Stone pines and bears

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ABSTRACT

Bears use stone pine (subsection Cembrae) seeds throughout the Northern Hemisphere, primarily Pinus sibirica, P. pumila, *and* P. koraiensis *in Eurasia, and* P. albicaulis *in North America. Bears make the greatest use of pine seeds in eastern Siberia and in the Northern Rocky Mountains of the United States. The pine seeds are important to bears because of their high nutritional value. During years of poor pine seed crops, Yellowstone area grizzly bears are trapped and killed more often; in Siberia, brown bears wander more and become more predatory.*

Grizzly use of pine seeds in the Yellowstone area is variable among years, in accord with the erratic seed production. Virtually all seeds used by bears are extracted from red squirrel caches. In many areas, the whitebark pine has nearly disappeared as a result of the double onslaught by white pine blister rust and mountain pine beetle infestations. This important food for some bears and populations has been nearly eliminated, and may not be available to bears despite human intervention for hundreds of years. Because the trees are so thinly distributed, silvicultural treatments hold little promise of appreciably enhancing pine seed availability to bears.

INTRODUCTION

The seeds of whitebark pine (*Pinus albicaulis*) and other stone pines (subsection Cembrae) are a high-quality wildlife food characterized by high triacerglycerol content (Craighead and others 1982; Hutchins and Lanner 1982; Mealey 1980; Shcherbina and Larionova 1963) and energy concentration comparable to that of fleshy fruits (Craighead and others 1982; Mealey 1980). Large seed size contributes to efficiencies of use by numerous species of birds and mammals (Hutchins and Lanner 1982; Tomback 1983). Because the cones are typically indehiscent (Arno and Hoff 1989; Lanner 1982), seeds remain concentrated in the cones and contribute to efficiencies of use, especially by red squirrels (*Tamiasciurus hudsonicus*) and bears (*Ursus* spp.). Where bears eat the entire cone, the fleshy pulp of the cone also contributes to their diet (Jonkel 1967).

Whitebark pine and other stone pine seeds are high-quality bear food for reasons in addition to their high energy content. Stone pine seeds mature by August and are available from then until bears hibernate (Hutchins and Lanner 1982; Iroshnikov 1963; Kendall 1983). This period corresponds with the critical hyperphaegic state during which bears accumulate the fat necessary to sustain them through hibernation and subsequent hypophaegia (Nelson and others 1983). Because of their high digestible lipid content, pine seeds very likely contribute more to efficiencies of body fat accumulation by bears than foods high in protein or sugar content (Allen 1976; Brody and Pelton 1988; Hadley 1985). Because of their durable nature, pine seeds can overwinter in or out of cones and provide high-quality food for bears the next spring and summer. Whitebark pine seeds and cones also contain estrogenic compounds (Jonkel 1967; Jonkel and Cowan 1971). These compounds could influence reproduction in bears, but effects are undocumented and the precise roles played by estrogens in delayed implantation are as yet unknown.

Bear use of stone pines is disadvantaged by frequent poor cone crops. Craighead and Mitchell (1982) recorded bumper cone crops of whitebark pine only 2 of 12 years in the Yellowstone National Park area and 2 of 7 years in the Scapegoat Mountains of Montana. In recent years we recorded good crops 2 and poor crops 4 out of 12 years in the Yellowstone area. Data from Weaver and Forcella (1986) suggested an average 2-year interval between poor crops and 6-year interval between good crops of whitebark pine in the Rocky Mountains during the 1970's. In Siberia, Nesvetailo (1987) estimated 10 good and 10 poor Siberian stone pine crops during a 58-year period. Together these observations suggest an average 2- to 6-year interval between both good and poor stone pine crops. It is also clear that this cycle is highly irregular among years, regions, and habitat types.

In areas where bears depend on stone pine seeds for fattening, and where there are typically few fleshy fruits available, years of poor pine seed crops result in increased conflict between bears and humans. In the Yellowstone area there is a predictable and dramatic increase in adult female bear deaths and management actions against bears during poor seed crop years (Blanchard, this proceedings). Similarly, in Siberia poor stone pine seed crops result in increased attacks on humans and increased livestock and agricultural crop depredations (Stroganov 1962; Ustinov 1965). This increased conflict probably results not only from an increased number of poor-condition bears (Ustinov 1965), but also because of the many human foods available in bear habitat that constitute high-quality alternatives to native fruit and seed crops (Mattson, in press).

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DISTRIBUTION OF USE

In common with other stone pines (including *P. sibirica*, *P. pumila*, and *P. koriaensis*), whitebark pine is used by bears wherever it is abundant (fig. 1). In North America this occurs south of the Canadian border in the cordillera of the western United States. Farther north, whitebark pine is only an incidental part of the forest vegetation (Arno and Hoff 1989).

Within the range of stone pines, bear use of stone pine seeds ranged from near zero in Glacier National Park, MT, (Kendall 1986) and the Mission Mountains of Montana (Mace and Jonkel 1986) to 18.3 percent and 28 percent of total sampled fecal volume in Yellowstone (Mattson and others, in preparation) and the Lake Baikal area of Ulan-Ude, U.S.S.R. (Ustinov 1965; Vereschagin 1976), respectively (table 1). Peak use consistently occurred from September through November. A secondary peak usually occurred in the spring, in association with use of overwintered pine seeds following large crops the previous fall. This pattern of use is typified by Yellowstone data for the years 1977-87 (fig. 2). When feeding on pine seeds, bears tend to consume the seeds to the near-exclusion of all other foods. This was consistently reflected in high mean percent volumes of pine seeds in scats—percent volume divided by percent frequency (fig. 2).

There is a remarkable correspondence between the current southern limit of the main distribution of brown bears (*Ursus arctos*) and stone pines (fig. 1). This correspondence almost certainly does not reflect dependence of either species on the other. More likely human (*Homo sapiens*) intolerance has relegated brown bears to the comparatively inhospitable and harsh environments characterized by stone pines (Mattson, in press). Nonetheless, within this area of overlap, stone pine seeds are an important food for numerous Asian and North American bear populations (Aune and Kasworm, in press; Bergman 1936; Bromlei 1965; Craighead and others 1982; Kendall 1983; Kistchinski 1972; Novikov 1956; Stroganov 1962; Ustinov 1965, 1976; and others), especially where there were few, irregularly available fleshy fruits (Mattson and others, in preparation).

