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Excavation of red squirrel middens by grizzly bears in the whitebark pine zone

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Summary

1. Whitebark pine seeds *Pinus albicaulis* are an important food of grizzly *Ursus arctos horribilis* bears wherever whitebark pine is abundant in the contiguous United States of America; availability of seeds affects the distribution of bears, and the level of conflict between bears and humans. Almost all of the seeds consumed by bears are excavated from middens where red squirrels *Tamiasciurus hudsonicus* have cached whitebark pine cones.
2. Relationships among the occupancy of middens by squirrels, the excavation of middens by bears, and site features were investigated in this study. Data were collected from radio-marked bears and from middens located from line transects on two study sites in the Yellowstone ecosystem.
3. Densities of active middens were positively related to lodgepole pine *Pinus contorta* basal area and negatively related to steepness of slope.
4. The probability that a midden was occupied by a squirrel (i.e. active) was positively related to lodgepole pine basal area in the surrounding stand, size of the midden and size of the whitebark pine cone crop, and negatively related to elevation and to bear excavation during the previous 2–12 months.
5. The probability that a midden had been excavated by a bear during the previous 12 months was positively related to size of the midden, and to whitebark pine basal area and cone crop, and negatively related to nearness of roads and town sites.
6. The influence of midden size on bear use was attributable to a positive relationship with the number of excavated cones. The positive association between bear excavations and whitebark pine basal area or cone crops was attributable to availability of pine seeds.
7. Grizzly bears would benefit from the minimization of roads and other human facilities in the whitebark pine zone and from increases in the availability of whitebark pine seeds, potentially achieved by increasing the numbers of cone-producing whitebark pine trees, especially in lower elevations of the whitebark pine zone where red squirrels are more abundant.

Key-words: avoidance of humans, diet selection, foraging strategies, habitat relationships, Yellowstone National Park.

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Introduction

Whitebark pine *Pinus albicaulis* Engelm. seeds are an important food of grizzly bears *Ursus arctos horribilis* Ord. in parts of the contiguous United States that experience a continental climate (Mattson & Reinhart 1994). When whitebark pine seeds are abundant, grizzly bears eat virtually nothing else (Craighead, Sumner & Scaggs 1982; Mattson, Blanchard & Knight 1991). Approximately one-half of the kernel of white-

bark pine seeds consists of fats (Lanner & Gilbert 1994) that are potentially important to the reproduction of female grizzly bears (Mattson & Reinhart 1994; Mattson 1997a).

Availability of whitebark pine seeds has a major indirect effect on grizzly bear survival in the Yellowstone ecosystem. When pine seeds are available, most grizzly bears forage in high-elevation whitebark pine stands that are typically remote from human facilities (Mattson, Blanchard & Knight 1992). When pine

seeds are scarce, grizzly bears are active closer to roads and town sites, and roughly two to three times as many bears are killed by humans compared to years when pine seeds are abundant (Mattson *et al.* 1992). Because humans kill between 80 and 90% of all adult and subadult grizzly bears that die in the contiguous United States (Mattson *et al.* 1996), use of whitebark pine seeds by grizzly bears has become a prominent management consideration, especially in the Yellowstone ecosystem.

Yellowstone grizzly bears obtain virtually all (> 90%) of the pine seeds they eat by excavating cone caches made by red squirrels *Tamiasciurus hudsonicus* (Mattson & Reinhart 1994). Whitebark pine cones require two years to mature and remain on the tree with seeds retained within unless harvested by seed or cone predators such as squirrels (McCaughy & Schmidt 1990). Red squirrels harvest the cones of whitebark pine after they mature, typically in early August, and cache them in larder hoards (Kendall 1983; Hutchins 1994). These hoards are identified by a prominent accumulation of cone debris from previous caches and typically mark the centre of a territory that is vigorously defended by a single resident squirrel (Smith 1968; Kemp & Keith 1970). The accumulated debris is called a 'midden' and constitutes the defining feature of squirrel territories which may persist through the tenures of several individuals (Rusch & Reeder 1978; Price *et al.* 1986). Red squirrels and their middens have thus become a focus of management attention in grizzly bear habitat.

Managers are also concerned with the under-use of available bear foods where grizzly bears seem to avoid humans and human facilities. Previous research in the contiguous United States has shown that grizzly bears routinely avoid areas within 500 m of roads, and within up to 5 km of town sites and major recreational developments (Mattson *et al.* 1996). Questions remain, however, whether this research based on day-time telemetry locations of radio-marked animals adequately documents night-time use. There is also concern that habitat selection primarily related to the distribution of native foods may be mistaken for 'avoidance' of humans, especially if poor quality habitat is spatially correlated with human facilities (Mattson *et al.* 1996).

This study was designed to provide managers with critical information on grizzly bear use of pine seeds and the potential under-use of habitat near humans by bears. To facilitate habitat assessments, information on the density of squirrel middens excavated by grizzly bears was stratified by commonly used classifications of site potential and forest stand structure. Data were collected to allow midden use by bears and midden occupancy by squirrels to be modelled. The models were designed to help managers anticipate the consequences of management actions and the reaction of grizzly bears to other phenomena, such as natural forest succession and global climate change.

Finally, this study provided an opportunity to test whether grizzly bears in the Yellowstone ecosystem were avoiding roads and town sites.

Whitebark pine seeds are the most abundant of only two high-quality foods commonly available to grizzly bears in forests at high elevations (> 2360 m). The other food source is meat obtained from ungulate carrion & kills (Mattson & Knight 1989; Mattson 1997a). Whitebark pine seeds are consumed by bears almost exclusively from middens. Middens therefore correlate well with the availability of high quality bear foods in whitebark pine forests. Because bear excavations are durable and visually prominent, they can be detected at any time, irrespective of the time of day that either bears or researchers are active.

Study area

The study area consisted of two sites located one each in the states of Wyoming and Montana, United States of America, in or near Yellowstone National Park. One site, 9.5 km² in size, was located on the Mt Washburn mountain massif in north-central Yellowstone Park (44°47'N 110°24'W). A second site, 12 km² in size, was located immediately north-east of the Park, within 2 km of the town of Cooke City (45°00'N 109°58'W). The Mt Washburn site was transected by a paved highway. During the study, Cooke City had a population of 100 year-round residents, although this number increased during the summer due to visitors and seasonal residents. The town was reached by a paved highway that defined the lower elevational boundary of the nearby study site. Neither site had been harvested for timber by humans.

Both sites encompassed the range of elevations where mature whitebark pine is common, between 2360 m and the upper extent of forest growth at 2870 m. Forest cover was broken by a few meadows and rock-strewn slopes and consisted primarily of lodgepole pine *Pinus contorta* Dougl., subalpine fir *Abies bifolia* A. Murray, Engelmann spruce *Picea engelmannii* Parry, and whitebark pine. Douglas-fir *Pseudotsuga menziesii* (Merbel) Franco was common in places on the Mt Washburn site. Whitebark pine and Douglas-fir usually occurred intermixed with other tree species, but they could dominate wind-exposed sites at high and low elevations, respectively (Mattson & Reinhart 1990). Undergrowth was short-statured (< 50 cm) and typically dominated by forbs such as western meadow-rue *Thalictrum occidentale* Gray, and ericaceous shrubs such as globe huckleberry *Vaccinium globulare* Rydb. and grouse-whortleberry *V. scoparium* Leiberger.

