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Variation in Production and Bear Use of Whitebark Pine Seeds in the Yellowstone Area

David J. Mattson
Interagency Grizzly Bear Study Team
Forestry Sciences Lab
Montana State University
Bozeman, MT 59717

Daniel P. Reinhart¹
Interagency Grizzly Bear Study Team
Forestry Sciences Lab
Montana State University
Bozeman, MT 59717

Bonnie M. Blanchard
Interagency Grizzly Bear Study Team
Forestry Sciences Lab
Montana State University
Bozeman, MT 59717

Abstract. We analyzed variation in counts of whitebark pine (*Pinus albicaulis*) cones from permanent transects and grizzly bear (*Ursus arctos horribilis*) use of whitebark pine seeds from radio-telemetry and line-transect samples. Cone production varied among years and sites during the 11 years of study, with typically 4- to 9-year intervals between the two largest crops on individual trees. Bears made widespread use of pine seeds only when > 21 cones were produced per tree, averaged over all transects. Use of overwintered seeds by bears was common and known to be substantial two out of six years. Sites used by bears to feed on pine seeds varied between successive large crops, with no duplication in aspect and elevation of the most intensive use over three crops. Techniques by which bears acquired seeds also varied, dependent on the presence of red squirrels. Our results suggest that Yellowstone grizzly bears will potentially make intensive use of the entire elevational and site range of whitebark pine, that no part of this range can be discounted as relatively unimportant to the grizzly bear population; and that habitats where bears use pine seeds need to be secure not only during the fall, but also during the summer and

¹Present address: U.S. National Park Service, Resource Management, Yellowstone National Park, WY 82190.

late spring. Our results also suggest the importance of long-term studies documenting variation in bear habitat use, in this case associated with foraging on a single important food.

Introduction

Whitebark pine seeds are an important food of bears in the Yellowstone area. Among other things, variation in seed crops has affected grizzly bear survival (Mattson, Blanchard, and Knight 1992). During poor seed crop years, grizzly bear conflicts with humans escalate, and more adult female and subadult male bears are killed, primarily because bears move to lower elevations nearer humans (Blanchard 1990; Mattson, Blanchard, and Knight 1992). During good seed crop years, most bears feed on seeds in whitebark pine's high-elevation range, farther from human facilities. When pine seeds are available, grizzly bears apparently feed almost exclusively on them, and seek out habitats where these seeds are available (Mattson and Jonkel 1990; Mattson, Blanchard, and Knight 1991).

Because of whitebark pine's importance to the threatened Yellowstone grizzly bear population, predicting seed crops and protecting productive whitebark pine stands have become an important part of grizzly bear habitat management (Blanchard 1990; Mattson and Jonkel 1990). Data collected by the Interagency Grizzly Bear Study Team from 1977 to 1987 suggested that mixed species conifer stands at low to mid-elevations of whitebark pine's range were used most intensively by grizzly bears, primarily because of higher red squirrel (*Tamiasciurus hudsonicus*) densities (Reinhart and Mattson 1990), and that bears got almost all of their pine seeds (97 percent) by raiding squirrel caches (Mattson and Jonkel 1990). At higher elevation, purer whitebark pine received very little bear use and were relatively unimportant to the grizzly bear population. Grizzly bear use of large whitebark pine seed crops during 1986 and 1987 also suggested among-years (that is, annual) differences in habitats where bears fed on pine seeds (Mattson and Jonkel 1990).

Most tree species exhibit considerable annual variation in seed production (U.S. Department of Agriculture, Forest Service 1974). Where investigated, additional substantial variation in seed production among sites has also been found (e.g., Alexander, Edminster, and Watkins 1986; Franklin 1968; Grisez 1975). This variation among sites within a given year (that is, within-years variation) tends to dampen annual variation in seed production at the landscape level (Kozhevnikov 1963; Nesvetailo 1987) and, consequently, variation in food supply of wide-ranging seed consumers.

Whitebark pine seed production is also known to vary considerably among years (Blanchard 1990; Knight, Blanchard, and Mattson 1991); however, site and regional variation has not been well studied. Weaver and Forcella (1986) concluded that most variation in whitebark pine cone production was among trees within a given stand and that production did not vary significantly among stands within or between regions. Given the potential importance of pine seed production to grizzly bear habitat management and protection, additional study of among-site variation in cone seed production is needed to validate the conclusions of Weaver and Forcella (1986) and to determine the adequate duration of grizzly bear habitat studies — whether 10 years of data collection is long enough to document most variations in habitat use associated with bear feeding on pine seeds.

It is not clear from the literature how often whitebark pine seeds overwinter in cones on trees and whether wildlife use these overwintered seeds. For example, Hutchins and Lanner (1982), Arno and Hoff (1989), Hutchins (1990), and McCaughey and Schmidt (1990) state that few if any intact cones fall naturally to the ground and that seed consumers use virtually all seeds during the year that they mature.

