USE OF PINE NUTS BY GRIZZLY AND BLACK BEARS IN THE YELLOWSTONE AREA

KATHERINE C. KENDALL, Research Office, Glacier National Park, West Glacier, Montana 59936

Abstract: Whitebark pine (*Pinus albicaulis*), an important tree of high altitudes in the northern Rocky Mountains and Sierra Nevada, produces nuts eaten by bears. Grizzly bear (*Ursus arctos*) and black bear (*U. americanus*) use of pine nuts was studied in Yellowstone National Park and adjacent areas during 1978 and 1979. Spring use appeared to be correlated with cone production in the preceding year, while fall use was correlated with the current crop. Most of the nuts eaten by bears came from cones cached by red squirrels (*Tamiasciurus hudsonicus*). Pine nuts were a nutritious food which was often present in early spring and late fall when alternate foods were scarce or low in digestible energy and when nutritional requirements of bears were high. No evidence was found that bears ate the nuts of limber pine (*P. flexilis*).

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The large seeds (pine nuts) of whitebark pine are commonly eaten in the spring (March–May) and fall (September–November) by grizzly and black bears in Yellowstone National Park and adjacent areas (Craighead and Craighead 1972, Blanchard 1978, Mealey 1980) and western Montana (Tisch 1961; J. Sumner and J. J. Craighead, unpubl. rep., Montana Coop. Wildl. Res. Unit, Univ. Montana, Missoula, 1973). Similar nuts from limber pine are eaten by grizzly bears on the east Rocky Mountain Front of northwestern Montana (Schallenberger and Jonkel, annual rep., Border Grizzly Project, Univ. Montana, Missoula, 1980). The nuts of the European stone pine (*P. cembra*) are an important food for brown bears (*U. arctos*) throughout the taiga zone in the Soviet Union (Pavlov and Zhdanov 1972, Ustinov 1972, Yazan 1972). Both the production of whitebark pine cones (Forcella 1977, Blanchard 1978, Mealey 1980) and the quantity of nuts consumed by bears vary annually (Mealey 1975, Blanchard 1978).

Pine nuts are also an important food for red squirrels in whitebark forests. In fall, squirrels remove cones from trees and cache them in middens. Bears as well as other mammalian and avian seed predators compete with squirrels for whitebark nuts (Forcella 1977, Tomback 1977).

Confusion about the ripening process of whitebark pine cones has resulted in errors in the literature on the availability of pine nuts as a bear food. Whitebark cones are indehiscent and do not disintegrate (Tomback 1981). Vertebrate foraging probably leaves few, if any, seed-bearing cones on trees by late fall; the cones remaining abscise sometime thereafter (Tomback 1981). Because cones do not abscise or release their seed in fall, bears may obtain pine nuts in 2 ways. Black bears may climb whitebark pine trees and break off cone-bearing branches to feed on cones (Tisch 1961, Mealey 1975, Forcella 1977); or both black bears and grizzly bears may raid squirrel caches to feed on pine nuts (Tisch 1961, Craighead and Craighead 1972, Blanchard 1978). The purpose of this study was to determine (1) the major source of pine nuts for bears, (2) why cone scales do not appear in bear scat containing pine nuts, and (3) what factors influence bear use of pine nuts.

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THE STUDY AREA

The study area was located in Yellowstone National Park and surrounding portions of Montana, Wyoming and Idaho (Fig. 1). Sites were located in whitebark pine forests in which bears fed on pine nuts. Whitebark pine occurred in upper subalpine and timberline areas between 2440 and 2870 m. Pure stands occurred on dry, exposed sites. On sheltered, moist sites, whitebark pine was mixed with subalpine fir (*Abies lasio-*

carpa) and Engelmann spruce (*Picea engelmannii*) (Weaver and Dale 1974). Limber pine occurred between 1580 and 2500 m in sparsely timbered stands on arid, rocky sites (Cooper 1975). Mature whitebark and limber pine were present in 8% and 0.4%, respectively, of the forested area of Yellowstone National Park (Civilian Conservation Corps, unpublished data). Similar information was not available for the rest of the study area.

