The relationships between forest structure and red squirrel midden density in the Mud Lake study area, Cooke City Basin, Montana.

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Acknowledgements

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Abstract

Whitebark pine (*Pinus albicaulis*) seeds are a very important food source for grizzly bears (*Ursus arctos horribilis*) and other species in the Greater Yellowstone Ecosystem. Whitebark pine is a long-lived stone pine of high-elevation forests in southwestern Canada and the western United States, with large nutrition-rich seeds. The cones do not abscise or release their seeds in fall, so bears have to raid red squirrel (*Tamiasciurus hudsonicus*) middens; a large site on the forest floor where squirrels open gathered cones and hide seeds.

In fall 2009 I documented forest structure, midden density and bear sign density on four transect lines near Mud Lake, Cooke City Basin, south-central Montana. These transect lines were originally part of a larger bear study with 27 transect lines, where data on bear sign were collected between June-October in 1990-1991 and between July-October in 1996, 1997, 2003, 2004, and 2007-2009.

My predictions where; (i) a higher density of middens in mixed forest; (ii) a positive relationship between bear sign and midden density; and (iii) a high density of trees with beetle infection in the Mud Lake study area. I found that the density of red squirrel middens were highest in mixed forest with a high content of whitebark pine trees. Midden density, both number of separate middens and midden area, increased with more cone-producing trees. Red squirrels are dependent on other conifers when the highly variable whitebark pine cone crops are low. I also found more bear sign in association with high densities of red squirrel middens, which shows that whitebark pine is an important habitat for bears. The amounts of dying and newly dead trees I found in my study can infer a coming epidemic of mountain pine beetle and blister rust. This can have enormous consequences for the animals that are so dependent on the food supply that whitebark pine offers. Whitebark pine as a keystone species supports a wide range of different species and a decrease of whitebark pine trees most likely will lead to less biodiversity.

Sammendrag

Frø fra Whitebark pine (*Pinus albicaulis*) er en veldig viktig matressurs for grizzlybjørn (*Ursus arctos horribilis*) og flere andre arter i Greater Yellowstone Ecosystem. Whitebark pine er en sakte voksende art i furufamilien med store og næringsrike frø som ligner pinjekjerner. Whitebark pine trær vokser i høyereliggende skogsområder i sydvestlige Canada og vestlige deler av U.S.A. Konglene faller ikke ned eller slipper frøene sine om høsten, så bjørn må plyndre amerikansk rødekorns (*Tamiasciurus hudsonicus*) hamstringsplass/"middens", som er områder på skogbunnen hvor ekorn åpner kongler og gjemmer frøene. Høsten 2009 gjennomførte jeg en studie av fire terrenglinjer/"transect" i nærheten av Mud Lake ved Cooke City i sørlige Montana. Jeg forsket på sammenhenger mellom skogstruktur, tettheten av middens og tettheten av bjørnetegn. Disse fire transectene var opprinnelig en del av et større bjørneprosjekt med 27 transect, som ble studert juni til oktober 1990-1991 og juli til oktober 1996, 1997, 2003, 2004, og 2007-2009.

Mine hypoteser var; (i) høyere tetthet av middens i blandet skog/"mixed forest", (ii) en positiv sammenheng mellom bjørnetegn og tettheten av middens og (iii) høy tetthet av trær infisert av barkebiller/"mountain pine beetles (*Dendroctonus ponderosae*)" i Mud Lake studieområde. Mine resultater viser at det var høyest tetthet av amerikansk rødekorn middens i blandet skog med en høy andel whitebark pine trær. Tettheten av middens, både i antall og areal, økte ved økt antall konglebærende trær. Amerikansk rødekorn er avhengig av andre konglebærende trær de årene den svært upålitelige whitebark pine produserer få kongler. Resultatene mine viser også en positiv assosiasjon mellom tettheten av bjørnetegn og tettheten av middens og det viser at whitebark pine frø er en meget viktig matressurs for bjørn. Mengden døende og nylig døde trær som jeg fant i mitt studieområde viser en mulig begynnende epidemi med barkebiller og "blister rust" (*Cronartium ribicola*). Dette kan ha enorme konsekvenser for dyrene som er så avhengig av den fôr tilgangen whitebark pine trær gir dem. Whitebark pine er en nøkkelart som påvirker en stor rekke arter. Minsket tilgjengelighet på whitebark pine trær vil muligens føre til mindre biologisk mangfold.

Nøkkelord: whitebark pine, Greater Yellowstone Ecosystem, grizzlybjørn, amerikansk rødekorn, middens, konglebærende trær, bjørnetegn, barkebiller, kongler, nøkkelart, blandet skog.