Lanner (1990) suggests that a number of undisturbed cones can overwinter on trees, but that they retain very little nutritional value. Conversely, circumstantial evidence from grizzly bear foraging activities suggests that many cones can overwinter on trees and in squirrel middens and that they provide enough nutrients to support heavy bear use (Kendall 1983; Mattson and Jonkel 1990; Mattson, Blanchard, and Knight 1991). Moreover, instances of bears scavenging fallen overwintered cones have been observed in the Yellowstone area and are quite common on seeds of other stone pines (subsection *Cembrae*) in Siberia (Mattson and Jonkel 1990). Resolution of this discrepancy is important to determining how much protection to offer foraging bears in whitebark pine stands during the spring and summer following good pine seed crops.

In this paper we present an analysis of grizzly bear feeding sites where bears fed on seeds of three successive large crops from 1985 to 1990. This analysis documents bear use of overwintered seeds and variation in habitat use and foraging strategies and, along with analysis of cone transect data, is the basis for hypotheses about site variation in cone production among successive large crops. We also elucidate the management implications of this site variation of crops and bear use of overwintered seeds.

Study Area and Methods

The 20,000-km² study area was centered on Yellowstone National Park and included portions of Wyoming, Montana, and Idaho. This area corresponded to the range of the Yellowstone grizzly bear population. Study area characteristics have been described by Knight and Eberhardt (1985), Blanchard and Knight (1991), and Mattson, Blanchard, and Knight (1991). Approximately 12 percent of Yellowstone Park consisted of habitat types in which whitebark pine was a major, long-persistent seral species and 2 percent of habitat types in which whitebark pine was climax (Despain 1990).

We collected cone production data annually from 1980 to 1990, from 10 trees each on permanent transects. The number of transects increased from 9 to 21 during the study period as we increased the elevational and geographic range of our sample. Methods for this study are further described by Blanchard (1990).

Radio-collared grizzly bears were located from the air once to twice a week throughout the active season, March-October. A subsample of these locations was visited and sampled, stratified by bear and geographic area. We ascribed data to a radio-telemetry location only if there was a high probability of association with the sampled bear and time, determined by nearness of the sign to the telemetry location, age of sign, and correspondence of bear-specific sign such as tracks to the sampled animal. Other grizzly bear feeding activity encountered while en route to or from these locations was also sampled. Site data from these locations included physical measurements (e.g., slope, aspect, and elevation); results from a variable-radius timber overstory plot; ocular and frequency plot estimates of total plant and individual species cover; laboratory analysis of collected feces; and measurements of bear feeding activity. At whitebark pine seed feeding sites these measurements included estimated extent of feeding activity; percent of area excavated; percent deadfall cover; number of cones estimated to have been used by bears, either total or in 5 × 5 m plots; and number of feces present. Fecal sampling and analysis methods are described by Mattson, Blanchard, and Knight (1991).

Data were also collected from a transect-based study conducted during 1990 and the fall of 1989 in the Cooke City area, immediately northeast of Yellowstone National Park. The study area was 108 km² in size and spanned elevations from 2,265 to 3,140 m. During 1990, 137 bear activity sites were sampled along a total of 97 km of line transects spaced at regular intervals, perpendicular to major drainages. The

same data were collected at these activity sites as at sites sampled in association with aerial telemetry locations. Approximately 30 percent of the total transect length intersected whitebark pine habitat types. Data from this study were attributable to both black (*Ursus americanus*) and grizzly bears because we could not consistently distinguish between sign of the two species.

We described the relationship between annual frequency of pine seeds in bear feces and mean number of cones per tree by nonlinear sigmoidal (e^x) regression (the NLIN procedure [SAS Institute, Inc. 1987]). Only the nine transects established in 1980 were used to estimate cone production for this analysis. Frequency of pine seeds in feces was calculated pooling September and October scats only for years when > 15 feces were collected during this period. Data for 1987 were not included because we suspected that cones matured early and had been heavily used by seed predators by the time cones were counted (Blanchard 1990).

We used unbalanced analysis of variance to test the hypothesis that cone production did not vary among years and sites and that variation among years was independent of variation among sites at whitebark pine cone transects (the GLM procedure [SAS Institute, Inc. 1987]). We also tested for equality of means and variances (t -test and f -test, respectively) of cone production between transects in areas where there had been high and low levels of pine seed use by bears during 1989 and 1990. Bear-related data were analyzed by contingency tables using the log-likelihood ratio (G statistic). This approach was used because most variables were categorical or, in the case of basal area and percent stand composition, data distributions were highly nonnormal.

We also analyzed the frequency (G test) of cone production by individual trees $>$ the current-year mean, relative to whether cone production had been above average the previous two moderate-to-large cone crops ($\bar{X} \geq 15$ cones per tree). We hypothesized that production $>$ the contemporaneous mean during two previous crops would decrease the probability of cone production by an individual tree $>$ the current crop mean because of depleted carbohydrate reserves. We assumed that small crops (all with $\bar{X} < 10$ cones per tree) would have little effect.

Results

Bear Use

Annual and Site Variation. The relationship between annual production of cones and frequency of pine seed use by bears, 1980 - 1989, was acutely sigmoidal (figure 1). Very little use occurred during years when mean number of cones per tree was < 21 and peak use occurred at > 27 cones per tree. This abrupt transition suggested a threshold.