Both sites were steep and predominantly west- to north-facing. As a consequence, much of the study area was exposed to the prevailing west- to south-west winds (Dirks & Martner 1982). This accentuated the harsh climate of the whitebark pine zone, typified by average annual temperatures near 0°C, annual pre-

precipitation of 600–800 mm and only 4 months without continuous snow cover (Weaver 1990). These conditions coincided with the extreme upper-elevational limits of red squirrel distribution (Streubel 1989).

Some data used in this analysis were collected in conjunction with a radio-telemetry study that included all of the known range of Yellowstone's grizzly bears. This range was *c.* 23000 km² in size, and consisted of high-elevation (>1650 m) mountains and plateaus surrounded by valleys and plains more intensively settled or used by humans. Features of this larger study area are described by Knight & Eberhardt (1985), Blanchard & Knight (1991) and Mattson *et al.* (1991).

Materials and Methods

FIELD METHODS

Data were collected from 1984 to 1987 along transects that were systematically placed throughout the elevational range of whitebark pine (Mattson & Reinhart 1996). Transects were 500–1000 m long, depending on topography and the occurrence of non-forest vegetation. Sampling occurred between 10 August and 28 September, during peak harvest and use of whitebark pine seeds by squirrels and bears (Kendall 1983; Mattson & Reinhart 1994), and before winter snow accumulation each year. Transects and sites were sampled in the same order each year. During 1984, 35 transects totalling 18.9 km and 15 transects totalling 16.4 km were sampled on the Mt Washburn and Cooke City sites, respectively. During the remaining years, 57 and 21 transects, totalling 29.8 and 21.1 km, were sampled at each respective site. More transects were established in 1985 to increase sample sizes in certain stand types (see below) especially in lower elevations of the whitebark pine zone.

These transects intersected 50 and 84 forest stands on Mt Washburn, and 57 and 69 stands on the Cooke City site (for 1984 and remaining years, respectively). Stands were delineated by interpretation of 1:20 000 aerial photographs and field checked for accuracy. Stands were classified according to habitat type (Steele *et al.* 1983) and cover type (Despain 1990). Habitat type reflected the biophysical site, and cover type described the current forest structure, including dominant species and successional status.

The stratification by habitat and cover type, and the related importance of sampling by stands, affected the layout of transects. Initial placement was systematic, parallel at about 150-m intervals. However, layout was subsequently adjusted to minimize the edge effects between different types of habitat and cover on parameter estimates by type (cf. Eberhardt 1978). This was done by maximizing the number of right-angle intersections with stand boundaries and the proportion of transects contained within stand interiors (Mattson & Reinhart 1996).

Two individuals sampled the transects; one observer (the co-author) sampled all years. All observed middens were noted, along with the perpendicular distance of each from the transect line. All but one of these middens were <50 m from a transect; the exception was 64 m away. Middens were distinguished according to whether they were currently used by a squirrel [based on the criteria of Finley (1969; fresh cones and clippings) and on sightings and vocalizations], and by whether they had been excavated by a bear within the previous 2 or 12 months. Excavations which were less than 2 months old were associated with use of the current year's crop of cones, while excavations 2–12 months old were associated with use of cones from the previous year's crop. Dimensions of the midden (length and width in decimetres) were also measured. The percentage of the midden surface disturbed by bear digging was assessed by eye.

Forest canopies were sampled by variable-radius plots placed at regular intervals along transect lines. Common US Forest Service techniques (cf. Finch 1957) were used to simplify subsequent management recommendations. The age of the oldest tree in a stand, based on counts of annual rings from an extracted core, was used to indicate the time since the last stand-replacement fire, excluding trees that had obviously survived this fire. Mature cones were also counted each year on 10 permanently marked whitebark pine trees at each of the Mt Washburn and Cooke City study sites. Blanchard (1990) describes the methods that were used for marking trees and counting cones.

Grizzly bears were radio-collared and tracked throughout the Yellowstone ecosystem from 1986 to 1992. These bears were located by aerial-telemetry and locations were subsequently visited by ground crews as part of a larger-scale study to document feeding behaviour and diet (Mattson 1997a,b). Wherever a radio-tagged bear had excavated a squirrel midden, the number of visible cones used by the bear was counted. These cones were identifiable by the ragged fracturing of bracts and by their close association with bear excavations. In small middens, all cones were counted. In larger middens, counts were based on subsamples from regularly placed (5-m spacing) 25-m² plots. Midden dimensions were also measured in the same way as for middens observed on transects. Knight & Eberhardt (1985), Blanchard & Knight (1991) and Mattson (1997b) provide further details on methods for radio-tagging bears and sampling telemetry locations.

ANALYSIS

Thirty-five habitat type/cover type combinations were present in the study area. These were consolidated into six classes (Table 1) based on similar forest structures. Consolidation was based on cluster analysis of data

Table 1. Description of forest types used to stratify the analysis of red squirrel habitat relationships and excavation of red squirrel middens by bears on the Mt Washburn and Cooke City sites, Yellowstone area, 1984–87

Type	Description*	Syntaxonomic composition†
WBP	High-elevation wind-exposed sites dominated by whitebark pine, immediately below upper timberline, but extending down exposed ridges.	Habitat types (hts) of the whitebark pine climax series.
WBP/LPP	High-elevation sites on northerly exposures with ground-layer vegetation dominated by ericaceous shrubs; whitebark pine abundant in diverse canopies.	Whitebark pine cover types (cts) of the subalpine fir/grouse-whortleberry ht, whitebark pine phase, and subalpine fir/globe-huckleberry ht.
LPP/WBP	Mid- to high-elevation sites on northerly or easterly exposures with diverse ground-layer vegetation; lodgepole and whitebark pines common or abundant in diverse canopies.	Lodgepole pine cts of the subalpine fir/grouse-whortleberry ht, whitebark pine phase and subalpine fir/globe huckleberry ht; subalpine fir/bluejoint reedgrass <i>Calamagrostis canadensis</i> and subalpine fir/twisted stalk <i>Streptopus amplexifolius</i> hts.
ABLA/VAGL	Mid-elevation sites on northerly or westerly exposures with ground-layer vegetation dominated by globe-huckleberry; lodge-pole pine abundant.	Lodgepole pine cts of the subalpine fir/globe-huckleberry ht.
LPP	Mid- to low-elevation sites on moderate to gentle slopes dominated by lodge-pole pine.	Subalpine fir/grouse-whortleberry ht, grouse-whortleberry phase, and lodgepole pine cts of the subalpine fir/western meadowrue ht.
ABLA/SPBE	Low- to mid-elevation wind-exposed sites with diverse ground-layer vegetation and Douglas-fir typically present.	Subalpine fir/birch-leaf spirea <i>Spirea betulifolia</i> ht.