METHODS

Radio transmitters were placed on 15 grizzly bears in 1978 and 1979 and on 2 black bears in 1979. Instrumented bears were relocated from the air (relocation sites) approximately 3 times a week using the radio-tracking equipment and techniques described by Judd and Knight (1977). A comparison of the number of relocation sites above 2440 m in 1978 and 1979 was used in conjunction with other data as an indicator of bear use of whitebark pine stands. Randomly selected relocation sites were investigated for evidence of bear feeding activity. Scats were collected at these sites and the age of all bear sign was estimated. Different digestion rates of food items were considered when percent volume of each scat item was estimated. Contents of scats collected during examination of relocation sites were assumed to be representative of the food habits of the bears in the study area. My analysis included scats collected by the IGBS between 1973 and 1977.

Thirteen whitebark and 3 limber pine stands different from those visited during relocation site examinations were studied for evidence of bear feeding activity. Observations of claw marks in trees, broken tree limbs, and excavated squirrel middens were recorded. Samples of bear hair were collected from middens disturbed between examinations and analyzed for bear species identification. Middens on Electric Peak were examined at 1-day to 1-week intervals from June through September 1979. Snow depth and cover at disturbed middens were noted during May and June 1979.

I observed squirrel caching behavior from August through October 1978 and August and September 1979. The length of observation periods, the numbers of cones and nuts cached, and the depth and location of caches were recorded. The

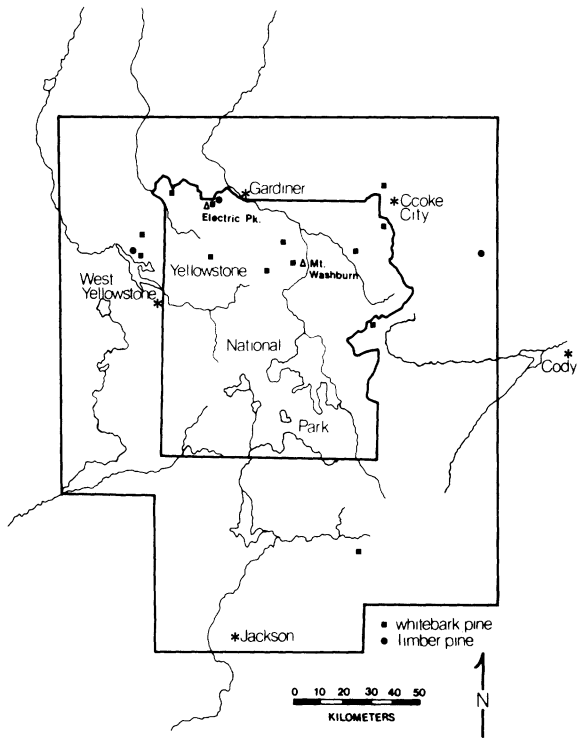

Fig. 1. Study area, including locations of 13 whitebark and 3 limber pine stands examined.

sizes of 25 squirrel caching areas were estimated visually. Randomly selected squirrel middens were examined in June–August 1978 and May–August 1979 to determine if cached cones and nuts were present. Pine nuts cached less than 3 months (nuts of the year) were distinguished from nuts cached for 6 months or more (old nuts) by color. Nuts of the year were tan; old nuts were dark brown.

Sample plots 10 × 25 m were established in squirrel caching areas on Electric Peak (7 plots) and Mt. Washburn (3 plots). The plots were searched for cached cones and nuts 2 to 4 times between 12 August and 9 October 1978 and once between 9 and 15 September 1979. The numbers of cones and nuts found in fall 1978 (between 27 September and 9 October) were compared with cones and nuts found in fall of 1979 because most cones had been harvested by these dates.

