' use of insect aggregations in alpine areas of the Yellowstone ecosystem.

Study area

In the 2 400 000-ha Yellowstone ecosystem, evidence of bear feeding on insect aggregations has been found only in the Absaroko Mountains between Clark's Fork of the Yellowstone River to the north and the Wind River to the south. A substantial portion of this country is above the timberline (3000–3250 m). The remainder of the area is forested except for valleys and south slopes in the drier eastern portion. Deep valleys and basins divide large, rugged mountain mass elevations range from about 1830 to 3960 m.

The mountains of this area originated with volcanic activity during the Late Eocene and Oligocene, and belong to the Absaroko volcanic formations. Most of the upper strata consist of basic and acidic breccia: a mass of cinders, ash, tuff, basalt, pumice, conglomerate, and other pyroclastic material (Love et al. 1955).

The alpine climate is characterized by frequent strong (>66 km/h) winds, typically westerly in winter and both westerly and southwesterly during summer (Dirks and Martner 1982). Precipitation varies considerably with latitude and longitude (Baker 1944), but most windward ridges and upslopes remain relatively snow-free during winter and deep drifts accumulate on lee slopes (Johnson and Billings 1962; Thilen and Smith 1985). The snow-free period therefore varies with aspect and landscape position. Mean July temperatures likely range from 7 to 9

(Johnson and Billings 1962), although no temperature records exist for the study area.

Methods

Bears were located from a fixed-wing aircraft during routine observation and flights to locate radiotelemetered grizzly bears. Bears were identified as to species, and their activities and other identifying characteristics (e.g., size, markings, and color) were noted. Subadults were distinguished by size and relative body proportions. Site characteristics (e.g., landform and vegetation) and location (Universal Transverse Mercator coordinates) were recorded. When estimating search effort by year, we included only flights flown substantially over areas with known or likely insect feeding sites.

We visited six alpine insect aggregation sites after most seasonal bear use had stopped. Another 12 sites were suspected to be insect aggregation sites used by bears, based on the similarity of bear behavior and site features to the 6 known sites. We know of no other food that bears would extensively dig for in alpine talus in the Yellowstone area. While visiting 1744 telemetry locations of radio-collared bears from 1977–1990, we found only 1 high-elevation excavation for rodents in alpine scree. Data collected at insect aggregation sites included measurements and descriptions of site characteristics (e.g., slope, aspect, elevation), vegetation type and coverage, and bear sign (e.g., dig dimensions and dig-site features, bed dimensions and locations). Feces in the vicinity were collected and later analyzed for frequency and volumetric content of identifiable diet items (cf. Mattson et al. 1991). We estimated volume ingested by adjusting scat contents, using corrections for differential digestibility of items (Hewitt 1989).

We interviewed 11 outfitters and 9 mountain sheep (*Ovis canadensis*) hunters who were thought to have used areas near known insect aggregation sites. Eight of the 20 respondents had consistently visited these areas between July and September for many years dating back to the 1950s. These individuals were asked if they remembered seeing aggregations of bears digging in talus between July and September.

We used the log-likelihood ratio (G) to test goodness of fit between observed and expected frequencies (Zar 1984, p. 52) of bear sightings among bear sex and age classes and elevation, aspect, and slope classes. Bonferroni confidence intervals were calculated to determine which classes differed significantly between observed and expected values (Byers et al. 1984), given a significant difference in overall frequency distributions. The expected distribution of sightings among bear classes, assuming representation was equal to theorized population proportions, was derived for a population with a stable age structure, a 3-year reproductive cycle, and a male:female ratio of 51:49 for litters (Knight et al. 1988¹). Expected distributions of observations for elevation, aspect, and slope classes were derived from map measurements at 344 random points above 3040 m elevation, the minimum elevation of documented sites of bears feeding on insects. Random points were restricted to the region where insect-feeding sites had been found. Measurements of elevation, slope, and aspect for individual bear sightings were also taken from maps. Distributions of bear sightings were pooled for analysis of habitat use, irrespective of known or suspected individual bear identity.