* Descriptions are based on Mattson & Reinhart (1990).

† Habitat types are described by Steele *et al.* (1983) and cover types by Despain (1990).

from each site [average linkage (SAS Institute, Inc. 1989)] using total forest basal area, whitebark pine basal area, and canopy species diversity [by the Margalef diversity index (D_{Mg}); Magurran 1988; Table 2]. Basal area was calculated as the cross-sectional area of

all stems > 1.4 m tall. Information on lodgepole pine basal area and stand age (Table 2) is relevant to explaining the results of the following statistical analyses.

Densities of middens were estimated using the computer program TRANSECT (Burnham, Anderson &

Table 2. Characteristics of canopies on forest types used to stratify the analysis of red squirrel habitat relationships and excavation of red squirrel middens by bears on the Mt Washburn and Cooke City sites, Yellowstone area, 1984–87. Sample size is for the number of plots. Canopies changed after the wild-fires of 1988. Means followed by the same letter in columns are not different among habitat types within sites at $\alpha = 0.1$

		Total Basal area (m ² ha ⁻¹)		Whitebark pine Basal area (m ² ha ⁻¹)		Lodgepole pine Basal area (m ² ha ⁻¹)		Margalef's Diversity Index (<i>D</i> _{Mg})		Age of oldest tree (years)	
Forest type*	<i>n</i>	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Mt Washburn											
WBP	34	23.7b†	14.2	16.0a‡	11.3	3.9c‡	8.6	0.385b‡	0.427	151b†	38
WBP/LPP	230	41.9a	19.0	23.4a	18.0	5.1c	9.7	0.550a	0.388	192a	36
LPP/WBP	314	43.2a	17.9	8.1b	11.8	16.8b	16.0	0.518a	0.333	182a	37
LPP	206	40.4a	17.4	2.2c	7.1	28.2a	17.5	0.313b	0.323	179a	35
ABLA/SPBE	96	28.7b	15.3	6.2bc	8.7	15.8b	12.8	0.416b	0.413	202a	76
Cooke City											
WBP/LPP	154	37.0ab	17.9	17.6a	15.9	6.8b	11.3	0.538a	0.358	158a	30
LPP/WBP	52	40.7a	21.3	7.1a	9.0	11.6b	16.1	0.528a	0.346	150a	40
ABLA/VAGL	267	34.9ab	16.5	3.4b	7.7	16.9a	15.4	0.458a	0.355	165a	34
LPP	72	32.4b	14.7	1.0b	5.0	16.6a	15.4	0.254b	0.326	148a	47

* Forest types are described in Table 1.

† Results of parametric tests that used natural log transformations of the data. Untransformed values are displayed.

‡ Results of non-parametric ANOVA (Kruskal–Wallis) and multiple comparisons (Zar 1984).

Laake 1980). Estimates were made for each of the six forest type classes on each site for each of the four study years. Stands rather than transects were used as replicates because the study was stratified by habitat types. Serial correlation did not pose a problem because adjacent stands were mapped as different types. In most cases, the Fourier series was used to estimate probability detection functions (Mattson & Reinhart 1996).

Analysis-of-variance (ANOVA) was used to test for differences in mean densities of middens and to test for differences in the means of forest canopy variables, among habitat types, sites and years. A type I error rate (α) of 0.1 was chosen for not rejecting differences, recognizing that P will always be an approximation of reality, and that α is chosen based on individual considerations and scientific norms (Gilbert 1989). Non-parametric ANOVA (the Kruskal–Wallis test) and a non-parametric equivalent of the Tukey multiple-comparisons test (Zar 1984) were used where data were *a priori* non-normal. An analogue of the Tukey test was also used for multiple-comparisons among proportions (Zar 1984). In all other cases, parametric ANOVA was used, followed by the Ryan Q or Tukey–Kramer multiple-comparisons test, depending upon whether cell sample sizes were equal or not (Day & Quinn 1989). Analyses for values averaged by habitat type were weighted by the length of transects (km) or number of plots to correct for the potential effects of unequal variances induced by unequal sampling of different habitat types.

Multiple linear regression was used to analyse the relationship of midden density to site and stand features. Observations were based on averages over all years by type for each site, excluding 1984 when fewer transects were sampled compared to 1985–87. Site effects were tested by analysis-of-covariance. Weighted regression (by km of transects) was used to account for unequal sampling effort among habitat types (Weisberg 1985). Linear regression was also used to analyse the relationship between the number of cones excavated per midden at aerial-telemetry locations of radio-tagged bears and midden size (length \times width).

Models were developed that related the probability of squirrel activity or bear excavations in each midden to site features, size of the whitebark pine cone crop, and midden dimensions. These probabilities were modelled as logits $\{\ln [p/(1-p)]\}$, able to be back-transformed by: $\hat{p} = e^{\beta}/(1 + e^{\beta})$ (Demaris 1992). Model fit was judged by the likelihood ratio statistic (Demaris 1992) and parameter significance was judged by the Wald χ^2 test (Wald 1943). Maximum likelihood estimates were used for all parameters. Logistic regression and contingency-table analyses, as appropriate, were used to describe single-factor relationships prior to building models with multiple independent variables. Independence was judged by the G^2 -test. Where independence was rejected, classes that

exhibited significant differences between dependent states were identified using simultaneous Bonferroni confidence intervals that varied with the sample sizes of each dependent class (Miller 1981).

Log-linear models with multiple independent variables allowed for a more reliable description of partial relationships because the effects of other factors could be controlled. Site and year effects attributable to differences in size of the whitebark pine seed crop and frequency of bear excavations were simultaneously considered. However, there were potential problems with this approach because observations were not wholly independent. Non-independence could have arisen from bears foraging in adjacent squirrel middens, from the occupancy of one midden by a squirrel affecting the occupancy of other middens around it and by repeat sampling of some middens during different years. Control of this potential effect was difficult because middens were not marked. As a result, the probability of type I error was underestimated (Garson & Moser 1995). A more conservative α (0.01) was adopted for these models.

Results

DISTRIBUTION OF ACTIVE MIDDENS

Densities of active middens were highest in forest types dominated by lodgepole pine (the LPP type) and lowest in forest types dominated by a mix of whitebark and lodgepole pines (the WBP/LPP type) on both the Mt Washburn and Cooke City sites (Tables 2 and 3). Densities were also low in forest types characterized by high coverages of Douglas-fir and birch-leaf spirea (the ABLA/SPBE type) and in the LPP/WBP type on the Cooke City site. Individual middens were consistently smallest (length \times width) in the ABLA/SPBE type and in forest types dominated by whitebark pine (the WBP type) (Table 3). Middens were largest on both sites in the WBP/LPP and LPP/WBP types.