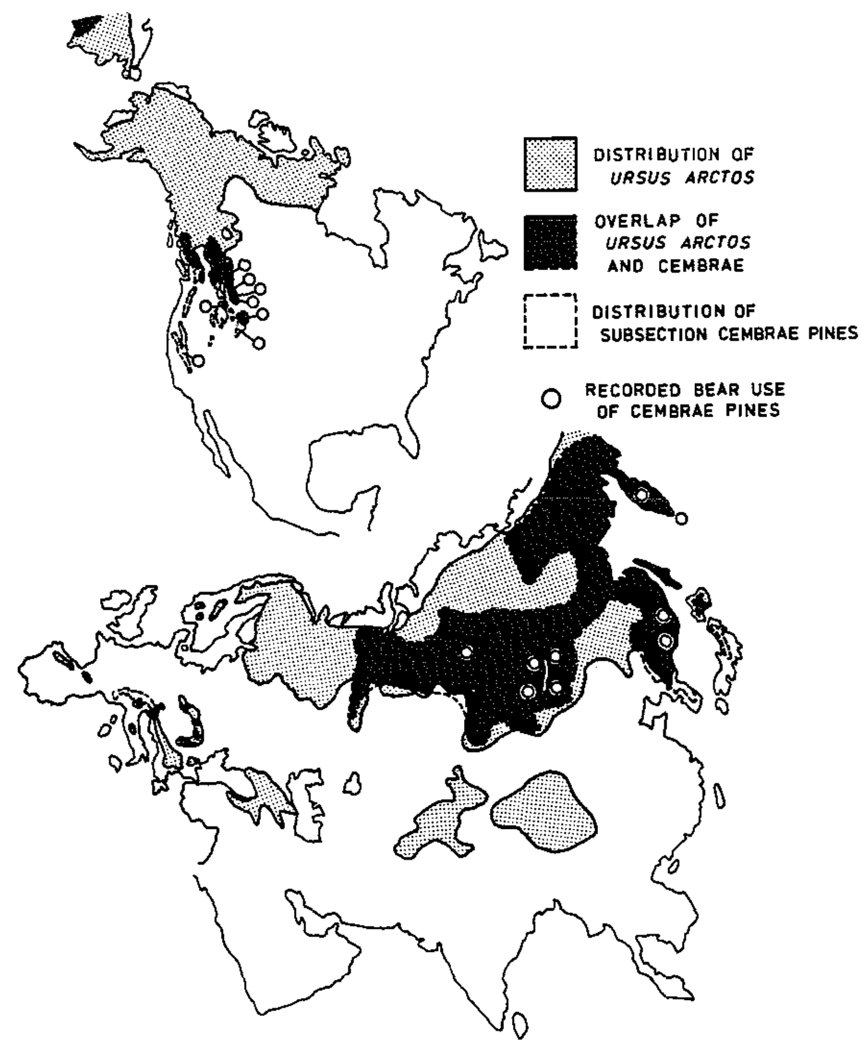

Figure 1—Distribution of brown bears (*Ursus arctos*) and stone pines (subsection Cembrae), and recorded instances of substantial stone pine seed use by bears (*Ursus* spp.) (Clevenger and others 1987; Critchfield and Little 1966; Elgmork 1987; Patnode and LeFranc 1987; Yi-Ching 1981; Zunino 1975).

Table 1—Percent frequency (%F) and volume (%V) of stone pine seeds in bear scats from study areas in the Rocky Mountains, Sierra Nevada, and Siberia

Study area	Total scat collection %F	Total scat collection %V	Maximum month or season %F	Maximum month or season %V	Month or season
Rocky Mountains					
Glacier NP, BC[1]	—	—	2	tr	Fall
North Fork of the Flathead, MT[2/11]	4.0	1.2	19.2	11.3	September
South Fork of the Flathead, MT[2]	.7	.4	—	—	
Glacier NP, MT[3]	0	0	—	—	
Mission Mtns, MT[2]	.3	.1	—	—	
East Front, MT[2/4]	14.6/5.1	12.6/4.5	33.3	31.0	October
Yellowstone, MT&WY[5]	30.3	18.4	42.8	39.2	October
Grays River Mtns,WY[6]	—	—	22.5	15.0	Fall
Sierra Nevada					
Yosemite NP, CA[7]	3	1	17	7	Fall
Siberia					
Kamchatka[8]	—	14	—	—	
Primore[8]	—	6	—	—	
Ussuri[9]	—	5.3	—	25.0	November
Baikal[8/10]	—	28	—	100.0	October

[1]Mundy (1963).
[2]Mace and Jonkel (1983).
[3]Kendall (1986).
[4]Aune and Kasworm (in press).
[5]Mattson and others (in preparation).
[6]Irwin and Hammond (1985).
[7]Graber and White (1983).
[8]Vereschagin (1976).
[9]Bromlei (1965).
[10]Ustinov (1965).
[11]Husby and others (1977).

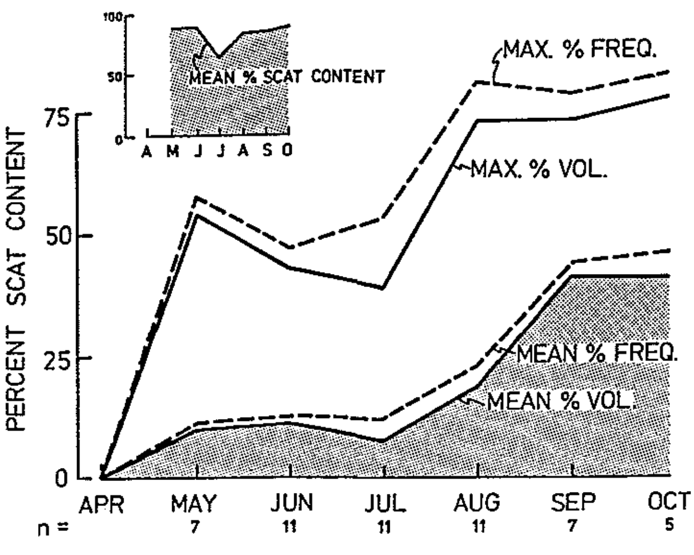

Figure 2—Percent frequency and volume of whitebark pine seeds in scats collected in the Yellowstone area, by month, 1977-87 (*n* = number of years). Inset diagram depicts mean percent pine seed volume in scats of occurrence, by month.

ACQUISITION OF PINE SEEDS

Bears employ several strategies to acquire stone pine seeds depending on the presence of rodent intermediaries, the density and stature of stone pine forests, and the bear's ability to climb. Black bears (*Ursus americanus* and *Selenarctos thibetanus*) are more adept climbers than brown bears (Herrero 1978) and are more likely to climb trees to consume seeds in the canopy, or to break limbs off and subsequently consume the seeds on the forest floor (Barnes and Bray 1967; Bromlei 1965; Mealey 1975; Stroganov 1962). In northwestern Montana, bears commonly climbed trees to acquire whitebark pine cones. These bears often had no hair on their entire front legs after a fall spent feeding on pine seeds (figs. 3 and 4). Pitch that built up on the feet and legs from clawing small whitebark pine trees peeled off when caked with dirt and debris, taking all the hair along.

Brown bears seem generally restricted to acquiring seeds that have fallen or been brought down to the forest floor by other animals. Scavenging on fallen cones is apparently common in Siberia (Bromlei 1965). In the Rocky Mountains, forest floor scavenging on cones is rare (Mattson, personal observation; Aune and Kasworm, in press). In the Yellowstone area only 3 percent of 193 instances where bears were known to have used pine seeds involved scavenging on fallen cones. These few

Figure 3—The front feet of this black bear are caked with pitch from feeding on whitebark pine cones and seeds (1959 photo by C. Jonkel).

