Bear use of pine nuts
by Katherine Clement Kendall

A thesis submitted in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in Fish and Wildlife Management
Montana State University
© Copyright by Katherine Clement Kendall (1981)

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).
STATEMENT OF PERMISSION TO COPY

In presenting this thesis in partial fulfillment of the requirements for an advanced degree at Montana State University, I agree that the Library shall make it freely available for inspection. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by my major professor, or, in his absence, by the Director of Libraries. It is understood that any copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Signature________________________________________

Date____________________________________________
BEAR USE OF PINE NUTS

by

KATHERINE CLEMENT KENDALL

A thesis submitted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

in

Fish and Wildlife Management

Approved:

Chairperson, Examining Committee

Head, Major Department

Graduate Dean

MONTANA STATE UNIVERSITY
Bozeman, Montana

March, 1981
iii

ACKNOWLEDGMENT

I wish to express my appreciation to Dr. Harold Picton, the chairman of my committee, for his advice and assistance in preparation of the manuscript, and Drs. Richard Knight, Theodore Weaver, William Gould, and Mary Meagher for reviewing the manuscript.

This study was conducted in conjunction with the Interagency Grizzly Bear Study (IGBS). Funding was provided by the National Park Service and the U. S. Fish and Wildlife Service. I am grateful for the cooperation of personnel from Yellowstone National Park and district U. S. Forest Service offices within the study area. I thank all the members of the IGBS who helped me with field work and D. Sizemore for conducting feeding trials on the Vancouver grizzlies.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>VITA</td>
<td>ii</td>
</tr>
<tr>
<td>ACKNOWLEDGMENT</td>
<td>iii</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>v</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>vi</td>
</tr>
<tr>
<td>ABSTRACT</td>
<td>vii</td>
</tr>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>THE STUDY AREA</td>
<td>3</td>
</tr>
<tr>
<td>METHODS</td>
<td>5</td>
</tr>
<tr>
<td>RESULTS</td>
<td>8</td>
</tr>
<tr>
<td>Cone Production</td>
<td>8</td>
</tr>
<tr>
<td>Squirrel Cone Caching Activity</td>
<td>8</td>
</tr>
<tr>
<td>Bear Use of Pine Nuts</td>
<td>9</td>
</tr>
<tr>
<td>Captive Bear Feeding Trials</td>
<td>14</td>
</tr>
<tr>
<td>DISCUSSION AND CONCLUSIONS</td>
<td>16</td>
</tr>
<tr>
<td>REFERENCES CITED</td>
<td>25</td>
</tr>
</tbody>
</table>
LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>ANALYSIS OF PINE NUT CONTENT IN BEAR SCATS COLLECTED BY</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>THE IGBS FROM THE YELLOWSTONE NATIONAL PARK AREA,</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1973-1979</td>
<td></td>
</tr>
<tr>
<td>2.</td>
<td>MONTHLY FREQUENCY AND PERCENT VOLUME OF PINE NUTS IN</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>BEAR SCATS FROM THE YELLOWSTONE NATIONAL PARK AREA,</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1978 AND 1979</td>
<td></td>
</tr>
<tr>
<td>Figure</td>
<td>Page</td>
<td></td>
</tr>
<tr>
<td>--------</td>
<td>------</td>
<td></td>
</tr>
<tr>
<td>1. The locations of 16 whitebark and limber pine stands examined in the study area</td>
<td>4</td>
<td></td>
</tr>
</tbody>
</table>
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*).
INTRODUCTION


Pine nuts are also an important food for red squirrels (*Tamiasciurus hudsonicus*) 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 1978).

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 two 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 raid squirrel caches to feed on pine nuts (Tisch 1961, Craighead and Craighead 1972, Knight 1977, 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.
THE STUDY AREA

The study area was located in Yellowstone National Park and surrounding portions of Montana, Wyoming, and Idaho (Figure 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 lasiocarpa) 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 0.04%, 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.

Stands were sampled for cone crop estimates and squirrel cone caching activity on ridges located 5 km north of Electric Peak on the northern boundary of Yellowstone National Park and in north-central Yellowstone on the west side of Mt. Washburn. These sites were 40 km apart.
Figure 1. The locations of 13 whitebark and 3 limber pine stands examined in 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 three times a week using the radio tracking equipment and techniques described by Judd and Knight (1976). 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 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 examinations 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 Interagency Grizzly Bear Study (IGBS) between 1973 and 1977.

Thirteen whitebark and three 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-September 1979.
Snow depth and cover at disturbed middens were noted during May and June 1979.