Based on experience, I indexed whitebark pine cone production as low, moderate, or high in 1978 and 1979. Mean number of nuts per cone was determined from 225 cones (25 cones from 9 sample plots) collected in September 1978.

Four captive grizzly bears and 3 captive black bears were fed whitebark pine cones to determine how bears obtain nuts from cones without consuming cone debris. Scats from these trials were collected and examined.

RESULTS

Cone Production

Cone production was higher in 1978 than in 1979. Although production data were not available prior to 1978, cone production appeared to be exceptionally high in 1978 and moderate in 1979. Cones averaged 88 (±26, SD) nuts per cone in 1978 and ripened earlier below 2550 m and on south-facing slopes than on higher-altitude sites and other aspects.

Squirrel Cone Caching Activity

Cone caching sites varied in size and in the number of cones buried and cached above ground. Placement of cones in 1978 caches ranged from sites with most cones buried to sites with most cones cached as surface piles. An extreme example of the latter was a cache with approximately 3000 cones on the surface in a 4-m^2 area. Caches for an individual squirrel were contained within areas of 100 to 626 m^2. Caching sites were more widely distributed at higher elevations where squirrel territories were larger and whitebark trees were smaller. Cones and nuts were present in randomly chosen sites searched in May, June, and July 1979 after the good cone year of 1978, but not in June and July 1978.

Squirrels cut cones from trees for immediate consumption in July when cones were immature, but squirrels were not observed caching cones until the 1st week of August. Sixty-three hours of observation showed cone caching by squirrels occurred from August through October. Squirrels buried cones 2.5 to 20.0 cm deep. One to 15 cones were cached per hole. When cones were plentiful in 1978, a large number of cones were left lying where they fell when cut in September and October or were placed at the bases of trees and logs and above buried cones. When cones were less plentiful in 1979, cones were not found on the surface.

In mid-September squirrels also began to cache whitebark pine nuts as opposed to cones. Caches of 3 to 176 nuts were found. Old caches were usable by bears because the endosperms of the nuts were still firm and white.

The number of cones and nuts cached in sample plots differed between years. More cones were cached in sample plots in 1978 than in 1979 ($P < 0.01$, Wilcoxen's Signed Rank test). The mean number of cones and nuts cached in sample plots in 1978 was 394 (±637, SD) and 55 (±71, SD), respectively. In 1979, the mean number of cones cached in plots were 48 (±49, SD) and the mean number of nuts was 293 (±573, SD).

Bear Use of Pine Nuts

Data from 633 and 745 relocations made in 1978 and 1979, respectively, indicated that the range of every radio-instrumented bear included stands of whitebark pine. Bear use of pine nuts varied seasonally and annually during the study period. In 1978 when nuts were relatively scarce, middens were raided at relocation sites in only 3 months: June, August, and September; in 1979 when nuts were plentiful, middens were raided in 6 months: April and June–October. Due to frequent snows, no evidence of bear feeding activity was found at November relocation site examinations. During March–August, 16% more bear relocations occurred above 2440 m in 1979 than in 1978 ($P < 0.005$), but in October–November, 34% more bear relocations occurred above 2440 m in 1978 than in 1979 ($P < 0.005$). Eighty-four percent of relocations occurred above 2440 m in September of both 1978 and 1979. Examination of 132 relocation sites in 1978 and 188 such sites in 1979 indicated that bears had raided caches to obtain nuts in 7% and 36% of the sites in 1978 and 1979, respectively.

No evidence of bear use of limber pine nuts was found in 3 limber pine stands examined. Few red squirrels and no squirrel middens or caches were observed in these stands.

The 13 additional whitebark stands studied provided more seasonal and annual use pattern data. In 1978 when few 1977 cones were present, no bear use of middens was found in these stands before the 1978 cone crop matured in August. Three raided middens were found on Electric Peak in August at an elevation of 2500 m. All cones cached in the raided middens were buried, so bears had to dig to obtain them. Bear use of pine nuts on Electric Peak between 2560 and

2800 m began in September as nuts became plentiful and increased through October. Because middens at those elevations had up to 3000 cones cached on the surface, bears seldom dug into middens. Bear use of squirrel caches was inferred from the presence of scat and tracks.