Figure 4—Cracking of the pitch, debris, and hair mat on this young black bear's front foot show the extent of whitebark pine cone and seed feeding by this bear, and the process whereby bears lost the hair from their front legs (1959 photo by C. Jonkel).

instances occurred in stands where whitebark pine comprised approximately 76 percent of total stand basal area ($\bar{X}$= 46.7 ± 10.6 m^2/ha), and following extreme weather that knocked cones out of the trees. Taylor (1964) similarly mentioned bears concentrating at and scavenging on cones on the forest floor in an area where whitebark pine cones were wind-thrown by a "violent storm." Bears also consumed cones directly from the canopy of dwarfed stone pines, commonly in Kamchatka (Bergman 1936; Kistchinski 1972) and less frequently near timberline in northwest Montana and Yellowstone (Mattson and Jonkel, personal observation; Craighead and others 1982; Jonkel 1967; Tisch 1961).

In most areas where brown bears make substantial use of stone pine seeds, rodents are a critical link. In the Rocky Mountains red squirrels preferentially harvest whitebark and limber pine seeds (Hutchins and Lanner 1982) and cache them in middens, typically in intact cones (Hutchins and Lanner 1982; Kendall 1983). Bears subsequently search out these middens and excavate the whitebark pine cones. This commonly occurs in the Yellowstone area (Kendall 1983) and along the East Front of the Rocky Mountains in Montana (Aune and Kasworm, in press; Schallenberger and Jonkel 1980). Excavation of squirrel middens by bears to obtain seed and fruits is also known from northern Idaho (whitebark pine seeds) (Kendall 1989), Yosemite National Park (whitebark pine seeds) (Graber and White 1983), and northern Minnesota (hazelnuts [*Corylus cornuta*]) (Rogers 1989). In the Yellowstone area, 97 percent of 196 pine seed feeding sites involved excavation of squirrel middens. A similar high percentage of squirrel midden use was characteristic on the East Front of Montana (Aune and Kasworm, in preparation; Schallenberger and Jonkel 1980).

In Siberia, the Siberian chipmunk (*Eutamias sibiricus*) appears to be the primary rodent intermediary between stone pine seeds and bears. As in North America, stone pine seeds are a preferred food of both chipmunks and squirrels (*Sciurus vulgaris*) in Siberia (Ognev 1940). Siberian chipmunks commonly make stone pine seed caches of 1.5 to 2 kg in size (up to 6 kg) for winter and spring consumption (Ognev 1940). And as in the Rocky Mountains, bears search out and excavate these rodent caches in spring and late fall (Bromlei 1965; Novikov 1956; Ognev 1940; Stroganov 1962; Ustinov 1976).

The much greater use of chipmunk rather than squirrel caches by Siberian bears is puzzling. In his monograph on Eurasian mammals, Ognev (1940) suggested that chipmunks commonly attained much higher densities than squirrels in the range of Siberian stone pines. He quoted an estimate for one area of only 0.14 squirrel "nests"/km of transects. This compared with 0.11 to 0.14 squirrel middens/km in pure whitebark pine stands of the Yellowstone area (Reinhart and Mattson, this proceedings). Significantly, virtually no bear use of squirrel middens was observed in pure whitebark pine stands of the Yellowstone area. This suggests that when squirrels are at such low densities bears use relatively few squirrel caches. By all indications Siberian squirrels more often cache cones in hollow trees, through elevated openings, than do squirrels in the Rocky Mountains. This would further complicate acquisition of squirrel caches by Siberian bears.

Bears are remarkably adept at extracting seeds from cones in the Yellowstone area; few cone remnants are ingested along with the seeds (Kendall 1983). One way that bears achieve this is by scraping away the cone scales with their claws and lapping up the seeds with their tongues from among the debris (Kendall 1983). Typical bear feces that result from consumption of pine seeds consist almost wholly of broken seed coats (Kendall 1983; Tisch 1961). Very few seeds pass through intact, and it is doubtful that bears serve as a significant dispersal agent for whitebark pine in most of the Rocky Mountains (Hutchins and Lanner 1982). This is especially likely given the poor germination potential of unburied whitebark pine seeds (McCaughey, this proceedings).

Interestingly, Siberian brown bears are apparently prone to ingest more cone scales when scavenging pine seeds out of cones from the forest floor (Semechkin 1963). This may be a consequence of their greater use of individual seeds extracted from chipmunk caches. The scavenging of cones may also be marginally profitable, providing little incentive to invest the added time and energy required to break apart the cones and pick out the individual seeds.

Of the three main seed-acquiring techniques, the excavation of rodent caches is on average the most energetically efficient process for bears. Unless there is a bumper crop, bears will expend considerably more energy than they acquire by breaking major tree limbs and harvesting seeds from the relatively few cones on each limb. Similarly, unless there is an unusual weather event, very few cones will survive depredations of chipmunks, nutcrackers (*Nucifraga* spp.), and other avifauna and fall intact to the forest floor (Hutchins and Lanner 1982; Kozhevnikov 1963). Rodents increase the foraging efficiencies for bears by harvesting otherwise unavailable, intact cones and seeds from trees, then concentrating them in caches. Red squirrels will use caching sites or middens for many years (Reinhart and Mattson, this proceedings), which in turn facilitates their location by bears. In the Yellowstone area individual middens receive repeat use by bears in the same and different years (Mattson, personal observation; Kendall 1983). Bear depredations may be so heavy in some habitats that many squirrels may not survive (Mattson and Reinhart 1987; Reinhart and Mattson, this proceedings). In these situations midden locations may be less predictable due to higher turnover of individuals in the squirrel population.

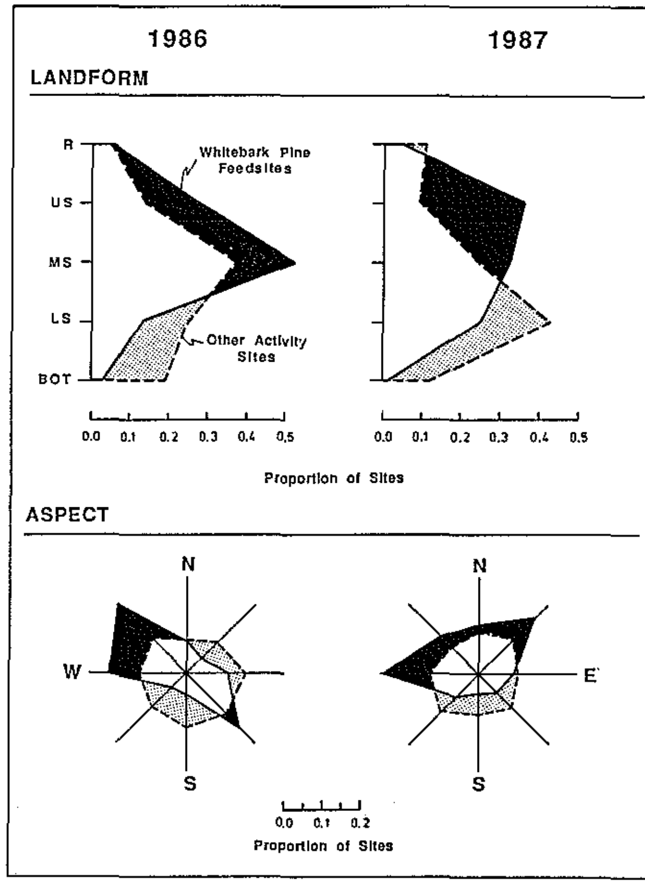

Figure 5—Proportionate distribution of whitebark pine seed feed sites and all other activity sites among landform and aspect classes in the Yellowstone area.