I observed squirrel caching behavior from August to October 1978 and August and September 1979. Length of observation periods, the numbers of cones and nuts cached, and depth and location of caches were recorded. The sizes of 25 squirrel caching areas were estimated visually. Randomly selected squirrel middens were examined 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 x 25 m were established in squirrel caching areas on Electric Peak (seven plots) and Mt. Washburn (three plots). The plots were searched for cached cones and nuts two to four 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 three 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) nuts per cone in 1978 and ripened earlier below 2550 m and on south-facing slopes than on higher altitude sites.

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 3,000 cones on the surface in a 4-m² area. Caches for an individual squirrel were contained within areas of 100 to 626 m². 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 first 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 ($P < 0.01$, Wilcoxon's Signed Rank). The mean number of cones and nuts cached in sample plots in 1978 was 394 ($±637$) and 55 ($±71$), respectively. In 1979, the mean number of cones cached in plots was 48 ($±49$) and the mean number of nuts was 293 ($±573$).

Bear Use of Pine Nuts

Data from 633 and 745 relocations made in 1978 and 1979, respectively, indicated 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 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 three 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 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 3,000 cones cached on the surface, bears seldom dug into middens. Bear use of squirrel caches was inferred by 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 that the use of cached pine nuts began approximately the first 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 depth on these slopes averaged 0.3 to 0.6 m 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 2620-2770 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 second and third 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 first 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–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.

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.

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
### TABLE 1. ANALYSIS OF PINE NUT CONTENT IN BEAR SCATS COLLECTED BY THE IGBS\(^1\) FROM THE YELLOWSTONE NATIONAL PARK AREA, 1973-1979.

<table>
<thead>
<tr>
<th>Year</th>
<th>No. of scats</th>
<th>Percent frequency of occurrence(^4)</th>
<th>Percent of scat volume(^5)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1973</td>
<td>22</td>
<td>8</td>
<td>5</td>
</tr>
<tr>
<td>1974</td>
<td>83</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>1975</td>
<td>68</td>
<td>9</td>
<td>4</td>
</tr>
<tr>
<td>1976</td>
<td>23</td>
<td>69</td>
<td>45</td>
</tr>
<tr>
<td>1977</td>
<td>474</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>1978</td>
<td>593</td>
<td>15</td>
<td>11</td>
</tr>
<tr>
<td>1979</td>
<td>752</td>
<td>47</td>
<td>40</td>
</tr>
</tbody>
</table>

1 Interagency Grizzly Bear Study.
2 Scats collected in Yellowstone National Park only.
3 From Mealey (1975).
4 Frequency occurrence percent = (total number of scats containing pine nuts/total number of scats) \(\times\) 100.
5 Percent of scat volume = sum of volume percent of pine nuts/total number of scats.

TABLE 2. MONTHLY FREQUENCY AND PERCENT VOLUME OF PINE NUTS IN BEAR SCATS FROM THE YELLOWSTONE NATIONAL PARK AREA, 1978 AND 1979

<table>
<thead>
<tr>
<th></th>
<th>May</th>
<th>June</th>
<th>July</th>
<th>Aug</th>
<th>Sep</th>
<th>Oct</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percent</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>frequency of</td>
<td>3/14*</td>
<td>1/13</td>
<td>2/36</td>
<td>19/51</td>
<td>70/80</td>
<td>91/69</td>
</tr>
<tr>
<td>occurrence</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Percent of scat volume</td>
<td>1/14</td>
<td>1/12</td>
<td>1/19</td>
<td>12/40</td>
<td>55/73</td>
<td>86/65</td>
</tr>
<tr>
<td>Total No. scats collected</td>
<td>35/63</td>
<td>142/117</td>
<td>175/112</td>
<td>138/63</td>
<td>37/145</td>
<td>11/68</td>
</tr>
</tbody>
</table>

* 1978 value/1979 value.

Scat collection efforts were not equally distributed in all seasons. From 1973 to 1977 scats were collected primarily from June through September (Knight, pers. comm.). 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.

Captive Bear Feeding Trials

Four captive grizzly bears and three 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 one year. None of the scats collected from feeding trials contained cone debris.
DISCUSSION AND CONCLUSIONS

Scat analysis and size 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 four 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 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, dessicated 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 two 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 two stages. Squirrels began to cache immature cones in the first 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, respectively. 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 1978). 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 first 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 (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 m 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 in 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 in 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, Knight 1980). 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 on pine nuts in summer, 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, Knight et al. 1980, 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 dessicated 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 dessication 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 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 attacks 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 three limber pine stands. Limber pine appeared to support few, if any, red squirrels. Although limber pine cones were dehiscent (Tombback 1980) 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 limber pine provided few, if any, suitable sites for squirrel middens (Finley 1969). Schallenberger and Jonkel (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.
REFERENCES CITED