In 1979 use of squirrel caches by bears on Electric Peak began in the spring below 2590 m and was related to snow depth. The estimated age of bear sign found 9-10 May indicated the use of cached pine nuts began approximately the 1st week of April or earlier. The earliest bear digging occurred where snow melted first; i.e., on slopes of greater than 25% with south to southeast aspects at elevations 2440 to 2590 m. By 9 May, snow on these slopes averaged 0.3 to 0.6 m deep and was melted around tree bases. Digging also occurred in early May in middens on slopes of 0 to 15% where snow depth was 0.9 to 1.2 m. One to 11 holes (0.5 to 1.0 m in diameter) were dug through snow into a squirrel's central caching area. No bear activity was found during May above 2590 m where snow depth averaged 1.5 m and snow cover was 100%.

Above 2590 m, bear digging in middens began in June 1979. The change coincided with decreased snow depth and cover. Caches were first raided on Electric Peak at 2620 to 2770 m in early to mid-June when snow depth varied from 0 to 1.0 m and snow cover ranged from 10 to 60%. Initial bear use of caches on Mt. Washburn at 2680 to 2740 m occurred between the 2nd and 3rd week of June when 0 to 1.0 m of snow was present.

Bears used middens at all elevations on Electric Peak after mid-June, but increasing activity was observed above 2620 m in July. After squirrels began caching cones in the 1st week of August 1979, bears apparently again raided middens at all elevations.

Bears rarely consumed all cones or nuts from a caching area during a single visit. They repeatedly visited middens from April to July and mid-September to October 1979 when new cones were not added to caches. One midden was raided at least 11 times between 11 May and 26 August 1979. Middens were also repeatedly raided in August and September 1978 and 1979 while squirrels were actively caching cones.

Grizzly bears and black bears fed in middens in the same area. Forty-five samples of bear hair were collected from excavated middens throughout the Electric Peak study area, 11 May to 22 September 1979. Black bear hair was found in 58% of these samples, and grizzly bear hair appeared in 42%. Commonly, grizzly bears and black bears fed in the same midden within 2 days or less of each other. No evidence was found that either grizzly bears or black bears broke off cone-bearing limbs to feed on cones.

Table 1. Pine nut content in bear scats collected by the IGBS[a] from the Yellowstone National Park area, 1973–1979.

Year	No. of scats	% of scats containing pine nuts	Pine nut content ($\bar{X}$% of scat volume)
1973[bc]	22	8	5
1974[bc]	83	4	2
1975[b]	68	9	4
1976[b]	23	69	45
1977	474	6	2
1978	593	15	11
1979	752	47	40

[a] Interagency Grizzly Bear Study.
[b] Scats collected in Yellowstone National Park only.
[c] From Mealey (1975).

Scat analyses suggest variation in the annual and seasonal importance of pine nuts as a bear food item. Annual pine nut content in bear scats from 1973 through 1979 (Table 1) ranged from 4% frequency of occurrence and 2% of total scat volume to 69% frequency of occurrence and 45% volume. The frequency of occurrence of pine nuts in 1979 scats increased 22% over 1978 levels in both spring and summer (June–August).

Approximately 75% of the scats contained pine nuts in the fall in 1978 and 1979. Pine nuts occurred more frequently and constituted a larger percent of scat volume in 1979 than in 1978 in all months except October (Table 2). Scats containing pine nuts rarely contained cone scales.

Scat collection efforts were not equally distributed in all seasons. From 1973 to 1977 scats were collected primarily from June through September (Knight, pers. commun.). In 1978, 8 and 9% of the scats collected were deposited in spring and fall, respectively. Scat results in 1979 were more representative of annual food habits with 22% and 34% of the scats from spring and fall, respectively.