CHARACTERISTICS OF PINE SEED FEEDING SITES

Topography

Bears exhibited different tendencies in their use of the landscape to acquire pine seeds depending on the year and study area. In the Yellowstone area, bears used mid-slopes and up-slopes to forage on pine seeds more than expected from distribution of all activity sites (fig. 5). However, they exhibited greater preference for mid-slopes during 1986, when using an overwintered crop, and up-slopes during 1987, when using a current year's crop. (Activity site and feed-site parameters were determined from visiting telemetry locations of radio-instrumented bears.) Greater use of mid- and up-slopes corresponded with the tendency for whitebark pine to occur at higher elevations in more wind-exposed habitats (Mattson and Reinhart, this proceedings). Interestingly, in the Yellowstone area bears used ridgetops relatively little for pine seed foraging; in past years, ridgetops were the main foraging area for bears in the Whitefish Range of northwestern Montana (Jonkel 1967).

Distribution of pine seed feed sites among aspects varied considerably among years, regions, and landforms. In the Yellowstone area, greater than expected use of west and northwest exposures occurred during 1986, and of west, northwest, and northeast exposures during 1987 (fig. 5). Use of west exposures occurred most often on mid- and low slopes. On the East Front of the Rockies, northeast, east-southeast, southwest, and west-southwest exposures were used most for foraging on pine seeds (Aune and Kasworm, in press).

The distribution of use among aspects in Yellowstone appeared to be related to environmental factors, depending on landform. (We derived estimates for environmental variables from published data.) Use of up-slopes and ridges was negatively related to estimated summer radiation (Buffo and others 1972) and estimated relative frequency of summer winds >8 k/h (Dirks and Martner 1982, Upper Rendezvous site) (fig. 6). This suggests that more exposed and "droughty" conditions did not favor bear use of pine seeds in convex topography. This effect was most likely mediated through the abundance of red squirrels; site favorability for squirrels was negatively

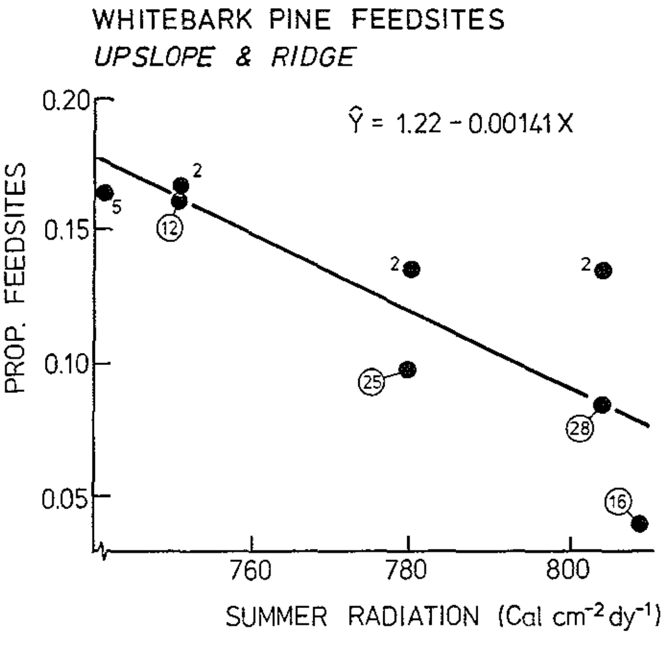

Figure 6—Relationship of proportionate pine seed feed-site distribution in Yellowstone among aspect classes, on convex landforms relative to summer radiation (June 22) and frequency of summer winds >8 k/h (numbers, with higher values circled).

related to wind exposure and positively related to stand basal area (Reinhart and Mattson, this proceedings). On mid- and low slopes, pine seed foraging increased exponentially with increased frequency of winter winds >8 k/h ($\hat{y} = 0.097 + 12.2\,x^4$, where y is the proportion of pine seed feed sites and x is the proportion of winter winds >8 k/h, in a given aspect class). This relationship was probably related to decreased or more irregularly drifted winter snowpack with increased winter wind exposure (Reinhart and Mattson, this proceedings). Given that spring and summer bear use of overwintered crops occurred more commonly on mid-slopes, a combination of shallower snowpack and more productive squirrel habitat probably favored early season bear use of overwintered squirrel caches on west slopes.

The elevational distribution of pine seed feed sites also varied among study areas and years, although in Yellowstone virtually all feed sites occurred above 2,425 m (8,000 ft) elevation (fig. 7). East Front feed sites averaged 455 m (1,500 ft) lower in elevation than Yellowstone feed sites, and partly reflected the 3° latitude difference in study areas (Aune and Kasworm, in press). The elevational distribution of pine seed feed sites was also much more dispersed on the East Front compared with Yellowstone. The much lower elevational range of East Front feed sites, between 1,515 and 1,879 m (5,000 and 6,200 ft), almost certainly reflected bear use of limber pine (*Pinus flexilis*) seeds. Bear use of limber pine seeds from squirrel caches was also recorded in Yellowstone, but only three times out of a total of 196 recorded instances of pine seed use.

Use of the overwintered Yellowstone pine seed crop during 1986 tended to occur at higher elevations than use of the current year's crops during 1979 and 1987 (fig. 7). The higher elevational distribution of feed sites during 1986 conformed more closely to the elevational distribution of whitebark pine (from the Mount Washburn massif; see Mattson and Reinhart, this proceedings) than did pine seed feed sites the other 2 years. This suggests that bears preferred stands with higher whitebark pine basal area when using overwintered seed crops.

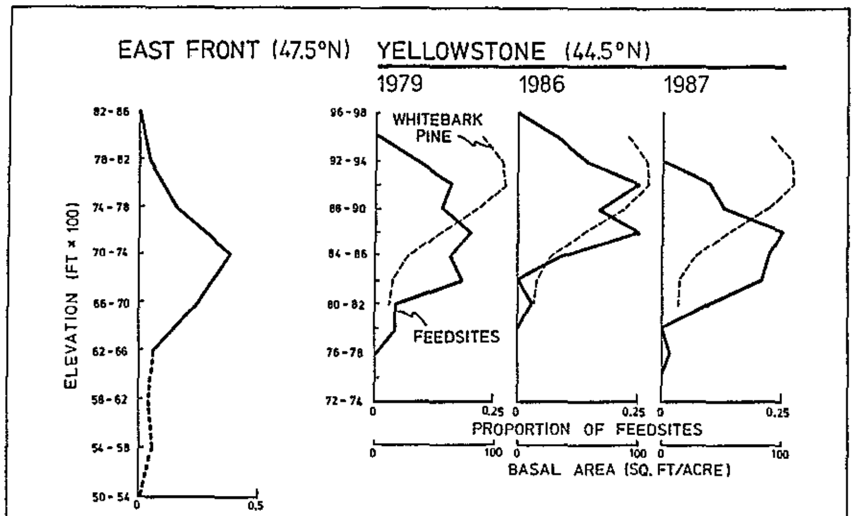

Figure 7—Proportionate distribution of East Front (Aune and Kasworm, in press) and Yellowstone (by year) pine seed feed sites by elevation, and mean whitebark pine basal area by elevation for the Yellowstone area (1 m = 3.28 ft; 1 m^2/ha = 0.2295 ft^2/acre).