Results

Site characteristics

We identified a total of 18 sites used by bears to feed on insect aggregations: 12 suspected and 6 known (Fig. 1). All but one of these sites were discovered between 1986 and 1989. We visited six of the sites a total of 8 times from 1987 to 1989.

¹Knight, R., Beecham, J., Blanchard, B., Eberhardt, L., Metzgar, L., Servheen, C., and Talbott, J. 1988. Report on the Yellowstone grizzly bear population task force: equivalent population size for 45 adult females. Unpublished Interagency Grizzly Bear Study Team Report. Interagency Grizzly Bear Study Team, Forestry Science Laboratory, Montana State University, Bozeman.

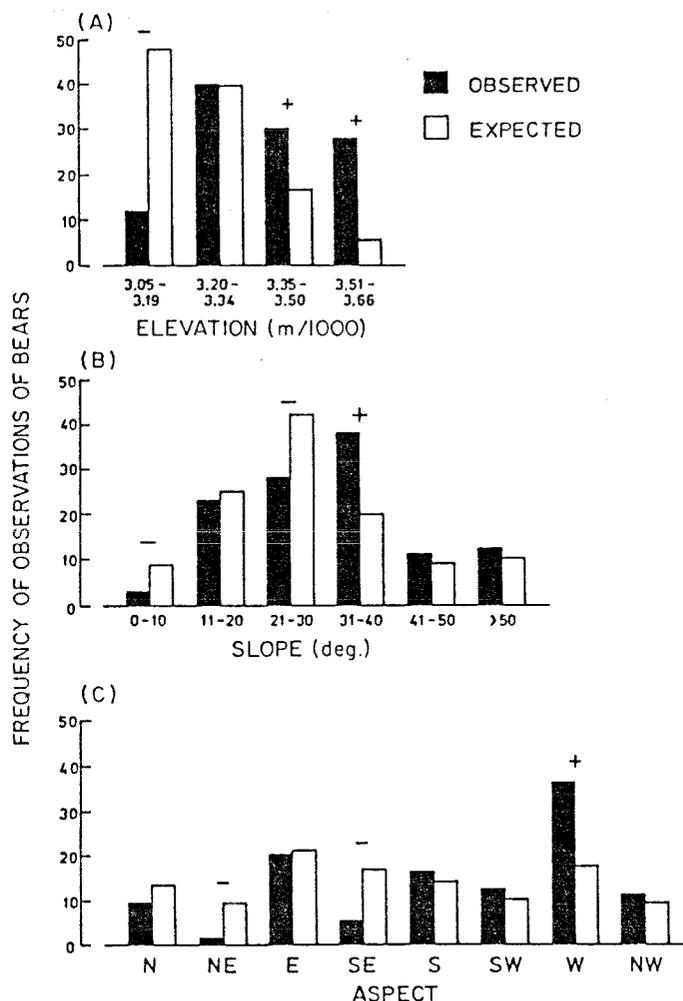


FIG. 1. Observed and expected frequencies of autonomous individual bears or family groups digging at known or likely insect aggregation sites, by elevation (A), slope (B), and aspect (C). A plus or a minus sign denotes observed frequencies significantly greater or less than expected, respectively ($P < 0.05$).

All 18 sites were located in glacial cirques on scree slopes (*sensu* Bloom 1978, p. 188) immediately below steeper headwalls or cliffs. The scree slopes at the sites we visited appeared to be active, with high rates of debris accumulation. Virtually none of the scree interstices were filled with finer debris, and deposition of fragments on these slopes was common while we were at the sites. The slightly rounded but angular scree ranged from 8 to 40 cm in size. Elevations at the 18 sites averaged 3356 ± 193 m (3024–3680 m), and slopes were $32 \pm 11^\circ$ (13–60°). Seven of the sites were on west aspects, six were on north aspects, four were on south aspects, and one was on an eastern aspect.