Table 2. Monthly frequency and percent volume of pine nuts in bear scats from the Yellowstone National Park area, 1978 and 1979.

Month and year	No. of scats	% of scats containing pine nuts	Pine nut content ($\bar{x}$% of scat volume)
May 1978	35	3	1
1979	63	14	14
Jun 1978	142	1	1
1979	117	13	12
Jul 1978	175	2	1
1979	112	36	19
Aug 1978	138	19	12
1979	63	51	40
Sep 1978	37	70	55
1979	145	80	73
Oct 1978	11	91	86
1979	68	69	65

Captive Bear Feeding Trials

Four captive grizzly bears and 3 black bears used similar means of extracting nuts from whitebark cones. Bears broke cones by either biting or stepping on the cones. Cone debris was spread out with a paw or muzzle and the nuts licked up. Nuts were retained while cone scales were expelled from the side of the mouth. Grizzly bears ate the nuts from all cones given to them, showing no preference between resinous cones of the year and old, often moldy cones which had been cached in a midden for 1 year. None of the scats collected from these feeding trials contained cone debris.

DISCUSSION AND CONCLUSIONS

Scat analysis and site examinations provided biased estimates of the extent of bear use of pine nuts. These techniques tended to underestimate bear use of nuts for at least 4 reasons: (1) High-elevation sites were not representatively sampled because snow depth and weather conditions hindered access to these areas. (2) In spring and fall, snows concealed scat and other sign. (3) With cones cached on the surface in the post-growing season of 1978, site examinations showed little evidence of feeding activity in whitebark stands because bears did not need to dig into middens to obtain cones. (4) From 1973 to 1978, scats from spring and fall were undersampled. Because bears ate pine nuts primarily in these seasons, the importance of pine nuts in the bears' annual diet was underestimated in previous studies. On the other hand, while scat analysis techniques attempted to compensate for variable digestibility, scat content results probably tended to underestimate the importance of highly digestible items (e.g., animal material, berries, succulent vegetation) and overestimate the importance of items with low digestibility (e.g., grasses, sedges, desiccated forbs). While the seed testae of pine nuts ranked high in digestibility (Mealey 1980), the woody seed coats were not digestible and may have inflated the percent of scat volume figures for pine nuts.

Squirrel caches were the only identified source of cones for bears. No evidence was found that bears climbed trees or broke off cone-bearing limbs to feed on cones. Blanchard (1978) reported that grizzly bears raided squirrel middens throughout fall and used pine nuts almost exclusively by the latter part of the season.

Mealey (1980) hypothesized 2 distinct use stages for grizzly bears eating whitebark pine nuts: (1) incidental and (2) exclusive. He believed that the cones eaten in the incidental stage in late August and September were those lying on the ground as a result of squirrel cuts and wind throw. Primary foods were forbs and grasses, and pine nuts were eaten incidentally. The cones were fed upon exclusively during October and November when, after cone fall, cones were abundant on the ground. His explanation is not valid because whitebark cones are indehiscent and abscise sometime after fall (Tomback 1981).

My observations supported an alternate explanation for 2 stages. Squirrels began to cache immature cones in the lst week of August and continued to add cones to middens into November in 1978 and through mid-September in 1979. Cones may have been present in squirrel middens in insufficient numbers in August for bears to eat only pine nuts. In the fall, bears could feed exclusively on pine nuts because more cached cones were available.

Bears obtained pine nuts from both cached cones and cached nuts. With an average of 88 nuts per cone, the cones cached in a typical sample plot contained 29,550 and 3,600 nuts in 1978 and 1979, respectively. Nut caches contained 55 and 293 nuts per plot in 1978 and 1979, respec-

tively. Nut caches probably provided a small proportion of nuts to bears, but cached cones were the major source. Absence of cone debris in scats containing pine nuts did not necessarily indicate that bears fed in nut caches. Black bears observed by Mealey (1975) fed on cones and ate only the nuts. Feeding trials of captive bears demonstrated that both grizzly bears and black bears could eat nuts from cones without ingesting cone scales.