Very few whitebark pine cones matured during 1986, 1988, and 1990, and we recorded only two instances of bear use of these crops (Knight, Blanchard, and Mattson 1991). However, grizzly bear use of the 1985, 1987, and 1989 crops was heavy ($n = 54, 75$, and 90 feeding sites, respectively). Aspects and elevations of sites used by grizzly bears to feed on pine seeds differed among periods when they used the large 1985, 1987, and 1989 crops ($G = 74.85$, $df = 22$, $p < 0.001$) (figure 2). Aspects and elevations differed between all individual time periods ($p \leq 0.005$), with the greatest difference between 1987 - 88 and 1989 - 90 ($G = 55.48$, $df = 11$, $p < 0.001$). During 1985 - 86 use was concentrated on east aspects at mid-elevations and on west aspects at high elevations of the whitebark pine zone. During 1987 use was concentrated on west and north aspects at low to mid-elevations, and during 1989 - 90, on east and south aspects at high elevations.

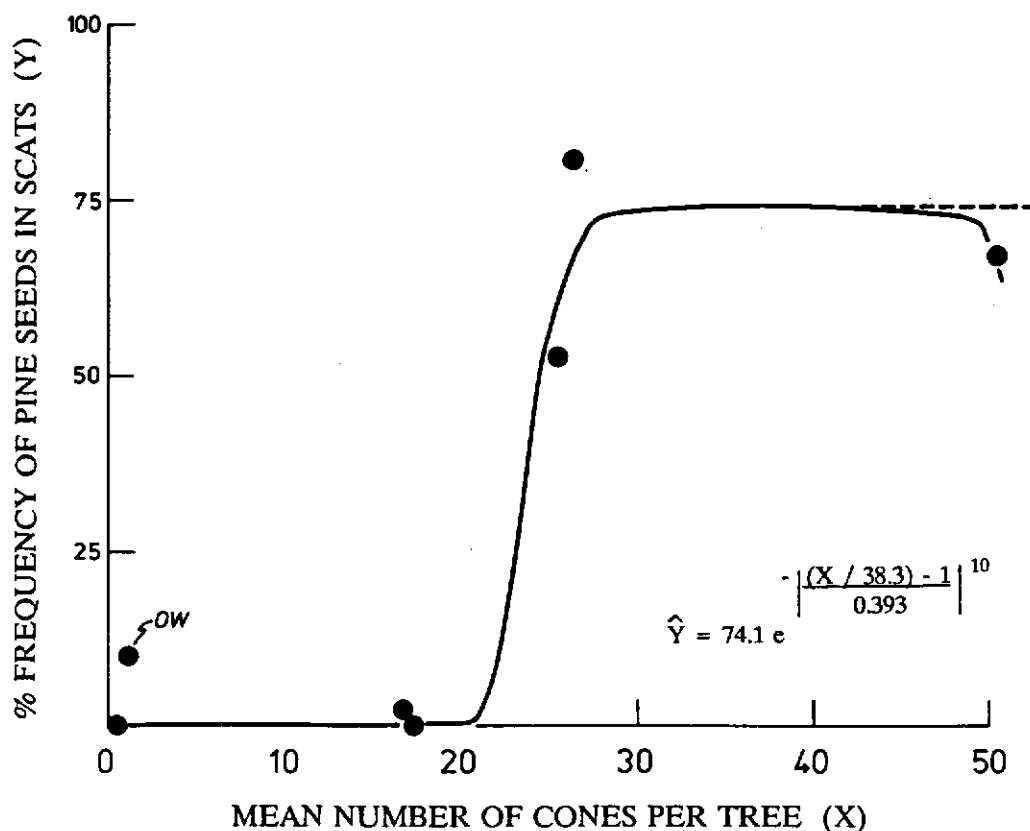


Figure 1. Relationship for the years 1980 through 1989 between percent frequency of pine seed remains in September and October grizzly bear feces and mean number of cones produced per tree on nine transects established in 1980. The data point labeled *OW* represents bear use of overwintered seeds rather than seeds that matured during the current year; frequency of current-year crop use was approximately zero. Data from 1987 were not used because of anomalous cone counts.

Other site characteristics varied with differences in aspect and elevation of intensive seed use by bears among the three periods. Distribution of feeding sites among landscape positions (ridge, upslope, midslope, and lowslope-bottom) differed among time periods ($G = 14.81$, $df = 6$, $p = 0.023$). Most of this variation was caused by proportionally more feeding sites on ridges during 1989 - 90 (11 percent, versus 4 percent and 6 percent during 1985 - 86 and 1987, respectively) and on lowslopes and bottoms during 1987 (38 percent versus 17 percent and 23 percent during 1985 - 86 and 1989 - 90, respectively). These differences are in accord with those expected by differences in elevation of use.