Timber Overstory

There was a weak positive association between intensity of midden use by bears and whitebark pine basal area (table 2). This was more evident during use of an over-wintered crop during 1986, when bears tended to use more stands with higher whitebark pine basal areas compared to 1987 ($x^2 = 12.81$, df = 5, $P = 0.025$; number of feed sites relative to six categories based on whitebark pine basal area). This difference is understandable given that stands with higher whitebark pine basal areas would have a higher probability of providing over-wintered seeds. However, there was very little correlation between number of cones excavated from middens by bears and whitebark pine basal area ($r = 0.194$, $n = 69$, $P = 0.106$).

Whitebark pine basal area was apparently only one of several habitat parameters that determined the location and intensity of pine seed foraging by bears. This was further implied by the relatively low average basal areas and percent composition of whitebark pine in stands used by bears for foraging on pine seeds (table 3). Stands with high percent whitebark pine composition and whitebark pine basal area were generally not preferentially selected by bears in the Yellowstone area.

We recorded no use of younger aged, early successional stands by bears for foraging on whitebark pine seeds in the Yellowstone area. All stands used by bears were classified as mature to overmature and mid-successional to climax. This is not surprising, given the probable late age at which whitebark pine produce an appreciable number of cones under normal stand conditions. Although the relationship between cone production and stand age is not known for whitebark pine, this relationship is well described for the related and morphologically similar Siberian stone pine (Axelrod 1986). Generally, Siberian stone pines do not produce appreciable numbers of cones until stands reach 90 to 120 years of age. Under exceptional conditions appreciable cone production begins as early as 30 years and, depending on stand and site conditions, high levels of cone production last 150 to 300 years (Iroshnikov and others 1963; Kozhevnikov 1963). It is reasonable, therefore, to assume that most habitat types used by bears for foraging on whitebark pine seeds do not produce sufficient numbers of seeds to sustain bear use until stands reach approximately 100 ± 20 years of age.

Table 2—Whitebark pine basal area associated with different intensities of midden use by bears in the Yellowstone area, 1986 and 1987

	Intensity of use								
	Low			Moderate			High		
Year	n	$\bar{X}$	S_x	n	$\bar{X}$	S_x	n	$\bar{X}$	S_x
1986	5	10.1	5.0	15	13.8	17.1	14	19.0	27.1
1987	14	9.1	7.8	20	15.8	15.4	19	14.0	15.7

Habitat Types

The majority of pine seed use by bears in the Yellowstone and East Front study areas occurred in the ABLA/VASC-PIAL h.t. phase (table 4). (This same type was designated the ABLA-PIAL/VASC h.t. in the East Front study area; see Appendix A for habitat type nomenclature). Proportionate use of the ABLA/VASC-PIAL phase in the Yellowstone area varied from year to year, primarily as a result of different levels of use in mesic mid-elevation and drier high-elevation habitat types. The proportionate distribution of pine seed feed sites among all habitat types in the East Front and in Yellowstone during 1987 was remarkably similar. Very little use of the PIAL series was documented in both study areas. These observations suggest that bear foraging on pine seeds in the various drier portions of the Rocky Mountains occurs in similar habitats for probably much the same reasons.

We quantified bear use of different habitat types by two different use-density indices for the Yellowstone area (table 5). These calculations used data collected at bear feed sites in 1986 and 1987. The estimated density of excavated material (D x E) indexed the density of bear use in sites selected for use by bears. (A/F) x E was dimensionless and quantified overall density of bear feeding on pine seeds in a given type within the whitebark pine zone (>2,545 m); it was not specific to sites selected by bears. The second index was not calculated for high-elevation, dry habitat types because we lacked an estimate of availability for this type.

Values of the second index suggest that overall density of pine seed feeding by bears at elevations >2,545 m (the whitebark pine zone) was highest in lodgepole pine (LP) cover types of the ABLA/VASC-PIAL phase and lowest in the ABLA/VAGL-VASC and ABLA/VASC-VASC phases. Intermediate levels of use characterized whitebark pine (WB) cover types of the ABLA/VASC-PIAL phase and the ABLA/THOC and ABLA/CACA h.t.'s.

Table 3—Whitebark pine and total stand basal area ($\bar{X} \pm S_x$), and whitebark pine as a percent of total stand basal area and cover for whitebark pine seed feed sites in the Yellowstone area, 1986 and 1987

	Basal area (m²/ha)				Mean percent whitebark pine	Percent whitebark pine canopy cover	
	Total		Whitebark pine				
Year	$\bar{X}$	S_x	$\bar{X}$	S_x		$\bar{X}$	S_x
1986	49.4	22.3	14.9	20.5	30.2	—	—
1987	46.6	23.0	12.9	15.1	27.8	33.3	13.7

The degree to which bears were selecting specific sites to feed on pine seeds within a habitat type is suggested by the ratio of estimated midden use density at bear-selected sites to the ratio of observed to expected proportionate use (D/(A/F)). A high value suggests that although relatively few sites were used by bears within a type, those few sites received relatively high-density use because of favorable combinations of squirrel densities and whitebark pine basal area. This was especially true for the ABLA/CACA h.t., and to a lesser extent for the ABLA/VAGL-VASC and ABLA/VASC-VASC phases and spruce-fir (SF) cover types of the ABLA/VASC-PIAL phase. In other habitat types bear use of pine seeds was more uniform.

Bears used the ABLA/VASC-PIAL phase and high-elevation dry types (ABLA/ARCO and ABLA/RIMO h.t.'s) during 1986 and 1987 primarily to feed on pine seeds (fig. 8). Very little bear activity in the whitebark pine (PIAL) series was devoted to use of pine seeds, principally because very few squirrels reside in this type (Reinhart and Mattson, this proceedings); most bear activity in the PIAL series was described as travel. This assessment emphasizes the importance of the ABLA/VASC-PIAL phase and, in areas where this phase is less common, the drier high-elevation *Abies lasiocarpa* (ABLA) series types.

The ratio of whitebark pine basal area at sites used to forage on pine nuts and whitebark pine basal area at all other activity sites within a given habitat type is shown in figure 8. These data indicate that bears selected pine seed feed sites in the ABLA/VASC-VASC phase and ABLA/ THOC h.t. principally on the basis of locally greater whitebark pine basal area; use of these types for pine seed foraging was restricted to anomalous sites at higher elevations where mature whitebark pine occurred in appreciable amounts.