Seasonal shifts in the location of feeding sites were partially related to cone availability. Bear digging began in August in middens at 2500 m because of the south and southeast aspects and low elevation of the stands and consequent earlier maturation of cones (Tomback 1977). Bears dug into middens on steep, south-facing slopes in April and May 1979 because nuts probably could be obtained with less effort. Snow was shallow and fell easily away from the digging site. Deep snow at high elevations apparently concentrated bear feeding activity below 2590 m prior to June in 1979. From June until the 1st week of August, bear activity was greatest between 2590 and 2870 m because more cones probably remained in high-elevation caches than in the frequently raided middens at lower elevations.

The availability of pine nuts appeared to affect bear feeding. Bears fed on pine nuts at more relocation sites in 1979 than in 1978. A lower proportion of scats containing pine nuts was found prior to August in 1978, but a higher proportion of scats containing pine nuts was found in fall 1978 and May through October 1979. Whitebark pine cones and nuts were not present in middens in the summer of 1978 until mid-August, but cones and nuts were present in spring, summer, and fall 1979. Consequently, the heavy cone production in fall 1978 affected bear food habits in both 1978 and 1979.

Differences between the elevations of relocation sites in 1978 and 1979 supported the observed relationship between pine nut availability and bear use of pine nuts. Bear movement to higher elevations coincident with increased feeding on whitebark pine nuts was reported by Mealey (1975), Blanchard (1978), and Schallenberger and Jonkel (annual rep., Border Grizzly Project, Univ. Montana, Missoula, 1980). In this study more instrumented bears were relocated above 2440 m during March through August of 1979 than in 1978. The move to higher elevations in spring and summer 1979 coincided with the presence of pine nuts in middens. There was no difference in the number of relocation sites above 2440 mm in September in 1978 and 1979, but in October and November bears were relocated less often above 2440 m in 1979 than 1978. The similar levels of bear activity at high elevations in September 1978 and 1979 corresponded with the initiation of cone caching. Because squirrels harvested all cones by the end of September 1979, the number of cones available in middens could only decrease during the remainder of the fall. In 1978, unharvested cones were present on trees and continued to be cached throughout the fall. The sustained level of bear activity at high elevations in October and November 1978 may have been due to the large quantity of cones present throughout fall. Cone supplies in late fall 1979 may not have been sufficient to support the level of bear activity observed in September.

Availability was not the only factor affecting bear use of pine nuts. Food selection by bears is based on food item nutritive value as well as availability (Sizemore 1980). The results of Mealey (1980) suggest that bears follow an energy-optimization path, as has been found for other animals (Pyke et al. 1977). Thus, high-energy foods are selected unless abundant supplies of lower-quality food result in a food source which provides more net energy.

Major spring foods of grizzly bears in the Yellowstone area vary annually and have been reported as meat, especially carrion (Cole 1972, Mealey 1980) and graminoids and forbs (Blanchard 1978). Herbaceous material is covered by snow in March and April and limited in quantity and distribution in May. Because meat is higher in digestibility and energy content than herbs (Mealey 1980) and plants are not usually abundant even when available in spring, bears select for animal material. However, during the pre-green-up period the relative scarcity of animal material may mean that there is an absolute limit of protein available to grizzly bears (Mealey 1980). Mealey did not sample in the mountains prior to June and, therefore, did not address the importance of pine nuts to bears in spring. Pine

nuts are rich in fat and protein and relatively high in digestibility (Mealey 1980) and may be a critical source of energy to bears in spring.