The density of active middens, by forest type ($n = 9$), was positively related to lodgepole pine basal area ($LPPBA$) and negatively related to steepness of slope ($SLOPE$):

$$\hat{y} = 1.32 + 0.116\sqrt{LPPBA} - 0.350 \ln(SLOPE)$$

($F_{2,6} = 33.5$, $R^2 = 0.918$, $P = 0.001$). There was no effect ($P = 0.796$) attributable to the study area site (Mt Washburn vs. Cooke City). $LPPBA$ and $SLOPE$ potentially conveyed information about other stand and site features, calculated as Pearson's correlations using square root transformations of basal areas and natural log transformation of $SLOPE$. $LPPBA$ was negatively correlated with whitebark pine basal area ($r = -0.836$, $P = 0.005$) and elevation ($r = -0.658$, $P = 0.058$). $SLOPE$ was positively correlated with Douglas-fir basal area ($r = 0.685$, $P = 0.042$), and negatively correlated with subalpine fir ($r = -0.869$,

Table 3. Sizes and densities of active middens and densities of middens excavated by grizzly bears, for forest types of the Mt Washburn and Cooke City sites, Yellowstone area, 1984–87. Coefficients of variation (CV) are expressed as SD mean⁻¹ and are for among-years' variation ($n = 4$). Means followed by the same letters in columns are not different among habitat types within sites, controlling for year effects where evident, at $\alpha = 0.1$

		Active midden density (<i>n</i> ha ⁻¹)		Active midden size (m ²)		Excavated midden density (<i>n</i> ha ⁻¹)	
Forest type*	<i>n</i>	Mean	CV	Mean	CV	Mean	CV
Mt Washburn							
WBP	8	0.50bc†	0.37	10.0c‡	0.001	0.057b†	1.12
WBP/LPP	34	0.23c	0.25	84.4a	0.02	0.138a	0.38
LPP/WBP	126	0.72ab	0.16	82.3a	0.06	0.291a	0.30
LPP	103	1.09a	0.19	56.7b	0.05	0.207a	0.42
ABLA/SPBE	4	0.37c	0.30	12.1c	0.08	0.000b	–
Cooke City							
WBP/LPP	50	0.44bc	0.22	81.3a	0.03	0.160a	0.76
LPP/WBP	12	0.44c	0.42	120.1a	0.03	0.048ab	2.10
ABLA/VAGL	83	0.66ab	0.24	42.5b	0.02	0.029b	1.16
LPP	24	0.86a	0.01	52.8b	0.02	0.000b	–

* Descriptions of forest types are given in Tables 1 and 2.

† Tests used square root transformations of the data. Untransformed values are displayed.

‡ Tests used natural log transformations of the data. Untransformed values are displayed.

$P = 0.002$) and Engelmann spruce ($r = -0.703$, $P = 0.035$) basal areas.

PROBABILITY OF SQUIRREL ACTIVITY

The probability that a midden was being used by squirrels to feed or cache cones was related to elevation, midden size, basal area of lodgepole pine in the surrounding stand, and whether the midden had been excavated within the last 2–12 months by bears (Table 4). The probability of activity was positively related

to lodgepole pine basal area and negatively related to elevation (Fig. 1). Of the more immediate features, the probability of activity was positively related to midden size and negatively related to excavation by bears (Fig. 2). The nature of these relationships was the same on the Mt Washburn and Cooke City sites. However, all of the relationships, except for midden size, were stronger on Mt Washburn (Table 4).

These relationships were evident in a log-linear model with multiple independent variables (Table 5). In addition, the probability of squirrel activity was

Table 4. Statistics for tests of goodness-of-fit and for whether parameters (β_1) = 0 (Wald χ^2 tests), for single-variable logistic regression models. The probability of a squirrel being active in a midden or that a midden was excavated by bears was related to site, stand or midden features. Models were developed for each of the Cooke City and Mt Washburn study sites from observations along transects, 1984–87

	Goodness-of-fit			β_1 (d.f. = 1)	
	d.f.	G^2	P	χ^2	P
<i>Probability of squirrel activity</i>					
Lodgepole pine basal area (m ² ha ⁻¹)					
Cooke City	40	36.3	0.638	1.9	0.172
Mt Washburn	61	68.0	0.250	43.0	<0.001
Elevation (m)					
Cooke City	51	53.4	0.380	3.7	0.056
Mt Washburn	52	59.2	0.231	47.8	<0.001
Midden length \times width (size) (m ²)					
Cooke City	92	101.8	0.228	28.4	<0.001
Mt Washburn	117	156.7	0.008	10.9	0.001
<i>Probability of bear excavation</i>					
Whitebark pine basal area (m ² ha ⁻¹)					
Cooke City	31	53.9	0.007	21.4	<0.001
Mt Washburn	42	100.1	<0.001	12.8	0.001
Midden length \times width (size) (m ²)					
Cooke City	78	71.2	0.693	18.3	<0.001
Mt Washburn	99	110.5	0.202	40.3	<0.001

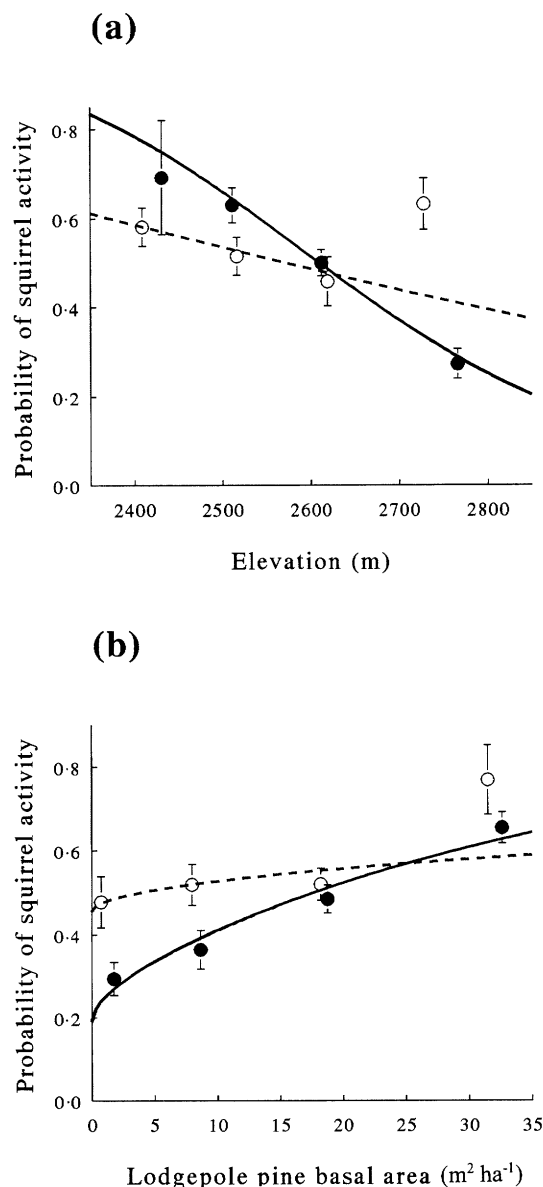


Fig. 1. Relationships between the probability of a red squirrel using a midden for caching or feeding and (a) elevation and (b) basal area of lodgepole pine in the surrounding forest stand, for two study sites in the Yellowstone ecosystem between 1984 and 1987. The curved lines depict relationships estimated by logistic regression. Point probability estimates (± 1 SE) are also shown for four percentiles, to illustrate the fit of regression lines to observed midden activity. The dashed line and open points depict the relationship for the Cooke City site and the solid line and points depict the relationship for Mt Washburn.

positively related to the size of the current-year's cone crop. At $\alpha > 0.01$, squirrel activity was also positively related to the previous year's whitebark pine cone crop and negatively related to being located on the Cooke City vs. Mt Washburn site (Table 4). Model fit was acceptable (d.f. = 666, $G^2 = 662.6$, $P = 0.530$).