Table 4—Proportional use (P) of habitat types and habitat type groups by bears for foraging on whitebark pine seeds in the Yellowstone area and East Front of the Rockies (data from Aune and Kasworm, in press)

	Yellowstone							
	1979		1986		1987		East Front	
Habitat types	P	*n*	P	*n*	P	*n*	P	*n*
ABLA/VASC-PIAL ABLA-PIAL/VASC	0.700	35	0.583	21	0.534	39	0.522	35
High-elevation, subxeric	.120	6	.250	9	.082	6	.104	7
Mesic-subhydric, mid-elev.	.180	9	.194	7	.315	23	.313	21
Mid-lower elev., subxeric	.000	0	.000	0	.068	5	.060	4
Total *n* =		50		36		73		67

Table 5—Whitebark pine basal area, estimated squirrel densities, and parameters of bear use for whitebark pine feed sites in habitat types of the whitebark pine zone

Habitat types	(A) *n*	(B) Estimated squirrel density (*n*/km)	(C) Whitebark pine basal area m²/ha $\bar{X}$	S_x	(D) Estimated density of midden use (*n*/km)	(E) Excavated material (*m*³/midden) $\bar{X}$	S_x	(D x E) Estimated density of excavated material (*m*³/km)	(F) Expected frequency[1]	(A/F) Ratio, observed/ expected	(A/F x E) Density of excavated material (dimensionless)	D/(A/F)
ABLA/VASC-PIAL LP cover types	14	2.76	4.3	5.8	1.24	6.6	4.0	8.18	6.7	2.09	13.8	0.59
ABLA/VASC-PIAL WB cover types	37	2.05	20.1	17.0	1.59	5.6	6.9	8.86	27.5	1.34	7.5	1.18
ABLA/VASC-PIAL SF cover types	6	2.36	10.7	9.0	1.43	3.5	3.8	5.00	7.8	.77	2.9	1.86
High elev., dry[2]	13	.85	14.9	25.0	.58	7.0	8.0	4.06	—	—	—	—
Low elev., dry[3]	5	2.23	9.2	9.7	1.25	1.8	—	2.25	4.1	1.22	2.2	1.02
ABLA/CACA	4	3.62	9.2	15.4	2.07	7.4	—	15.32	6.7	.60	4.4	3.45
ABLA/THOC	19	2.62	10.2	11.5	1.56	5.3	5.1	8.21	18.2	1.04	5.5	1.50
ABLA/VAGL-VASC	4	1.32	5.7	6.9	.65	2.8	—	1.82	11.7	.34	1.0	1.91
ABLA/VASC-VASC	5	2.92	.9	2.0	1.00	2.3	3.9	2.30	9.9	.50	1.2	2.00
PIAL series	6	.14	40.2	4.4	.14	2.4	—	.34	7.3	.82	2.0	.17

[1]From Mount Washburn study area, Yellowstone National Park ($n = 835$).
[2]ABLA/ARCO, ABLA/RIMO h.t.'s.
[3]ABLA/SPBE, ABLA/JUCO, and ABLA/BERE h.t.'s.

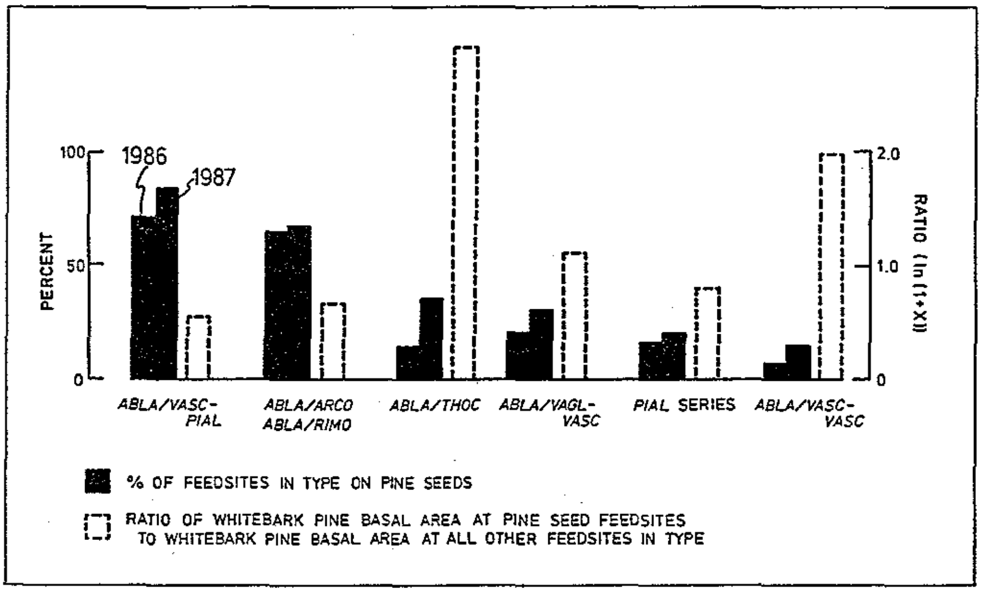

Figure 8—Percent of activity sites devoted to pine seed use in Yellowstone habitat types, for 1986 and 1987, and the ratio (ln (1 + *X*)) of whitebark pine basal area at pine seed feed sites to whitebark pine basal area at all other activity sites for 1986 and 1987 combined (1986, $n = 36$; 1987, $n = 73$ pine seed feed sites).

USE OF SQUIRREL MIDDENS

Most bear use of pine seeds in the Yellowstone area was from cones cached in squirrel middens. A major portion of bear excavations in middens were <2.0 m^3 in size, and could be characterized as incidental or exploratory (fig. 9). A few midden excavations ($n = 3$) were extensive (30 to 51 m^3). The number of cones excavated by bears per midden ($\hat{y}$) during 1987 was positively and significantly related to total excavated volume (x) ($\hat{y} = 33.2 + 13.6x$; $r^2 = 0.676$, $n = 52$, $F = 219.8$, $P < 0.000$); excavated volume reflected the relative number of seeds acquired by bears from a midden. The volume of excavated material did not vary significantly among middens from different habitat types.

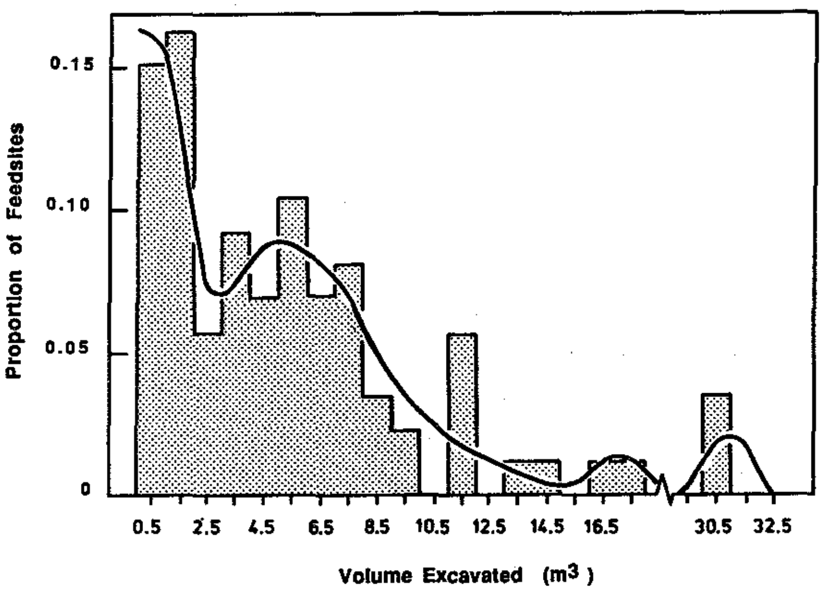

Figure 9—Proportionate distribution of Yellowstone pine seed feed sites, for 1986 and 1987 combined, with respect to estimated excavated volume ($n = 109$).