Scree slopes used for feeding by bears were essentially devoid of vegetation; even the lichen cover on rocks was sparse. However, there were alpine tundra-covered benches and plateaus above and below many of the sites. The tundra plateaus were dominated by forbs, most commonly *Geum rossii*, *Trifolium nanum*, *T. dasyphyllum*, *Phlox multiflora*, and *Eritrichium nanum*. Graminoids, including *Deschampsia cespitosa*, *Poa* spp., *Phleum alpinum*, and *Carex* spp. were more common on the moister, lower elevation benches.

TABLE 1. Observed and expected numbers of grizzly bears at known or likely insect aggregation sites

	Observed	Population expected	Adults expected
Subadult	17 ^a	67.5 ^b	
Lone adult	61 ^a	30.5 ^b	60.5 ^a
Female with cub(s) of the year	16 ^a	10.5 ^a	20.7 ^a
Female with yearling(s)	25 ^a	10.5 ^b	20.7 ^a

NOTE: Expected proportions were derived from Knight et al. (1988, see footnote 1), assuming a male : female ratio of 51:49 for litters and a 3-year reproductive cycle. Values in rows followed by a different letter are significantly different ($P < 0.05$); tested by proportions (Byers et al. 1984).

Characteristics of bears using sites

Subadults (<5 years old), lone adults, adult females with cubs of the year, and adult females with yearlings were observed at known or likely sites of feeding on insects. Of the 146 observations of bears (family groups were counted as a single observation), 18% were of black bears (*Ursus americanus*) and the rest (119) were of grizzly bears. All observations of black bears were on a single mountain massif located peripherally with respect to the study area boundaries and to occupied grizzly bear habitat.

Frequencies of observed and expected grizzly bear classes differed significantly ($G = 94.14$, $df = 3$, $P < 0.001$) (Table 1). Most of this difference was attributable to underrepresentation of subadults. There was no significant difference between observed and expected frequencies among adult classes only ($G = 2.20$, $df = 2$, $P = 0.353$), although there was a tendency for females with cubs of the year to be underrepresented.

The ranges of 17 radio-collared grizzly bears included or were close to (5–15 km) known alpine insect aggregation sites; mean life range (minimum convex polygon) of adult females in the Yellowstone area is 884 km² (Blanchard and Knight 1991). Five of the nine collared adults fed at insect sites, whereas only one of eight subadults was even suspected of doing so.

Chronology of bear use

The numbers of bears observed at known or likely insect aggregation sites during flights increased between 1981 and 1989 (Table 2), not only when bear observations were averaged over all flights, but particularly when only those flights where bears were observed at an insect site were taken into account. No bears were observed from 1974 to 1981, but few of these flights included the part of the study area containing sites where bears fed on insects. None of the outfitters or mountain sheep hunters we interviewed remembered seeing aggregations of bears at or near likely insect sites in the 1950s and 1960s, and only one recalled bears feeding at a known site in the mid-1970s.

The mean number of observations per flight when a bear was seen was lowest between 15 June and 15 July (Table 3). All observations of bears digging at known or likely insect sites were made between 15 July and 15 September. The proportion of females with young decreased over the three time periods analyzed (15 June – 15 July, 16 July – 15 August, 16 August – 15 September), whereas the proportion of subadults increased. The frequency of observations among bear classes differed significantly between the mid and late time periods ($G = 8.84$, $df = 2$, $P = 0.013$), primarily because of a significant drop in the proportion of females with young during the late time period.

Characteristics of bear use

Four radio-collared grizzly bears monitored for >1 year and known to feed at insect sites used those sites in each of the years

TABLE 2. Numbers of observation and tracking flights over the study area, and numbers of individual bears or family groups observed flight at known and likely insect aggregation sites, by year