It was unlikely that increased feeding on pine nuts in summer 1979 was due to a change in the availability of alternate foods between 1978 and 1979. Important summer bear foods (i.e., succulent vegetation and corms and roots of graminoids and forbs) are stable and abundant in the Yellowstone area (Blanchard 1978, Mealey 1980). The higher digestibility and energy content of pine nuts compared to herbs and a decrease in the succulence of vegetation (i.e., in a dry year) would combine to cause bears to feed in summer on pine nuts, if present.

Pine nuts and meat are consistently the most important fall bear food in the Yellowstone area, especially in October and November (Blanchard 1978, Mealey 1980). In September, bears begin feeding on pine nuts but continue to feed on succulent vegetation found in moist sites (Graham 1978). In October when most herbs are desiccated and low in nutritive value, large quantities of pine nuts are eaten, supplemented by small amounts of Umbelliferae roots, grasses, and animal matter (Mealey 1980). Berries are highly nutritious and are eaten primarily from August through October; but such small quantities are probably consumed that they contribute little to the nutrition of bears in Yellowstone (Mealey 1980). Fall movement of bears to high elevations may be due in part to the later maturation and desiccation of high-elevation plants. However, scat results indicate feeding is almost exclusively on pine nuts regardless of other available food sources.

The importance of pine nuts to bears in the Yellowstone area appears to be that nuts are high in food value and are generally available at times when alternate foods are either scarce or low in digestible energy, or both. Bears must put on fat in fall to survive hibernation and early spring (Folk et al. 1976). Delayed hibernation and failure to hibernate occurred when Russian brown bears were malnourished in fall due to nut and berry failures (Pavlov and Zhdanov 1972, Ustinov 1972). When available, caches of pine nuts provide a concentrated source of highly nutritious food at times when rapid weight gain is necessary for bears. Picton (1978) found that reproductive rates of grizzly bears in Yellowstone National Park were high when weather was favorable in October, winter, and spring. Warm, snowy winters reduced energy needs of bears during winter. Warm, dry weather in October, April, and May implied bears were in good condition due to an extended period of feeding on pine nuts in fall and improved availability of food in spring. Mealey (1980) believed that the pre-green-up period may be the primary time in which natural grizzly bear population regulation takes place. Regulation operates through nutritional shortage and occurs because the availability of food sources in the pre-green-up period (i.e., meat and pine nuts) fluctuates. The presence of pine nuts prior to green-up offsets the nutritional stress experienced by bears in a spring with little or no carrion available. The absence of both carrion and pine nuts throughout spring would result in bears entering summer in poor condition. Malnourishment of bears in Russia resulted in increased numbers of bears entering settlements and attack on humans and livestock (Pavlov and Zhdanov 1972, Ustinov 1972).

More information is needed on annual whitebark cone production, subsequent spring availability of nuts in squirrel middens, spring carrion availability, and bear foraging efficiency to measure the effects on bears of cone abundance and to determine the role nutrition plays in the natural regulation of grizzly bear and black bear populations in Yellowstone National Park.

No evidence was found that limber pine supplied a portion of the pine nuts eaten by bears in the Yellowstone National Park area. It was not possible to distinguish between whitebark and limber pine nut remains in bear scats, but no sign of bear use of nuts was observed in 3 limber pine stands. Limber pine appeared to support few, if any, red squirrels. Although limber pine cones were dehiscent (Tomback 1981) and nuts dropped to the ground without the aid of squirrels, scattered nuts or sparse numbers of nut caches may not have been as attractive to bears as more abundant whitebark cone and nut caches. In Colorado, sparse low-elevation stands such as those of limber pine provided few, if any, suitable sites for squirrel middens (Finley 1969). Schallenberger and Jonkel (annual rep., Border Grizzly Project, Univ. Montana, Missoula, 1980) hypothesized that the limber pine stands were not dense enough to harbor as many red squirrels as

the more densely timbered whitebark stands, and as a result of the lack of squirrel caches, grizzly bears ignored equally abundant limber pine nuts to feed on whitebark pine nuts.

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