Proportional use of habitat types ($G = 24.50$, $df = 8$, $p = 0.002$) and cover types ($G = 14.43$, $df = 8$, $p = 0.045$) also differed as expected, primarily by differences in feeding sites between 1987 and other years. Feeding sites occurred in fewer high elevation dry habitat types (ABLA/ARCO, ABLA/ARLA, and ABLA/RIMO; see Steele et al. 1983 for acronym definitions) during 1987 than in other years (5 percent versus 12 percent and 19 percent during 1989 - 90 and 1985 - 86, respectively). Feeding also occurred in more low elevation dry types (ABLA/SPBE, ABLA/BERE, and ABLA/JUCO) (7 percent versus 0 percent

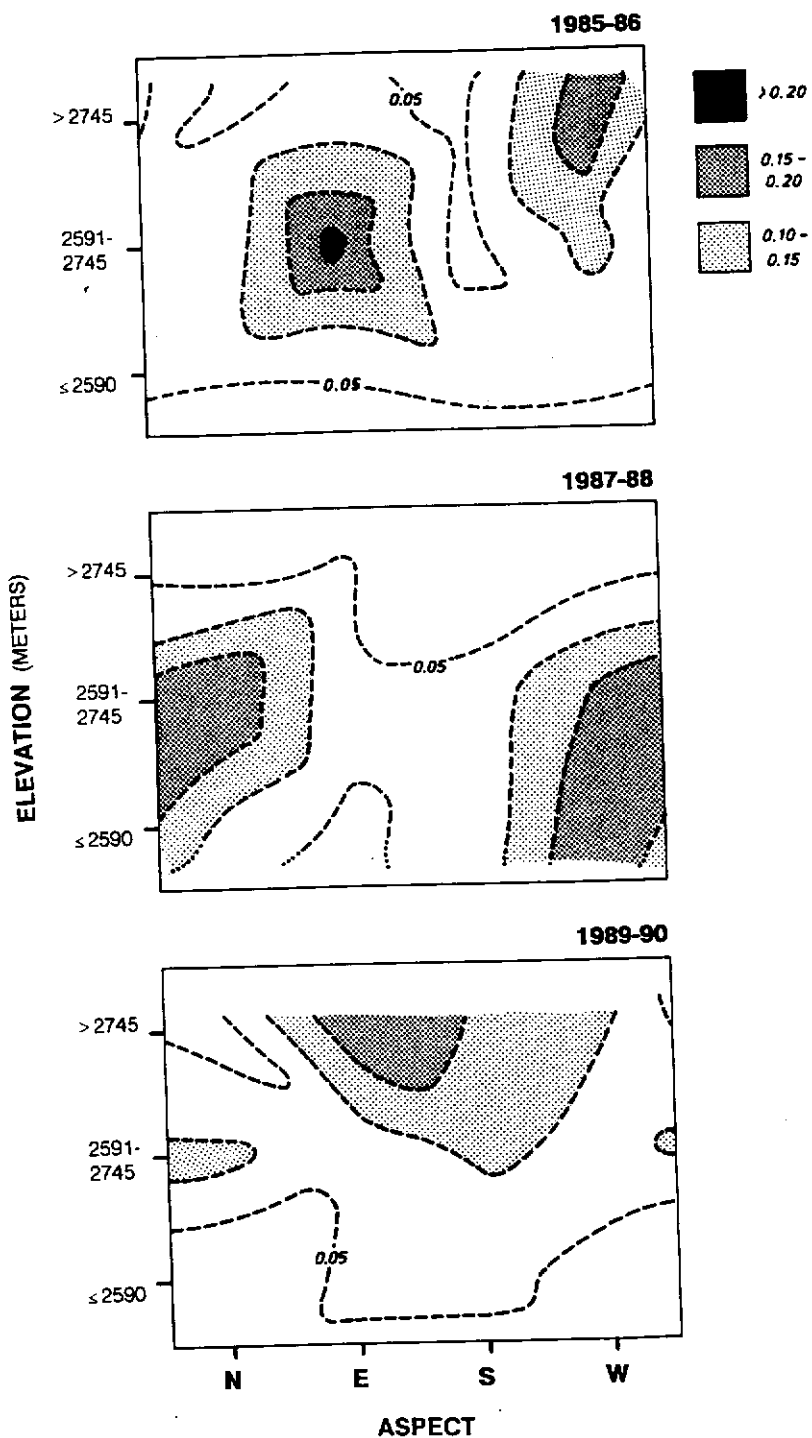


Figure 2. Proportional distribution of grizzly bear feeding on whitebark pine seeds, by four aspect and three elevation categories, for use of the 1985, 1987, and 1989 seed crops. Isolines were interpolated.

in other years). Use during 1989 - 90 also differed from the other periods by more feeding sites in the whitebark pine climax series (12 percent versus 2 percent and 3 percent during 1985 - 86 and 1987, respectively). Cover type use differed only between 1987 and 1989 - 90 by greater use of Douglas-fir (*Pseudotsuga menziesii*) cover types during 1987 and by greater use of whitebark pine dominated cover types during 1989 - 90 (see Despain 1990 for cover type descriptions).

Major features of the forest overstory associated with pine seed use sites did not differ among time periods, including total basal area ($G = 3.01$, $df = 6$, $p = 0.80$) and percent of total basal area in whitebark pine ($G = 7.66$, $df = 8$, $p = 0.47$). Although no significant differences were evident, there was a tendency for more stands used during 1989 - 90 to have >75 percent and fewer stands to have ≤ 25 percent whitebark pine basal area compared to both 1985 - 86 and 1987.

Variation in Use Strategies. Techniques by which grizzly bears acquired pine seeds at sampled radio-telemetry locations differed between 1989 - 90 and the other time periods ($G_c = 16.28$, $df = 1$, $p < 0.001$). Direct acquisition of seeds by scavenging fallen cones or, less often, by feeding directly off the tree canopy was more common during 1989 - 90 compared to 1985 - 86 and 1987 (23 percent versus 4 percent for the other periods combined). Similarly 52 percent of 62 whitebark pine seed feeding sites found along transects in the Cooke City area during 1990 involved black and grizzly bears scavenging fallen cones or breaking tree limbs to obtain cones (8 percent of the total).