DISTRIBUTION OF BEAR EXCAVATIONS

Bears consumed whitebark pine seeds exclusively from cones excavated in middens. In no instance were they

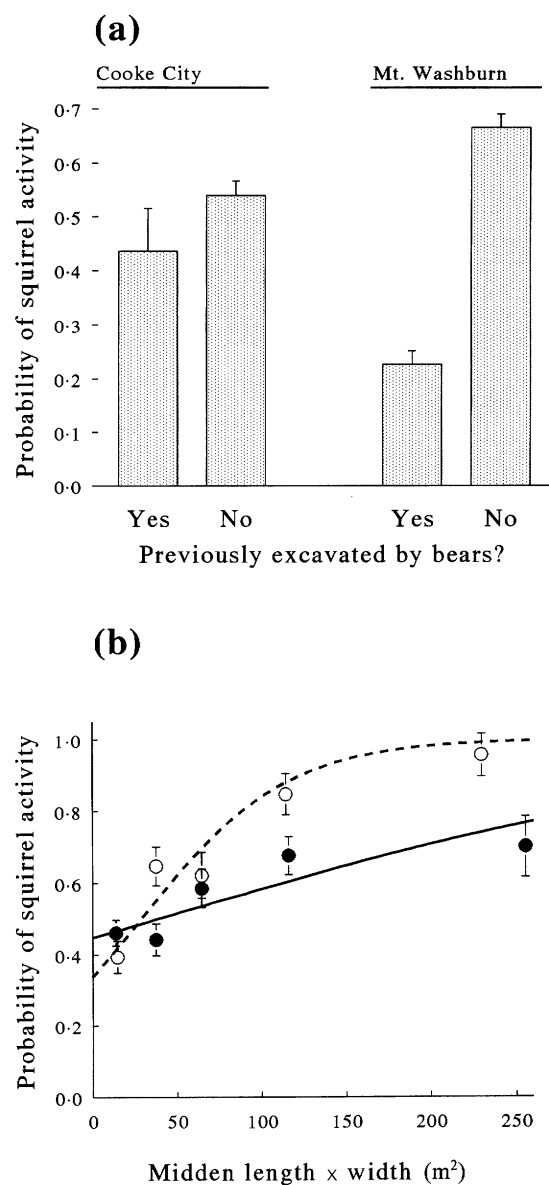


Fig. 2. Relationships between the probability of a red squirrel using a midden for caching or feeding and (a) excavation by bears within the previous 2–12 months and (b) midden size, for two study sites in the Yellowstone ecosystem between 1984 and 1987. The curved lines depict relationships estimated by logistic regression. Point probability estimates (± 1 SE) are also shown for five percentiles, to illustrate the fit of regression lines to observed midden activity. The dashed line and open points depict the relationship for the Cooke City site, and the solid line and points depict the relationship for Mt Washburn.

observed to consume seeds from fallen cones or cones obtained directly from tree canopies. Excavations therefore represented total consumption of pine seeds by bears in the transect study area. The density of middens excavated by bears was highest in forest types dominated by a mix of whitebark and lodgepole pines (the WBP/LPP and LPP/WBP types) on both study sites (Table 3). Densities were lowest in stands dominated by whitebark pine (the WBP type) or where Douglas-fir was abundant (the ABLA/SPBE) on the Mt Washburn site, and in stands dominated by lodge-

Table 5. Estimates of β parameters and the results of tests (P -values from Wald χ^2 tests with d.f. = 1) for whether parameters = 0 for two multi-variable log-linear models. These models describe relationships between the probability of a squirrel being active in a midden or the probability that a midden was excavated by bears and site features, stand features, size of the whitebark pine cone crop and midden characteristics. Data were collected from middens observed along transects on the Mt Washburn and Cooke City study sites from 1984–87

Parameter	Probability of squirrel activity (coefficients)			Probability of bear excavation (coefficients)		
	Estimate	SE	P	Estimate	SE	P
Intercept	98.8	24.5	<0.001	−7.98	0.73	<0.001
Midden length \times width (size) (m^2)	0.016	0.0023	<0.001	1.12*	0.14	<0.001
Current-year's whitebark pine cone crop ($n \text{ tree}^{-1}$)	0.191	0.030	<0.001	0.072	0.020	<0.001
Previous-year's whitebark pine cone crop ($n \text{ tree}^{-1}$)	0.034	0.014	0.014	0.053	0.017	0.002
Lodgepole pine basal area ($\text{m}^2 \text{ ha}^{-1}$)	0.211†	0.074	0.005	—		
Elevation (m)	−12.9*	3.11	<0.001	—		
Bear excavation within the previous 2–12 months						
Yes	−0.846	0.125	<0.001			
No	0.846‡					
Site effect						
Cooke City	−0.320	0.130	0.014	—		
Mt Washburn	0.320‡					
Whitebark pine basal area ($\text{m}^2 \text{ ha}^{-1}$)	—			0.374†	0.080	<0.001
Squirrel active in the midden						
Yes	—			0.664	0.142	<0.001
No	—			−0.664‡		
Within 500 m of a road						
Yes	—			−0.877	0.288	0.002
No	—			0.877‡		
Within 5 km of a town site						
Yes	—			−1.67	0.310	<0.001
No	—			1.67‡		

* Coefficient estimated for natural-log transformed values.

† Coefficient estimated for square-root transformed values.

‡ Coefficient calculated by difference.

pole pine (the LPP type) on the Cooke City site. The lowest densities of bear excavations coincided with the smallest mean sizes of middens on both sites.

Based on observations of radio-tagged grizzly bears, the number of cones excavated per midden was highest in the WBP and LPP/WBP types, and lowest in the ABLA/SPBE and LPP types (Table 6). Thus,

Table 6. Number of cones, by forest type, that were excavated by grizzly bears from red squirrel middens. The sample was obtained while visiting telemetry locations of radio-tagged bears in the Yellowstone area from 1986 to 1992. Means followed by the same letter are not different, controlling for year effects where evident, at $\alpha = 0.1$. Natural log transformations of the data were used, although untransformed values are displayed

Forest type*	Cones excavation ^{−1}		
	Mean	SD	n
WBP	137a	132	27
WBP/LPP	74ab	65	46
LPP/WBP	83a	74	28
LPP	57b	17	37
ABLA/SPBE	56b	74	3

* Forest types are described in Tables 1 and 2.

even though bear excavations could be relatively common in lodgepole pine-dominated stands (as on Mt Washburn), food rewards tended to be small. Conversely, even though middens were small and excavations relatively infrequent in whitebark pine-dominated stands, food rewards tended to be large. Overall, however, the LPP/WBP and WBP/LPP types were distinguished by the highest unit-area densities of cones excavated by bears.