Year	Number of bears				Total no. of flights	No. of flights with bear sighted
	All flights		Flights with bear sighted			
	Mean	SD	Mean	SD		
1981	0.3	0.5	1.0	—	7	2
1982	0.3	—	1.0	—	3	1
1983	0	—	0	—	7	0
1984	0.6	0.8	1.3	0.5	14	6
1985	0.2	0.6	1.5	—	12	2
1986	0.7	1.2	2.0	1.4	15	5
1987	2.3	2.4	3.6	2.1	11	7
1988	3.4	2.9	4.1	2.7	12	10
1989	2.7	2.9	4.6	2.3	19	11

they were monitored (13 bear years). The longest record of consistent use by a single bear was 6 years, 1984–1989. Each bear used only one site during any given year. The bear with 6 years' use and another with 3 years returned to the same site each year. Another bear shifted among sites between years, but all the sites were on the same massif. Of 53 radiotelemetry locations of these four bears from 15 July to 15 September, 64% were within 1.5 km of a known insect aggregation site. A significantly smaller portion, 5.3%, of the total aggregate range (minimum convex polygon) of these bears was within 1.5 km of insect sites ($G_c = 129.4$, $df = 1$, $P < 0.001$).

Bears ate mainly army cutworm moths at or near insect sites; although the exclusivity of moth use differed among years (Table 4). Graminoids and whitebark pine seeds were also eaten, and there was some grazing in adjacent mesic areas.

Bear excavations were 1–6 dm, typically 1.5–5 dm, deep. We could not consistently determine total volumes excavated because bears often backfilled previous excavations as they dug others. Moths were abundant and lethargic because of chilling when we collected them at dig sites, in one case less than an hour after bears had fed there. When two or more bears or bear families fed at an insect site, they were separated by 40–200 m with the exception of paired subadults or suspected mating adults. Bear use tended to be concentrated within areas of about 200 × 100 m. We found up to 40+ scats in these areas; others were undoubtedly covered as bears dug.

Bears observed digging for moths ($n = 110$) were not distributed randomly with respect to elevation, slope, or aspect (Fig. 1). More digging than expected occurred above 3354 m and less than expected below 3201 m. Digging was also more frequent than expected on slopes >30°, but significantly more only on slopes of 31–40°. Frequency of digging was much greater than expected on western aspects, and significantly less than expected on northeastern and southeastern aspects.

The majority of moth-seeking bears apparently bedded at or near insect sites. Some beds were excavated in open tundra and averaged 2.8 dm deep ($n = 3$). Others were located in the open scree feeding sites ($n = 8$). Most beds or bedding sites ($n = 22$) were situated in closely set clusters of 3–11 and were shaded by either an adjacent cliff or overhanging massive boulders 1.8–6 m high. These beds were typically shallow (≤ 1 dm deep, compared with an average of 1.6 dm ecosystem-wide (Knight and Blanchard 1983)) and were shaped from scree or rocky soil.

TABLE 3. Number of grizzly bear observations and proportionate representation of bear classes at known or likely insect aggregation sites, by monthly period, 1986–1989

	No. of observations of bears	No. of flights with bears observed	Bear class proportion		
			Subadults	Lone adults	Females with young
15 June – 15 July	9	7	0*	0.444*	0.555*
16 July – 15 August	73	16	0.137 _a	0.466 _a	0.397 _a
16 August – 15 September	37	10	0.210 _a	0.605 _a	0.184 _b

NOTE: Values in columns followed by a different letter are significantly different ($P < 0.05$). Values are proportions of total observations of bears, by time period.

*Sample size <24.

TABLE 4. Average content of bear scats collected at moth-feeding sites in 1987 ($n = 25$), 1988 ($n = 38$), and 1989 ($n = 53$)

	% frequency			% volume			% ingested volume		
	1987	1988	1989	1987	1988	1989	1987	1988	1989
Moths	64.0	92.1	73.6	42.0	77.2	57.5	66.6	92.1	80.2
Graminoids (Graminales)	76.0	23.7	35.8	46.2	9.3	23.4	13.8	2.1	6.3
Debris	36.0	42.1	37.7	4.8	8.4	9.7	—	—	—
Pine seeds (<i>Pinus albicaulis</i>)	8.0	2.6	7.5	5.4	2.6	6.6	14.2	5.2	11.4
Clover (<i>Trifolium</i> spp.)	4.0	2.6	3.8	1.4	2.4	0.9	0.4	0.6	0.3
Deer hair (<i>Odocoileus hemionus</i>)	4.0	0.0	0.0	2.2	0.0	0.0	4.6	0.0	0.0
Ants (Formicidae)	4.0	0.0	5.7	0.4	0.0	1.7	0.4	0.0	1.7

NOTE: Ingested volume was estimated by applying the correction factors of Hewitt (1989), excluding debris.