Cone remnants and intact cones were found on the ground at sites where bears scavenged fallen cones. In 18 of the 20 instances at telemetry sites during 1989 - 90, no squirrel middens or other squirrel activity were evident in the vicinity. At telemetry-related locations where bears had scavenged fallen cones, identifiable remnant and intact cones on the ground averaged $2.28/m^2$ ($n = 13$, standard deviation (SD) = 2.29), and where the distinction had been made, density of intact cones retaining most of their seeds averaged $0.49/m^2$ ($n = 5$, SD = 0.52). In the Cooke City study area, consumed or disintegrated cones averaged $0.82/m^2$ ($n = 13$, SD = 0.93), and intact cones averaged $0.35/m^2$ ($n = 5$, SD = 0.42). Most of the consumed or disintegrated cones found at these sites had scales closely associated with the cone axis, suggesting that disintegration by wildlife feeding or other causes had occurred on the ground. Cone densities were measured throughout the summer and fall, with the probability that proportionally fewer intact cones were likely to be found as scavenging progressed.

Use of Overwintered Seeds. Telemetry-specific fecal and feeding site analyses show that grizzly bears made substantial use of overwintered whitebark pine seeds from May through September of 1986 and 1990 (figure 3). We noted bear use of a few current-year cones during September 1990, but most seeds used at that time were from the previous year's crop. Similarly heavy use of the overwintered 1978 seed crop by bears during 1979 was documented by Kendall (1983). Results specific to the Cooke City area corroborated the use of overwintered cones during 1990, declining from a June peak to a September low (figure 4).

Our telemetry-related data also show that advent and duration of heavy pine seed use by bears varied, especially between 1987 and 1989. In 1987 use was heavy by August and peaked in September, whereas in 1989 heavy pine seed use occurred only after August and peaked in October. Apparently the moderately large 1987 seed crop was close to fully exploited by October, and few seeds overwintered and were used during 1988 (figure 3) (Mattson and Jonkel 1990).