PROBABILITY OF BEAR EXCAVATION

The probability that a bear had excavated a midden within the previous 12 months was positively related to the size of the midden and the basal area of whitebark pine in the surrounding stand (Fig. 3), and negatively related to its location within 500 m of road or 5 km of Cooke City (Fig. 4). Single-variable relationships based on logistic regression analyses were strong on both sites, although the fit of these single-variable models was sometimes not adequate (Table 4). The probability of bear excavation increased with midden size and whitebark pine basal area on both the Mt Washburn and Cooke City sites.

Pooling observations from both study sites and

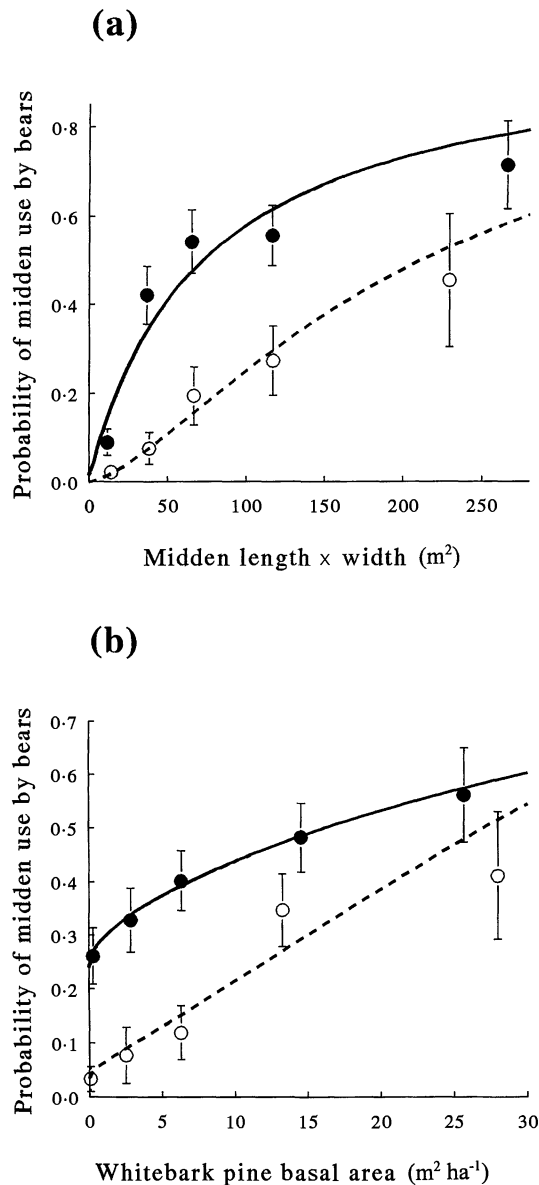


Fig. 3. Relationships between the probability of a red squirrel midden being excavated by bears during the previous 12 months, and (a) midden size and (b) basal area of whitebark pine in the surrounding forest stand, for two study sites in the Yellowstone ecosystem, 1984–87. The curved lines depict relationships estimated by logistic regression. Point probability estimates (± 1 SE) are also shown for five percentiles, to illustrate the fit of regression lines to observed bear excavations. The dashed line and open points depict the relationship for the Cooke City site, and the solid line and points depict the relationship for Mt Washburn.

jointly considering hypothesized zones of influence (ZOIs) associated with roads and town sites, no midden excavations were observed within overlapping road and town site ZOIs, and excavation was 1.3 and 2.6 times as likely away from road and town site ZOIs, respectively. Coefficients associated with town site, but not road, effects were significant (d.f. = 1, $\chi^2 = 19.6$, $P < 0.001$, and $\chi^2 = 5.5$, $P = 0.019$, respectively). At $\alpha > 0.01$, road effects were also significant. Model fit was not acceptable (d.f. = 1, $G^2 = 5.3$, $P = 0.021$).

These relationships were strong in a log-linear model that included multiple independent variables and provided a very good fit to the observed patterns (d.f. = 657, $G^2 = 507.0$, $P = 1.000$) (Table 5). The probability of excavation by bears within the previous 12 months was also positively related to the size of the whitebark pine cone crop during the previous and current year, and to the probability that a midden was being used by a squirrel at the time of observation. No effects attributable to study site were evident ($P > 0.25$). Holding all other effects constant at mean values for the study area, this model predicted that nearness to roads and town sites reduced the probability of bear use by 66 and 92%, respectively. Overlapping ZOIs from roads and town sites reduced bear use by 98%.

CORRELATES OF MIDDEN AND CONE CROP SIZE

The number of cones excavated from a midden by radio-tagged grizzly bears was positively related to midden size ($r^2 = 0.151$, $F_{1,126} = 68.0$, $P < 0.001$) (Fig. 5). The relationship was calculated for natural log transformed values of midden area and number of cones, excluding seven potentially anomalous very large (> 600 m²) middens.

The percentage of midden area disturbed by bear digging was recorded during 1986 and 1987, following large and small whitebark pine cone crops during the previous year, respectively (Table 7). Most bear excavations recorded during these years were attributable to bears foraging on the previous year's crop during the preceding 12 months. The relative frequency of different digging intensities differed between the two years (d.f. = 4, $G^2 = 15.1$, $P = 0.005$) (Fig. 6). Excavations were more extensive during 1986 compared to 1987, and differed in that relatively more excavations disturbed 61–80% of the midden and relatively few disturbed 21–40% of the midden during 1986. Excavations were also relatively more common during the year that preceded sampling in 1986 compared to all other years, including 1987 (Table 7). Midden densities were lower, especially on the Mt Washburn site, during 1986 compared to 1985.

Discussion

RED SQUIRREL ACTIVITY AND ABUNDANCE

The number of resident territorial red squirrels is closely associated with the number of active middens in an area (Kilham 1954; Smith 1968; Wolff & Zasada 1975; Vahle & Patton 1983). Active middens are thereby good indicators of red squirrel abundance (Mattson & Reinhart 1996) and inferences about populations of territorial red squirrels based on observations of middens are justified.

The establishment and use of middens by red squir-

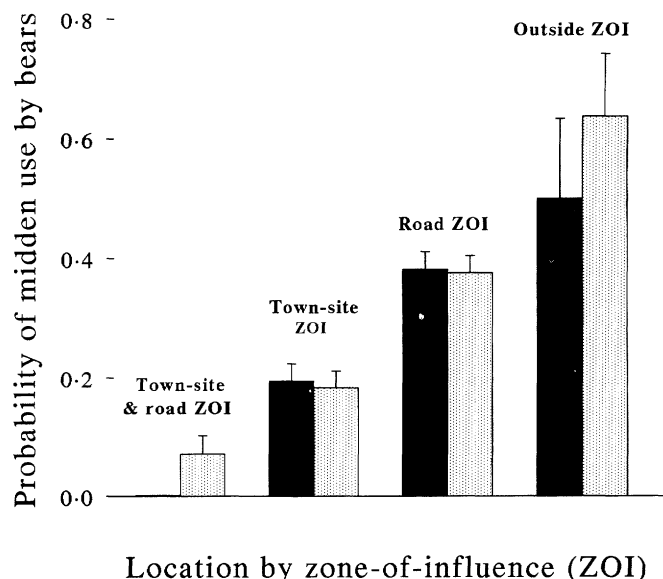


Fig. 4. The relationship between the probability (± 1 SE) of a red squirrel midden being excavated by bears during the previous 12 months and its location within zones-of-influence (ZOIs) for roads and town sites that had been identified by previous research with grizzly bears. Data were pooled from the Mt Washburn and Cooke City study sites in the Yellowstone ecosystem from 1984–87. The road ZOI included areas within 500 m and the town site ZOI included areas within 5 km. The black bars depict observed proportional use by bears and the stippled bars depict use predicted by a maximum-likelihood log-linear model.