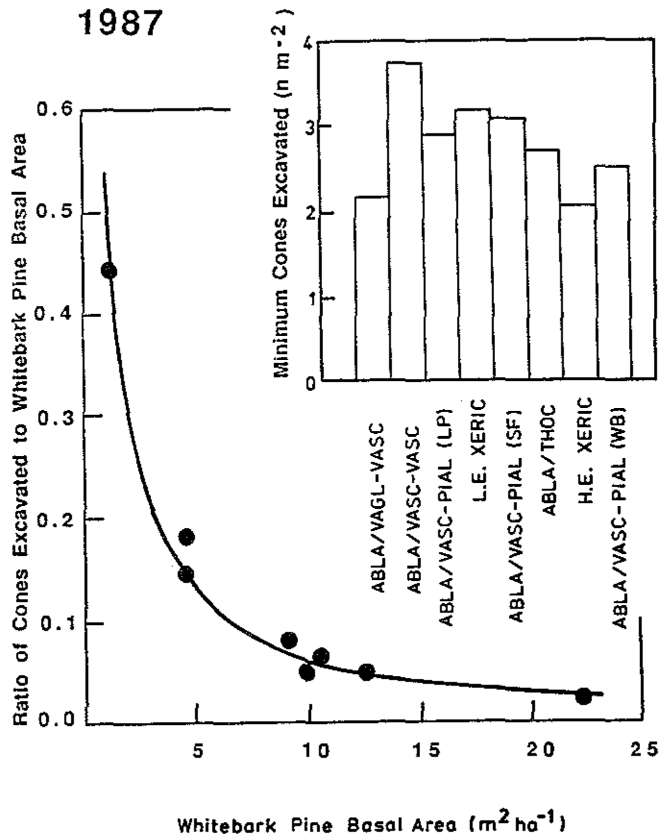

Figure 10—Relationship of the ratio of excavated cone density to whitebark pine basal area averaged for Yellowstone area habitat types, for 1987. Inset depicts mean estimated number of cones excavated/m^2 for Yellowstone area habitat types.

The apparent preferential harvest of whitebark pine cones by squirrels tended to minimize differences in the densities of whitebark pine cones in middens, relative to stand whitebark pine basal area. Absolute densities of cones excavated by bears in Yellowstone varied relatively little among habitat types (between 2 and 4 cones/m^2), regardless of characteristic whitebark pine basal area (fig. 10). This was reflected in an asymptotic increase in the ratio of excavated cone density to whitebark pine basal area as basal area decreased. At low densities of mature whitebark pine, fewer squirrels' territories contained cone-producing trees, and despite preferential caching of whitebark pine cones by squirrels, there were fewer middens with whitebark pine cones available to bears. This phenomenon was evident in the positive relationship between stand whitebark basal area (x, in m^2/ha) and the probability of a midden being excavated by a bear ($\hat{y}$) ($\hat{y}$ = (942.8 + 13.36 X^{-2})) (Mattson and Reinhart 1987).

FORAGING STRATEGIES

Bear pine seed foraging, squirrel midden densities, and whitebark pine abundance are clearly related. A chronology of the trade-offs between midden density and whitebark pine basal area is evidenced by bear use of the 1987 pine seed crop in the Yellowstone area (table 6). During the earliest period of bear use in July, the number of cones excavated per cubic meter of excavation was higher than during August. These earliest feed sites occurred in a few favored, lower elevation habitats on south and southeast exposures, primarily in the ABLA/SPBE, ABLA/BERE, and ABLA/JUCO habitat types. These types were restricted to anomalous sites above 2,425 m elevation, and were more common at lower elevations. Whitebark pine cones probably matured earlier in these habitats, and because of high whitebark pine basal areas, the resident squirrels may have started caching whitebark pine cones earlier than in other stands with relatively less whitebark pine. Use through the first half of August was oriented toward stands with higher whitebark pine basal area and lower squirrel densities. The density of excavated material and cones was comparatively low during this period, as would be expected with the low rate of caching during early phases of whitebark pine cone harvest by squirrels (Hutchins and Lanner 1982). Peak use of pine seeds occurred between the middle of August and the middle of September, when bears used stands with higher squirrel densities. Bears excavated a higher density of cones during the last half of August, compared with the previous month, despite the lowest average number of excavated cones per cubic meter of excavation. By this time squirrel caching was at a uniformly high level (Hutchins and Lanner 1982), and squirrel midden density was probably most limiting to bear use of pine seeds. Although densities of excavations and excavated cones remained high during the last half of September, use generally declined. By this time marginal habitats had probably been fully exploited, and bears turned to using other foods or pine seed sites with relatively more whitebark pine and fewer squirrels. Full exploitation of the modest 1987 pine seed crop (Blanchard, this proceedings) by bears probably occurred by the end of September; subsequent October bear use of pine seeds dropped to very low levels.

We examined the relationship of various measures of cone-use density in habitats selected by bears to relative fecal volumes of pine seeds for different 1987 time periods (fig. 11). Although we had few data points, the derived relationships suggest constraints on bear use of pine seeds that were related to minimum densities of available whitebark cones in favored habitats. Such relationships further suggest that bears did not forage on pine seeds during 1987 when densities were less than approximately 39 available cones/midden and 56 available cones/km. The relationship of mean cones excavated per investigated telemetry location (relative pine seed use as documented by feed-site investigation) to relative pine seed scat volume, suggests that at <9 excavated cones/investigated relocation, pine seed use was likely to go undetected by scat analysis, at least at the 1987 sampling intensity (n = 472).

Table 6—Whitebark pine basal area, estimated squirrel densities, and parameters of bear use for whitebark pine feed sites for seasonal time periods, 1987. Squirrel midden densities were estimated by a site favorability index (Reinhart and Mattson, this proceedings), and use of any given midden was predicted from stand whitebark pine basal area (Mattson and Reinhart 1987)

Time period	*n*	(A) Estimated squirrel density (*n*/km)	(B) Whitebark pine basal area m²/ha $\bar{X}$	s_x	Estimated density of midden use (*n*/km)	(D) Excavated material (m³/midden) $\bar{X}$	s_x	(C x D) Estimated density of excavated material (m³/km)	(E) Minimum No. of excavated cones (*n*/midden) $\bar{X}$	s_x	(C x E) Est. minimum density of excavated cones (*n*/km)	(E/D) Mean number of excavated cones per m³ of excavation
07/15-07/31	7	2.04	22.3	17.5	1.66	1.8	0.9	2.99	37.3	7.5	61.9	20.7
08/01-08/15	14	2.04	16.1	16.1	1.44	5.0	5.1	7.20	75.5	76.4	108.7	15.1
08/16-08/31	19	2.80	11.4	15.7	1.73	6.5	8.7	11.24	81.2	91.0	140.5	12.5
09/01-09/15	24	2.42	9.1	9.9	1.38	4.8	4.2	6.62	116.6	103.7	161.0	24.3
09/16-09/30	2	1.98	9.2	—	1.13	2.6	—	2.94	50.5	—	57.1	19.4