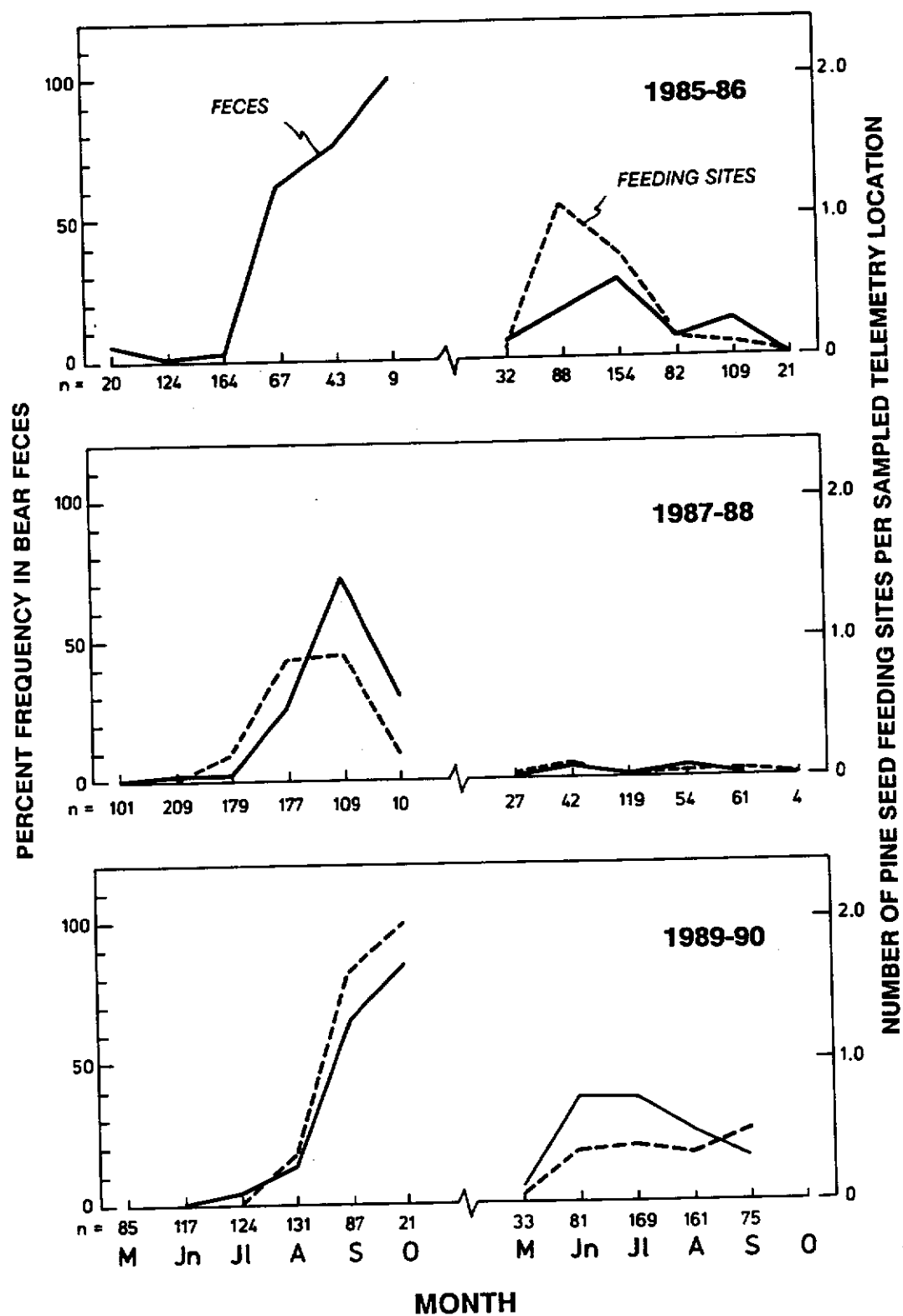


Figure 3. Percent frequency of whitebark pine seeds in Yellowstone grizzly bear feces and number of pine seed feeding sites per sampled telemetry location, by year and month. Criteria for sampling feeding sites were different during 1985, and so feeding site data are not shown. Monthly sample sizes are for feces.

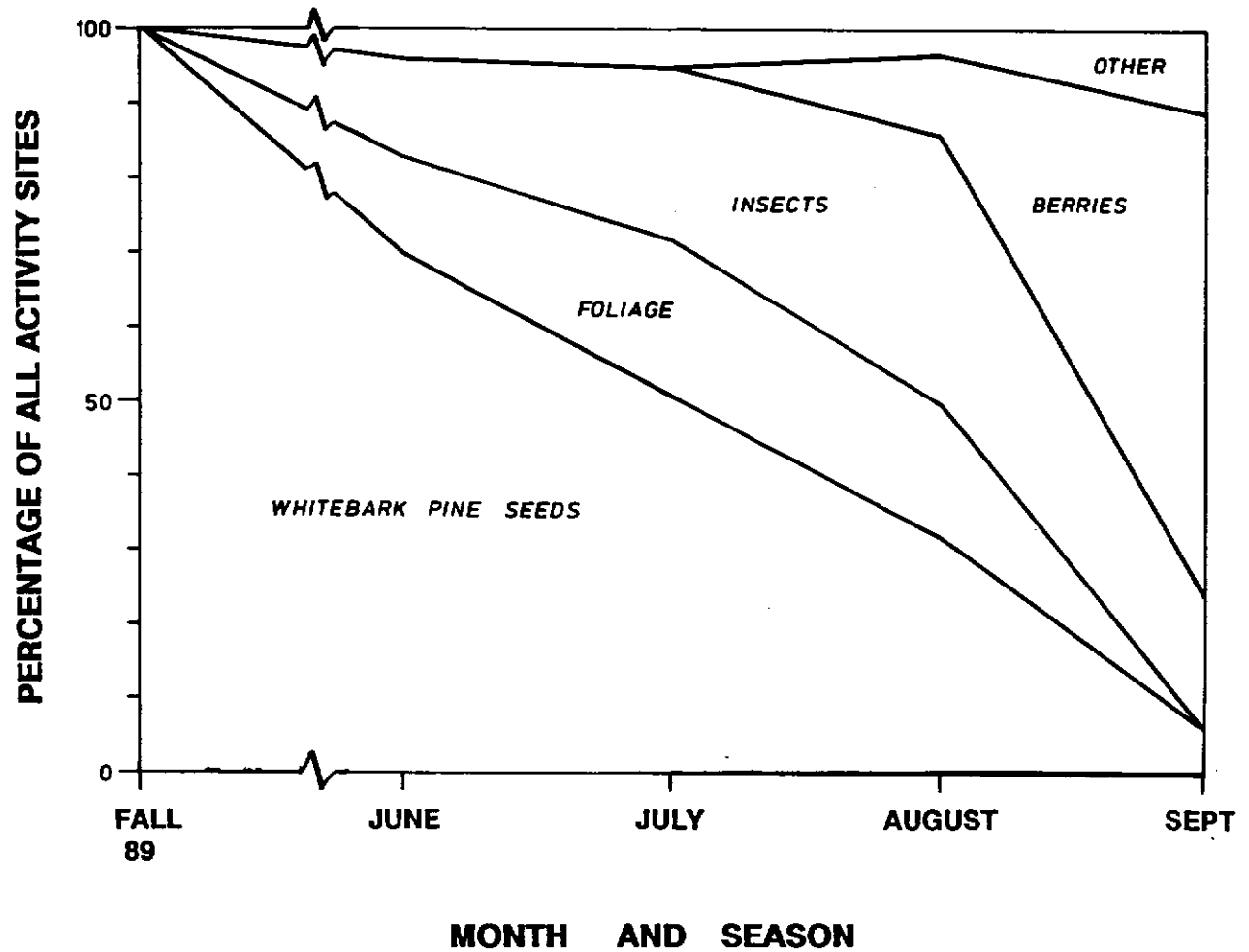


Figure 4. Relative percentage of different feeding activities encountered on bear sign transects in the Cooke City area during 1989 and 1990, by month and pooled for fall of 1989.