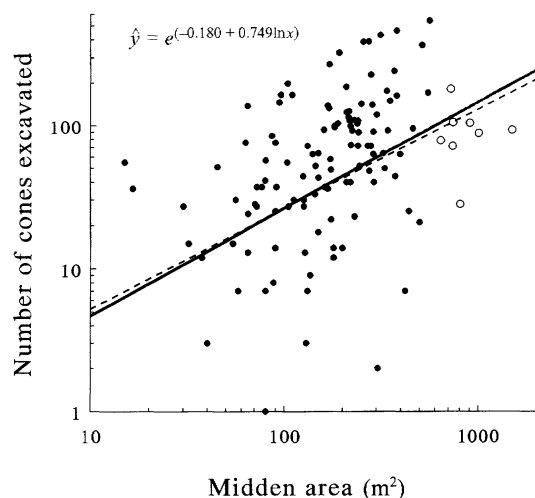


Fig. 5. The relationship between the number of cones excavated by radio-marked grizzly bears from red squirrel middens and the surface area of the midden for the Yellowstone ecosystem between 1986 and 1992. The solid line depicts the estimated relationship, excluding potentially anomalous very large (> 600 m²) middens (shown as ○). The dashed line depicts the relationship including these middens.

rels in the whitebark pine zone was positively associated with lodgepole pine basal area. Previous work with squirrels in conifer forests found that similar relationships existed between squirrel abundance or midden-site selection and the basal area of either the entire stand or of certain species within the stand (Wolff & Zasada 1975; Vahle & Patton 1983; Sullivan & Moses 1986; Smith & Mannan 1994). The mechanism behind these relationships was assumed to be unit-area food abundance or micro-site amelioration. However, the energetic benefits of using lodgepole

pine seeds are less than those of using the seeds of any other tree species in the study area (Smith 1968; Finley 1969; Lanner & Gilbert 1994). Other studies have also found that red squirrels living in stands dominated by lodgepole pine or the closely related jack pine *Pinus banksiana* Lamb. existed at much lower densities compared to squirrels living in Douglas-fir or spruce-dominated stands (Smith 1968, 1970; Finley 1969; Rusch & Reeder 1978). Thus, interpreting the positive relationship observed in this study between squirrels and lodgepole pine is complicated because it both contradicts and agrees with expectations based on previous research.

The relationship between red squirrel activity or abundance and lodgepole pine basal area was probably caused, in part, by non-biotic features that were correlated under natural conditions with abundance of lodgepole pine in the whitebark zone. Within this zone, lodgepole pine was more abundant at lower elevations or, more generally, where climate was less extreme (Mattson & Reinhart 1990). Comparatively mild conditions probably also favoured red squirrels in an otherwise harsh environment (Gurnell 1987). If so, then these results should not be construed to imply that red squirrel populations can be increased simply by increasing the abundance of lodgepole pine on a site. On the other hand, red squirrels may have directly benefitted from lodgepole pine because seed crops of this species are comparatively stable from one year to the next (Finley 1969; Smith 1970). As evidence of this potential effect, densities of active middens were least variable among years on sites where lodgepole pine was most abundant.

Annual variation in the frequency of red squirrel

Table 7. Annual estimates of the whitebark pine cone crop, percentage of active middens that were excavated by grizzly bears during the previous 2 months, and density of active middens, Mt Washburn and Cooke City sites, Yellowstone area, 1984–87. Sample size is for the number of active middens. Percentages followed by the same letter in columns are not different among years within sites at $\alpha = 0.1$, controlling for habitat type effects

Year	<i>n</i>	Cone crop (<i>n</i> tree ⁻¹)		Excavated middens (%)	Active midden density (<i>n</i> ha ⁻¹)
		Mean	SD		
Mt Washburn					
84	50	7.5b	2.6	26.0bc	0.447
85	90	28.3a	6.8	48.9a	0.557
86	65	0.9c	1.6	16.9c	0.219
87	138	3.4c	3.6	27.5b	0.453
Cooke City					
84	30	—	—	6.7b	0.428
85	54	46.6a	9.3	24.1a	0.682
86	40	3.8c	2.4	0.0c	0.548
87	39	11.8b	2.6	13.3ab	0.544

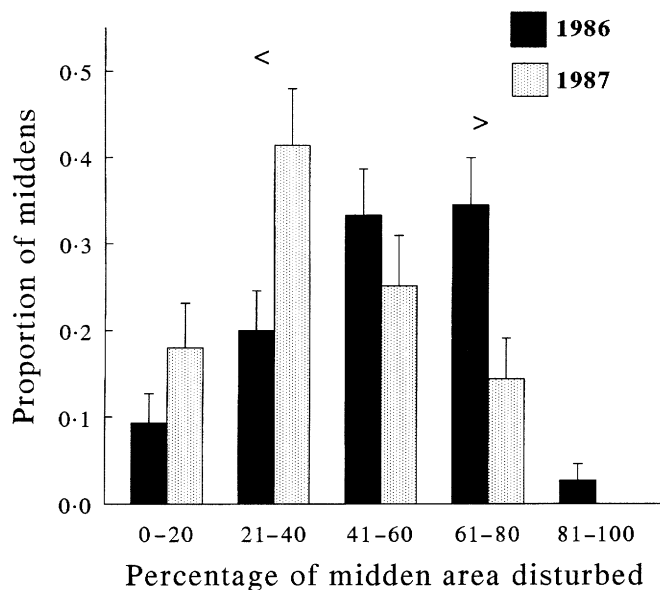


Fig. 6. The proportion of red squirrel middens excavated by bears during 1986 and 1987 relative to different levels of disturbance. Data were pooled from the Mt Washburn and Cooke City study sites in the Yellowstone ecosystem. Disturbance was measured as the percentage of a midden's surface that had been excavated or covered with back-cast debris by the bear. The '<' denotes a category where the relative frequency during 1987 exceeded that during 1986 while the '>' denotes the opposite.

activity in established middens was positively related to the size of whitebark pine cone crops and negatively related to the frequency of bear excavations. Both of these relationships were plausible. Whitebark pine seeds are large, fatty and favoured by squirrels over the seeds of other tree species (Kendall 1983; Hutchins 1994). Greater amounts of a high energy-content food, such as whitebark pine seeds, probably allowed a greater number of vulnerable and otherwise dispersing juveniles to survive and establish middens (Klenner & Krebs 1991).