We also observed bears climbing cliff slopes, apparently to bed in clefts, although we did not find or measure beds at these sites. We found clusters of 2–6 scats (mean 2.6) around all the beds.

Discussion

During July, adult army cutworm moths typically undertake massive migrations from agricultural lands to often far-distant mountains (Cook 1927; Pepper 1932; Pruess 1967; Burton et al. 1980). The moths apparently aggregate at high elevations and feed on nectar (Burton et al. 1980). Usually by mid-September to mid-October, the adults return to agricultural lands to lay eggs (Cook 1927; Pruess 1967).

Bears probably ate army cutworm moths or ecologically similar moths at all known and suspected sites. Army cutworm moths or their remains were found at all six of the sites we visited, and the timing of bear activity apparently coincided with the presence of army cutworm moths in the mountains. Bear foraging behavior and site characteristics were similar in all instances.

These sites were not documented in pre-1981 flights, probably because detection of alpine insect use by bears seems to require radio-collaring of bears and ground inspection, which was hindered by the relative inaccessibility of virtually all our sites. Other alpine sites in Rocky Mountains used by bears to feed on insect aggregations have probably not been detected or verified for similar reasons.

The rate of bear observations at alpine insect aggregation sites has increased in our study area since 1981. This is consistent with the recollections of hunters and outfitters using the study area during the previous three decades. Increased sightings could have resulted from a relative increase in use by bears, an increase in the bear population, an increase in our efficiency of sighting bears at these sites, or a shift in bears' use of sites from evening to daylight hours. Given the magnitude of the increase in

sightings and the history of the bear population in the Shoshone National Forest (SNF) (Knight and Eberhardt 1985), we suspect that all four factors have played a role.

We have little doubt that alpine insect aggregations are important to grizzly bears in the SNF. Army cutworm moths are predictably a high-quality food; during July and August, fat content of the abdomen can reach 64% (Pruess 1967), and soft-bodied insects such as these are highly digestible (Hewitt 1989). These insects are also abundant during hyperphagia, when bears accumulate the body fat necessary for surviving winter hibernation and spring hypophagia. The onset of hyperphagia for bears in Yellowstone is probably during late July (Mattson et al. 1991). Grizzly bears concentrate at insect aggregations for extended periods during early hyperphagia, and while there they primarily ingest the insects.

The underrepresentation of subadult bears on insect aggregation sites in our study area is in accord with observations of bears feeding and concentrating at high-quality native food sources reported in other studies (Stonorov and Stokes 1972; Egbert and Stokes 1976; Kendall 1986; Reinhart and Mattson 1990). The reason for this underrepresentation is unclear, but presumably the subadults are avoiding adults. Several studies have suggested that adult bears can dominate higher quality food resources and aggressively exclude smaller, often subadult bears (Hornocker 1962; Stonorov and Stokes 1972; Egbert and Stokes 1976; Herrero 1983). To some extent underrepresentation of subadults could have resulted from lower visibility because of their smaller size; however, this bias probably does not explain the magnitude of the underrepresentation. It is also possible that females with young were more sightable than lone bears, simply because groups are more likely to be seen than single bears. It is possible, therefore, that females with young used insect sites proportionately less often than indicated by our observations.

Our results concerning proportionate representation of bear

classes are in contrast to those of Klaver et al. (1986) from insect aggregation sites in the Mission Mountains of Montana. The frequencies of observation of adults versus females with young versus subadults were significantly different between the two studies ($G = 7.87$, $df = 2$, $P = 0.021$). The differences are attributable to proportionately more observations of lone adults and fewer of subadults during our study. This agrees with the hypothesis of Klaver et al. (1986) that the more security-conscious or subordinate bears disproportionately used insect aggregation sites in their study area, and that these sites afforded refuge from lone adults.