Cone Transects

Cone production varied among years ($F = 53.13$, $df = 10$, $p < 0.0001$) and among sites ($F = 9.64$, $df = 8$, $p < 0.0001$) at the nine transects established in 1980, for which we had 11 years of data. Variation in production among these sites was not independent of variation among years ($F = 8.20$, $df = 67$, $p < 0.0001$).

We did not find statistically significant differences in cone production among low, moderate, and high elevations during 1985, 1987, and 1989. Sample sizes were small, and among-site variation in cone production was high. However, elevational means did not contradict the hypothesis that cone production during these three crop years varied in accord with distribution of bear use. Production tended to be concentrated at low to mid-elevations during 1985, low elevations during 1987, and mid- to high elevations during 1989 (table 1).

Table 1. Mean number and standard deviation (SD) of whitebark pine cones produced per tree, averaged across transects and by year and elevational zone. Elevational zones were delimited differently than for grizzly bear use to equalize transect sample sizes among zones.

Year	Elevation (m)								
	2,561 - 2,683			2,684 - 2,805			2,805 +		
	\bar{X}	SD	n	\bar{X}	SD	n	\bar{X}	SD	n
1985	27.2	—	2	31.2	24.5	5	13.0	—	2
1987*	4.5	—	3	2.8	4.0	8	1.0	0.9	5
1989	27.5	15.4	7	61.8	41.7	9	54.3	52.1	5

*Low counts during 1987 probably resulted from early maturation and consumption of the seed crop prior to transect counts.

We stratified transects by aspects and elevations of high and low proportionate bear use during 1989 - 90 to test the hypothesis that mean and variance of cone production at transects did not vary between these areas of high and low bear use. We did not do a comparable analysis for the other periods because of insufficient transect sample sizes. Mean cone production did not differ between the two strata defined by bear use during 1989-90 (Cochran's $T = -1.52$, $df = 11.2$, $p = 0.155$); however, variance among transects was higher in the stratum associated with lower use ($SD = 50.06$ versus $SD = 16.07$; $F' = 9.70$; $df = 9,7$; $p = 0.007$).

We tabulated yearly intervals between the two largest cone crops observed on individual trees at the nine transects established in 1980. We observed no major difference in intervals depending on whether the largest or second largest crop had occurred first ($G = 8.88$, $df = 4$, $p = 0.068$) and so we pooled the data ($n = 88$ intervals). Modal intervals occurred at four years (20 percent of the total) and nine years (19 percent). Only 24 percent of the intervals were ≤ 2 years.

Frequency of cone production by individual trees $>$ the current-year mean was inconclusively related to above-average production for the previous two moderate-to-large cone crops (table 2). No relationship was evident for the 1985 crop. Based on other results we could both accept (1987) or reject (1989) the null hypothesis, that above-average current-year cone production was independent of above-average cone production during the two previous crops.

Table 2. Proportion of whitebark pine trees producing above-average cone crops, considering production relative to the contemporaneous mean during the previous two moderate to large crops,* and statistics for analysis of independence.

Previous Cone Crops	Proportion of Trees $>\bar{X}$		
	1985	1987	1989
$>\bar{X}$ Previous two crops	0.385	0.500	0.071
$>\bar{X}$ Most recent crop only	0.294	0.562	0.182
$>\bar{X}$ 2nd most recent crop only	0.500	0.250	0.250
$<\bar{X}$ Previous two crops	0.231	0.154	0.421
Statistics			
<i>G</i>	3.73	11.210	7.910
<i>p</i>	0.29	0.011	0.048
<i>n</i>	83	85	75

*Mean cone production of all trees ≥ 15 .

Discussion

Cone production at our permanent transects varied significantly among sites, trees, and years. Site variation was also associated with annual variation. These results suggest that even during years of heavy to average cone crops, nonrandom among-stand variation in production was substantial. Other studies of tree fruit and seed production have yielded similar results (e.g., Alexander, Edminster, and Watkins 1986; Franklin 1968; Grisez 1975; Kozhevnikov 1963). However, Weaver and Forcella (1986) found no significant among-stand or region variation in their study of whitebark pine cone production. Discrepancy between our results and those of Weaver and Forcella (1986) could be a consequence of their focus on higher elevation stands or differences in study years.

Bear use of pine seed crops also varied considerably. Widespread fall bear use was apparently contingent on substantial cone production, in excess of an average 21 cones per tree. This happened only three or four times (depending on actual production during 1987) in the 11 years from 1980 through 1990. However, during at least three years (1981, 1986, and 1990), cone crops the previous year were large enough to sustain substantial bear use during the summer. Thus, pine seeds were not available to most bears during 7 of the 11 years.

Sites used by bears to forage on large pine seed crops differed between successive crop years. Our analysis of how site variation in bear use related to cone production was compromised by inadequate transect sample sizes. However, our results do not contradict the plausible hypothesis that bears tended to more heavily use areas with more average cone production and less among-stand variation. During 1989 - 90, when cone production tended to be concentrated at higher elevations, bears used more high elevation stands with whitebark pine cover types, of the whitebark pine habitat type series. During 1987, when cone production occurred at lower elevations, bears also used more low-elevation stands with Douglas-fir cover types, of drier subalpine fir (*Abies lasiocarpa*) habitat types.