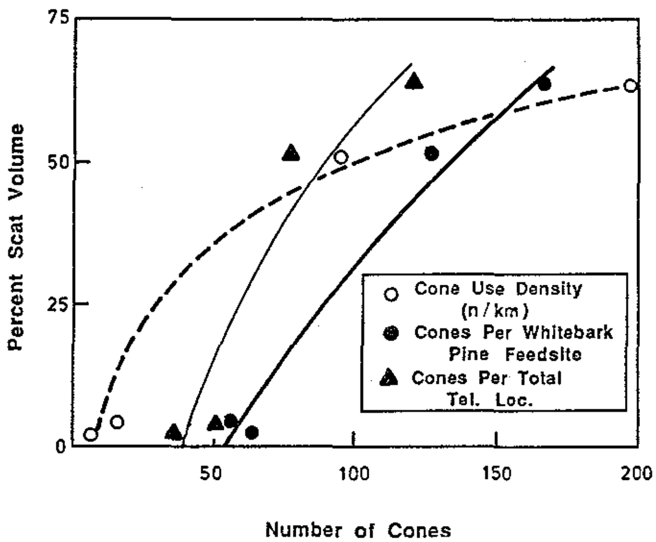

Figure 11—Relationships between percent scat volume, by month for 1987, and estimated excavated cone densities; per km, per whitebark pine seed feed site, and per telemetry location visited.

SUMMARY AND MANAGEMENT RECOMMENDATIONS

Stone pine seeds are a high-quality bear food because of their high triacerglycerol and energy content, relatively large size, and intermittent abundance. Wherever stone pines are relatively abundant, bears use them. Indehiscent stone pine cones are collected by arboreal rodents, principally red squirrels and Siberian chipmunks, into middens or caches. Preferential caching by these rodents, to a certain extent, minimizes the variation in stone pine seed production among sites and years. These rodents, therefore, are a key to the bear's ability to use pine seeds in most areas and to management of bear habitat for pine seed use.

Bears, midden locations and densities, the seasonal activities of squirrels, and whitebark pine abundance affect the seasonal foraging strategies of bears. Yellowstone bears were found to forage seeds primarily within the constraints of whitebark pine availability and squirrel midden densities. Bears made substantial use of stands with relatively low numbers of mature cone-producing whitebark pine, and were limited primarily by the absence of these trees altogether over substantial areas (more than approximately 1/2 ha). The greatest use of pine seeds typically occurred in LP cover types of the ABLA/VASC-PIAL phase because both squirrels and whitebark pine were relatively abundant in this type. At elevations >2,425 m, use of the ABLA/VAGL-VASC and ABLA/VASC-VASC h.t. phases was limited primarily by the lack of cone-producing whitebark pine, while use of the PIAL series was limited by lack of squirrels.

Management of bear habitat in drier portions of the Rocky Mountains for pine seed feeding depends on integrating squirrel and whitebark pine densities with bear foraging strategies. Stands of pure whitebark pine are of little use to most bears for pine seed foraging. However, these less fire-prone stands of pure whitebark pine may serve as important reservoirs of seed for dispersal by Clark's nutcrackers (*Nucifraga columbiana*) into burned areas.

Timber harvest has the potential to substantially impact bears through effects on squirrels and whitebark pine in habitats characterized by appreciable squirrel densities and mixed conifer species overstories that include whitebark pine. In many areas, stands and habitats important to bears for pine seed foraging occur at lower elevations of the whitebark pine zone and may contain few enough whitebark pine that their significance to bears is not recognized. Although whitebark pine is seral in much of the habitat used by bears to feed on pine seeds (Arno and Hoff 1989; Mattson and Reinhart, this proceedings), it may persist in stands for several hundred years as an appreciable cone producer. In addition, significant seed production is not likely to occur until trees are approximately 100 years old. Assuming 250 to 300 years to senescence of whitebark pine, 3 to 4 percent harvest of a landscape per decade would be sufficient to maintain productive whitebark pine stands. A few large-scale natural fires would serve the same purpose. Selective thinning of stands, even in favor of whitebark pine, would not necessarily benefit bears because a reduction in stand basal area under most circumstances predictably results in a reduction of red squirrel density (Reinhart and Mattson, this proceedings). Because squirrels require mixed-species conifer stands to achieve even moderate densities (Reinhart and Mattson, this proceedings), cutting and replanting stands to pure or near-pure whitebark pine has little promise of enhancing bear habitat, even in 100 years. In conclusion, there seems little that active timber management can do to augment bear use of whitebark pine in drier portions of the Rocky Mountains, although in areas where timber harvest has already occurred or is planned for other reasons, judicious planting of whitebark pine in mixtures with other tree species will very likely benefit bears in the future.

In northwestern Montana, whitebark pine has been seriously depleted by (1) extensive infections of white pine blister rust (*Cronartium ribicola*), (2) the massive mountain pine beetle (*Dendroctonus ponderosae*) outbreaks of the 1970's and 1980's, and (3) by extensive logging of old-growth whitebark stands, especially in the Whitefish Range. Extensive use of whitebark pine cones and seeds in this area by both black and grizzly bears, as during the 1950's and 1960's (Jonkel 1967; Kendall and Arno, this proceedings; Tisch 1961), does not occur any more.

Cutting practices that favor whitebark pine are urgently needed in northwestern Montana. The mechanics of whitebark pine regeneration are poorly understood; extensive periods (100 or 1,000 years) may be required before optimal conditions for reseeding and survival may occur. The elimination of old-growth stands, even though the trees are slowly dying from blister rust, may doom whitebark pine in its northern range and cause the permanent loss of an important bear food.

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APPENDIX A. HABITAT TYPE NOMENCLATURE AND ACRONYMS (STEELE AND OTHERS 1983)

Acronym	Common name	Scientific name
PIAL series	Whitebark pine series	*Pinus albicaulis* series
ABLA/VASC-PIAL phase	Subalpine fir/Grouse whortleberry-Whitebark pine phase	*Abies lasiocarpa/ Vaccinium scoparium- P. albicaulis* phase
ABLA/VASC-VASC phase	Subalpine fir/Grouse whortleberry-Grouse whortleberry phase	*A. lasiocarpa / V. scoparium-V. scoparium* phase
ABLA/VAGL-VASC phase	Subalpine fir/Globe huckleberry-Grouse whortleberry phase	*A. lasiocarpa / V. globulare-V. scoparium* phase
ABLA/THOC h.t.	Subalpine fir/Western meadowrue h.t.	*A. lasiocarpa / Thalictrum occidentale* h.t.
ABLA/SPBE h.t.	Subalpine fir/Shiny-leaf spiraea h.t.	*A. lasiocarpa/Spiraea betulifolia* h.t.
ABLA/BERE h.t.	Subalpine fir/Oregon-grape h.t.	*A. lasiocarpa/Berberis repens* h.t.
ABLA/JUCO h.t.	Subalpine fir/Common juniper h.t.	*A. lasiocarpa/Juniperus communis* h.t.
ABLA/RIMO h.t.	Subalpine fir/Mountain gooseberry h.t.	*A. lasiocarpa/Ribes montigenum* h.t.
ABLA/ARCO h.t.	Subalpine fir/Heart-leaf arnica h.t.	*A. lasiocarpa/Arnica cordifolia* h.t.
ABLA/CACA h.t.	Subalpine fir/ bluejoint h.t.	*A. lasiocarpa/ Calamagrostis canadensis* h.t.