The differences between the Mission Mountains and SNF study areas are likely best understood in the context of habitat differences. In the Mission Mountains there is an abundance of fleshy fruits in August and September, typically at moderate to low elevations (Servheen 1983). Alpine insect aggregations are probably of lesser or comparable quality relative to fruits, and fruits are very likely exploited much more heavily by lone adult bears (Servheen 1983). In the SNF, fleshy fruits are scarce, and during most years bears rely on whitebark pine seeds for fattening during hyperphagia (Mattson et al. 1991). Whitebark pine seeds are typically available only after the 3rd week in August at elevations above 2425 m (Mattson and Jonkel 1990). Thus, bears are afforded fewer options for high-quality food at lower elevations during August and September in the SNF, and dominant bears appear to rely much more heavily on alpine insect aggregations.

Many, if not most, bears in the SNF feed on alpine insect aggregations for at least a month each summer. As in the Mission Mountains, these sites might provide useful sampling locations for monitoring the population via aerial surveys from 15 July to 15 August (assuming that observer bias is corrected).

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- BAKER, F. S. 1944. Mountain climates of the western United States. *Ecol. Monogr.* **14**: 223–254.
- BLANCHARD, B. M., and KNIGHT, R. R. 1991. Movements of Yellowstone grizzly bears. *Biol. Conserv.* **58**: 41–67.
- BLOOM, A. L. 1978. *Geomorphology*. Prentice Hall, Inc., Englewood, Cliffs, NJ.
- BURTON, R. L., STARKS, K. J., and PETERS, D. C. 1980. The army cutworm. *Okla. Agric. Exp. Stn. Bull.* No. B749.
- BYERS, C. R., STEINHORST, R. K., and KRAUSMAN, P. R. 1984. Clarification of a technique for analysis of utilization-availability data. *J. Wildl. Manage.* **48**: 1050–1053.
- CHAPMAN, J. A., ROMER, J. I., and STARK, J. 1955. Ladybird and army cutworm adults as food for grizzly bears in Montana. *Ecology*, **36**: 156–158.
- COOK, W. C. 1927. Studies in the ecology of Montana cutworms (Phalaenidae). *Ecology*, **8**: 158–173.
- CRAIGHEAD, J. J., SUMNER, J. S., and SCAGGS, G. B. 1982. A definitive system for analysis of grizzly bear habitat and other wilderness resources. Monogr. No. 1, Wildlife-Wildlands Institute, University of Montana Foundation, University of Montana, Missoula.
- DIRKS, R. A., and MARTNER, B. E. 1982. The climate of Yellowstone and Grand Teton National Parks. Occas. Pap. No. 6. U.S. Department of the Interior, National Park Service, Yellowstone National Park, WY.
- EGBERT, A. L., and STOKES, A. W. 1976. The social behavior of brown bears on an Alaskan salmon stream. In *Bears—Their Biology and Management: Proceedings of the Second International Conference on Bear Research and Management*, Calgary, Alta., 6–9 November 1970. Edited by S. Herrero. International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland. pp. 232–241.
- GURNEY, A. B. 1953. Grasshopper glacier of Montana and its relation to long-distance flights of grasshoppers. *Smithson. Inst. Ann. Rej.* 1952. (Publ. No. 4111.) pp. 305–525.
- HERRERO, S. 1983. Social behavior of black bears at a garbage dump in Jasper National Park. In *Bears—Their Biology and Management: Proceedings of the Fifth International Conference on Bear Research and Management*, Madison, WI, February 1980. Edited by E. C. Meslow. International Association for Bear Research and Management, Madison, WI. pp. 54–70.