Although intraspecific competition could mask selection for "optimal" foraging sites (Rosenzweig 1991), we suspect that large seed crops exceed demand and that observed bear use was sensitive to favorable site conditions. This supposition is partly based on other analyses showing that most grizzly bear mortality in the Yellowstone area, of which virtually all is human-caused, occurs during years of poor pine seed crops (Mattson, Blanchard, and Knight, 1992). Thus, we have hypothesized that availability and distribution of other foods used by bears during years of poor pine seed crops more directly limit the bear population than does availability of the episodic large pine seed crops (Mattson, Blanchard, and Knight 1991; Mattson, Blanchard, and Knight 1992).

If variation in bear habitat use does reflect availability of seeds, then bear use of the large 1985, 1987, and 1989 crops suggests interesting differences in whitebark pine cone production between successive large crop years. Specifically, distribution of bear feeding sites is a basis for hypothesizing that peak production does not occur at the same general elevation and aspect between successive large crops, especially, as during the period from 1985 through 1989, when crops occurred at two-year intervals.

As stated previously, results from our analysis of cone-count transects suggest synchronous variation of cone production among sites and years. Our analysis of cone production on individual trees also suggests that intervals between large crops were most commonly four and nine years. Both of these results lend further weight to the hypothesis suggested by bear use that peak production is nonrepetitive among sites between successive large crops. Because seed and fruit production by trees is known to be at least partly dependent on carbohydrate reserves (Fraser 1966; Kramer and Kozlowski 1960; Nesvetailo 1987; and others), availability of these reserves is the most likely proximal cause of this among-site variation in production. The frequent 4- to 9-year intervals between large crops on individual trees suggest that under most circumstances whitebark pine in our study area required this time to replenish the carbohydrate reserves needed to produce large crops. Under circumstances where large crops were produced in our study area at two- to three-year intervals, we expected that the same trees would not be contributing equally to successive large crops. However, our analysis of this specific question was inconclusive.

Variation in bear habitat use and presumably peak production of cones between successive large crops resulted in fundamental differences in how bears acquired pine seeds. The most striking difference occurred during 1989 - 90 when bears obtained far more seeds by scavenging on fallen cones compared to other years. Results from the Cooke City area corroborate a high frequency of scavenging on fallen overwintered cones, although the more frequent incidence of this behavior around Cooke City could be caused by the inclusion of black bear feeding in our sample. Nonetheless, these results reconcile what appeared to be major differences in how brown bears in Siberia and grizzly bears in the Yellowstone area acquired stone pine seeds (Mattson and Jonkel 1990).

The greater incidence of cone scavenging during 1989 - 90 appeared to derive from greater bear use of whitebark pine stands at elevations above the range of red squirrels (cf. Reinhart and Mattson 1990).

Thus red squirrels were apparently not present to harvest and cache cones in many areas and were also not major competitors for seeds. Hutchins and Lanner (1982) observed that red squirrels were one of the major consumers of whitebark pine seeds, and so their absence probably translated into a greater number of cones overwintering on trees and being available for bears to scavenge when they fell the next year. We could not conclude from our observations to what extent cone fall was caused by natural dehiscence, wind-throw, or animals.

Bear use of pine seeds during 1989 - 90 also contradicted the conclusions of Mattson and Jonkel (1990) to the effect that Yellowstone grizzly bears made very little use of high elevation whitebark pine stands where red squirrels were scarce. During 1989 - 90 grizzly bears did use high elevation whitebark stands, and in two instances were observed for the first time during our study to use cones directly off the crowns of elfin trees at upper timberline. Use of cones directly from the crown by grizzly bears was also observed by Jonkel and Cowen (1971) in the Whitefish Range of northwestern Montana and by Mealey (1975) in the Yellowstone area.

Management Implications

Our results point to the pitfalls of short-term studies of bear habitat use. Mattson, Blanchard, and Knight (1991) arrived at the same conclusion based on large annual variation in grizzly bear food habits and suggested that five to seven years of study were needed to adequately document significant variation. It is clear from our analysis that strategies and habitat use associated with bear foraging on even a single food can be so varied that > six to nine years may be required to adequately document annual variation. A shorter duration, two- to three-year study of pine seed use by Yellowstone grizzly bears could have produced misleading or erroneous conclusions about specifically how and where bears acquired pine seeds. Some of the conclusions reached by Mattson and Jonkel (1990), based primarily on bear use of two seed crops, are an example of this risk. To date, no published study has given significant consideration to long-term annual variation in bear food habits (Mattson, Blanchard, and Knight 1991) or habitat use, much less habitat use associated with acquisition of a single important food.

From results presented here, we conclude that Yellowstone grizzly bears will potentially make intensive use of the entire elevational and site range of whitebark pine. No part of this range can be discounted as relatively unimportant to the grizzly bear population. However, bear use of pine seeds any given year will be highly varied and probably contingent on where and how much cone production has occurred. This conclusion is also a basis for hypothesizing that, as the duration of a bear habitat use study increases, fewer sites will be found to be unimportant to bears, at least during some year.

Our results also confirm that the substantial use of overwintered pine seeds by Yellowstone grizzly bears first recorded by Kendall (1983) is relatively frequent. Thus, habitats where bears use pine seeds need to be secure not only during the fall, but also potentially during the summer and late spring. Some bear use of overwintered pine seeds may persist into early fall and contradict use expected from the current year's seed crop.

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