Bears, on the other hand, deprived squirrels of food that represented a substantial amount of invested energy. Bear excavations in middens were often exten-

sive and affected more than one-half of the middens in some forest types during some years. Kendall (1983) observed that some middens were repeatedly excavated during a given year. Mattson & Jonkel (1990) also noted that some squirrels were killed and eaten by bears in the process. It is therefore possible that red squirrel populations declined after heavy exploitation of middens by bears. If so, then bears induced changes in squirrel populations that were detrimental to their own future foraging success.

Evidence of squirrel demography and behaviour from this study was largely circumstantial. Because we did not collect information on the total number of whitebark pine cones cached in middens, the import-

ance of whitebark pine seeds to red squirrel reproduction and survival is not clear; although the results of Kendall (1983) and Hutchins (1994) suggest they represent a major influence. The summary of information on hoarding by North American and Eurasian red squirrels *Sciurus vulgaris* Linnaeus by Wauters & Casale (1996) similarly suggests that larger hoards, in general, may be critical to red squirrel survival (cf. Smith 1968; Kemp & Keith 1970; Rusch & Reeder 1978). Although the percentage of middens disturbed by bear excavations was indicative, we did not directly estimate the percentage of cached cones that were consumed by bears, and so do not have a direct estimate of depredation. Also, as we did not observe marked squirrels, it is unclear what induced midden abandonment by the squirrels, and the extent to which this was due to mortality rather than movement to a new territory. The currently unknown relationship between midden size and age has additional bearing on this issue.

BEAR EXCAVATIONS

Both black bears *Ursus americanus* Pallas and grizzly bears excavate whitebark pine cones from red squirrel middens (Kendall 1983). Some of the excavations observed during this study were therefore attributable to black bears. However, this fraction is probably small. Black bears are inherently less prone to dig compared to grizzly bears (Herrero 1978). Grizzly bears also comprised 65% of the 168 bear sightings made in or near the Mt Washburn study site from 1984 to 1989 (K. Gunther, Bear Management Office, Yellowstone National Park, personal communication). In addition, where signs of bears were identified to species level in and near the Cooke City site during 1991, grizzly bears accounted for twice as many observations as black bears [D. P. Reinhart & D. J. Mattson, 1992, unpublished Interagency Grizzly Bear Study Team Report, Bozeman, Montana).

Midden size was important in determining whether bears excavated a midden; larger middens were used relatively more often than smaller middens. It may be that bears were more likely to excavate larger middens simply because they encountered them proportionately more often. On the other hand, large middens were more likely to be the site of squirrel activity and also tended to yield more excavated cones compared to small middens. It is possible therefore that bears selected for large middens, and that this behaviour was rewarded and reinforced. However, it is unclear whether red squirrels cached more cones in larger middens compared to smaller middens, given that we did not count the total number of exploited and unexploited cones in sampled middens.

The frequency of bear excavation was apparently affected by spatial and temporal variation in the availability of whitebark pine seeds. Availability of seeds would be obvious from the size of the cone crop.

Although seed production was less obviously related to whitebark pine basal area, Forcella & Weaver (1980), Weaver & Forcella (1986) and Shimanyuk (1963; for the closely related Siberian stone pine *Pinus sibirica* Rupr.) found good correlation between unit-area cone production and abundance of mature trees.

Assuming that whitebark pine basal area indicated the availability of seeds, bears excavated middens more often during years when, and on sites where, seed crops were larger. These results also suggest that bears excavated a given midden more intensively during years when more pine cones were available and presumably more were cached by squirrels. Given the plausible assumption that duration use and spatial extent of excavations in a given midden were correlated, bears resided longer in a 'patch' when resources were concentrated and more abundant. All of these patterns are consistent with the general predictions of optimal foraging theory (Stephens & Krebs 1986).

The results of this study are consistent with previous observations of grizzly bears avoiding roads and town sites. In common with bears foraging on ungulate carcasses during the spring (Green, Mattson & Peek, in press) and bears foraging on spawning cut-throat trout *Oncorhynchus clarki* Richardson during the early summer (Reinhart & Mattson 1990), bears during this study made virtually no use of resources in areas affected by close proximity to both a road and a town site. Proximity to town sites had a greater apparent impact on bears than did proximity to roads. These results also corroborate a previous assessment of human impacts in Yellowstone Park based on the analysis of telemetry locations from radio-tagged bears (Mattson, Knight & Blanchard 1987). This study is thus part of a growing body of research indicating that grizzly bears avoid areas near human facilities (Mattson *et al.* 1996).

In conclusion, grizzly bears will be affected both by human activity and management of forest stands in the whitebark pine zone. For example, a recent proposal which would have placed a gold mine near Cooke City, largely in or near areas used by bears to forage on whitebark pine seeds (Mattson 1995), would have had a negative impact on access by bears to this important food. Timber harvest also occurs in the whitebark pine zone, especially on lower-elevation sites (Eggers 1990). Depending on the harvest system, squirrel abundance as well as the numbers of whitebark pine cones cached in squirrel middens may be reduced, as may the opportunities for bears to obtain seeds. Two other factors, global climate change and white pine blister rust *Cronartium ribicola* J.C. Fisch. ex Rabenh. could also have a negative impact on grizzly bear abundance. Both pose major threats to whitebark pine in areas where grizzly bears currently consume substantial amounts of whitebark pine seeds. Under predicted scenarios of global climate warming, the whitebark pine zone would diminish to approximately one-tenth of its current extent (Romme &

Turner 1991). Blister rust has also virtually eliminated whitebark pine from much of its former range and is present in the Yellowstone ecosystem (Kendall 1995). Even a small increase in mortality of mature whitebark pine could negatively affect both the occupancy of pre-established middens by squirrels and the excavation of cones by bears.

MANAGEMENT IMPLICATIONS

This study is one of several confirming that grizzly bears avoid human facilities even when using high quality foods. By controlling for a number of intervening habitat-related factors, these results, along with those of Reinhart & Mattson (1990) and Green *et al.* (in press), indicate that the location of human facilities in the whitebark pine zone will almost certainly have a detrimental effect on grizzly bear access to an important food. Given that grizzly bears obtain more pine seeds per unit area under diverse canopies containing substantial amounts of both whitebark and lodgepole pines, these types of stands should receive protection.

In addition, these results suggest that grizzly bears would probably benefit from the propagation of blister rust-resistant whitebark pine in lower elevations of the whitebark pine zone (cf. Hoff, Hagle & Krebill 1994), in areas where red squirrel middens are more abundant. Similarly, grizzly bears would be vulnerable to incremental losses of cone-producing whitebark pine, whether due to forest succession, blister rust or climate warming. Managers should consider the potential effects of future losses of whitebark pine in their strategic conservation planning (Mattson & Reid 1991); the prospect of such losses introduces added uncertainty into population and habitat projections (Mattson & Reinhart 1994).

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