- HEWITT, D. G. 1989. Correcting grizzly bear fecal analysis to actual food habits. M.S. thesis, Washington State University, Pullman.
- HORNOCKER, M. G. 1962. Population characteristics and social and reproductive behavior of the grizzly bear in Yellowstone National Park. M.S. thesis, Montana State University, Bozeman.
- JOHNSON, P. L., and BILLINGS, W. D. 1962. The alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. *Ecol. Monogr.* **32**: 105–135.
- KENDALL, K. C. 1986. Grizzly bear population trend study; Appendix 1. U.S. National Park Service, Glacier National Park.
- KLAVER, R. W., CLAAR, J. J., ROCKWELL, D. B., MAYS, H. R., and ACEVEDO, C. F. 1986. Grizzly bears, insects, and people: bear management in the McDonald Peak region, Montana. In *Proceedings of a Grizzly Bear Habitat Symposium*, Missoula, MT, April 30–May 2, 1985. Compiled by G. P. Contreras and K. E. Evans. U.S. For. Serv. Gen. Tech. Rep. INT-207. pp. 205–211.
- KNIGHT, R., and BLANCHARD, B. M. 1983. Yellowstone grizzly bear investigations: report of the Interagency Study Team, 1982. U.S. National Park Service, Bozeman, MT.
- KNIGHT, R., and EBERHARDT, L. L. 1985. Population dynamics of Yellowstone grizzly bears. *Ecology*, **66**: 323–334.
- LOVE, J. D., WEITZ, J. L., and HOSE, R. K. 1955. *Geologic map of Wyoming*. U.S. Department of the Interior Geological Survey, Denver, CO.
- MATTSON, D. J., and JONKEL, C. 1990. Stone pines and bears. In *Proceedings of a Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-mountain Resource*, Bozeman, MT, March 29–31, 1989. Compiled by W. C. Schmidt and K. J. McDonald. U.S. For. Serv. Gen. Tech. Rep. INT-270. pp. 223–236.
- MATTSON, D. J., BLANCHARD, B. M., and KNIGHT, R. R. 1991. Food habits of Yellowstone grizzly bears, 1977–1987. *Can. J. Zool.* **69**: 1619–1629.
- PEPPER, J. H. 1932. Observations of a unidirectional flight of army cutworm moths and their possible bearing on aestivation. *Can. Entomol.* **64**: 241–242.
- PRUESS, K. P. 1967. Migration of the army cutworm, *Chorizagrotis auxiliaris* (Lepidoptera: Noctuidae). I. Evidence for migration. *Ann. Entomol. Soc. Am.* **60**: 910–920.
- REINHART, D. P., and MATTSON, D. J. 1990. Bear use of cutthroat trout spawning streams in Yellowstone National Park. In *Bears—Their Biology and Management: a selection of papers from the Eighth International Conference on Bear Research and Management*, Victoria, B.C., February 1989. Edited by L. M. Darling and W. R. Archibald. International Association for Bear Research and Management. pp. 343–350.
- SERVHEEN, C. W. 1983. Grizzly bear food habits, movements, and habitat selection in the Mission Mountains, Montana. *J. Wildl. Manage.* **47**: 1026–1035.

- STONOROV, D., and STOKES, A. W. 1972. Social behavior of the Alaskan brown bear. *In* Bears—Their Biology and Management: Proceedings of the Second International Conference on Bear Research and Management, Calgary, Alta., 6–9 November 1970, Edited by S. Herrero. International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland. pp. 232–242.
- THILENIUS, J. F., and SMITH, D. R. 1985. Vegetation and soils of an alpine range in the Absaroka Mountains, Wyoming. U.S. For. Serv. Gen. Tech. Rep. RM-121.
- USTINOV, S. K. 1965. Biology of grizzly bear in eastern Siberia. Okhotnich'e-promyslovye zveri. *Biologiya i khozyaistvennoe ispol'zovanie*, No. 1, Moskovskaya Veterinarnaya Akademiya. pp. 229–234. (Translated from Russian, Canada Department of the Secretary of State, Translation Bureau, Foreign Languages Division, Ottawa, 1969.)
- ZAR, J. H. 1984. Biostatistical analysis. 2nd ed. Prentice Hall, Inc., Englewood Cliffs, NJ.