Content

1. Introduction

The world is in rapid ecological change and humans are causing species extinctions at a record rate due to overconsumption of resources, habitat destruction, introduction of alien species, and other factors (Ellison et al. 2005). In nature species depend on each other for survival, but some species can be especially important for many others. Whitebark pine (*Pinus albicaulis*) is a primary producer that is so important for its community that it is called a keystone species (Tomback et al. 2001). A keystone species determines its community structure, is very important for other species' survival, and therefore the ecosystem function and stability and the perception of the landscape. When a keystone species is lost it will have strong effects on community diversity and composition (Krebs 2001), and initiate an ecological cascade, with a series of secondary extinctions of species dependent upon the keystone species (Krebs 2001). In other words, a keystone species increases the biodiversity in its community (Tomback et al. 2001).

Whitebark pine is a slow-growing and long-lived stone pine of high-elevation forests at the timberline in southwestern Canada and the western United States. It is of limited commercial use, but is very important for wildlife, because of its nutrition-rich seeds, and because it provides hiding and thermal cover for animals (Arno and Hoff 1989). Whitebark pine can help stabilize snow, rocks, and soil on steep mountainsides (Arno and Hoff 1989). The tree is also very picturesque and is a hallmark of high-elevation forests in the western United States. It is a masting species that produces annually fluctuating crops (McCaughey and Schmidt 1990). In 2009 the Interagency Grizzly Bear Study Team counted as many as 630 cones on one tree, but another tree had none (Haroldson and Prodruzny 2010). Whitebark pine is typically found in harsh, cold, and generally moist climatic zones and it is considered intolerant to moderately intolerant of shade (Steele 1986). Whitebark pine has the conservation status "vulnerable" according to the US Endangered Species Act, and is threatened by the fungal disease white pine blister rust (*Cronartium ribicola*), by mountain pine beetle (*Dendroctonus ponderosae*), and by fire-suppression policies (Ellison et al. 2005, Kendall and Keane 2001)

Red squirrels (*Tamiasciurus hudsonicus*) forage on whitebark pine cones whenever they are available. However, in nearly pure stands of whitebark pine, the squirrel population tends to

be low (Mattson et al. 2001). In mixed forest Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) provide an alternate and more predictable food source, allowing for a more stable squirrel production. Red squirrels defend non-overlapping territories by vocalization and chasing intruders (Rusch and Reeder 1978). Centralized in these territories lies the midden; a large site on the forest floor where squirrels traditionally open gathered cones and hide the seeds., and are typically associated with only one adult squirrel (Mattson and Reinhart 1996). Middens consist of large amounts of cone clippings and are easily observed (Fig. 2). Red squirrels use up to 80 percent of their daily activity from August through November to gather cones within their territories and store them in middens (Smith 1968). The density of active middens is the best way to estimate red squirrel density (Mattson and Reinhart 1996). Red squirrel middens are commonly found in association with whitebark pines, but the relationship between midden density and forest structure is not known.

The Cooke City Basin of south-central Montana is an area of highly productive bear habitat, in spite of high levels of human use. It is believed that dense populations of bears occur there, because of the adjacent whitebark pine forests and their associated cones (Tyers et al. *in prep.*), which are an important food source for bears in the Greater Yellowstone Ecosystem (GYA) (Keane 2000, Kendall 1983). The seeds are high in digestibility and approximately one-half of the kernel of the seeds consists of fat (Mattson and Reinhart 1997). Whitebark cones do not abscise or release their seeds in fall (Kendall 1983), so bears have to climb trees to secure them or find fallen cones. More often, bears raid red squirrel middens. Whitebark cone seeds are an especially important energy source for bears before and after hibernation, when bears are in need of rapid weight gain (Kendall 1983).

Grizzly bears (*Ursus arctos horribilis*) are prone to extinction, and are listed as threatened according to the US Endangered Species Act. It is therefore important to understand their ecology to be able to secure the species. Bears have a diverse diet and follow the season's variations (Reed-Eckert et al. 2004). In years when the cone crops are very low, bears search for other food sources, often in lower areas, resulting in conflicts with humans (Mattson et al. 1992). Bear have basically no natural enemies (Shaffer 1978), but are dependent on adequate food and shelter.

The aim of this study was to investigate the relationship between forest structure and the occurrence of red squirrel middens, both by area and number, and bear sign. I also documented the status of conifers of cone-bearing age in relation to mountain pine beetle infestation. Based on the above, I made the following predictions; there will be (i) a higher density of middens in mixed forest; (ii) a positive relationship between bear sign and midden density; and (iii) a high density of beetle infected trees in the Mud Lake study area

2. Study area

2.1 Geography

The 91 km² Cooke City study area is located 6 km from the north entrance to Yellowstone National Park (YNP), Montana. To the north the study area is surrounded by the Absaroka-Beartooth Wilderness of the Gallatin and Custer National Forests. South of the study area lies the north Absaroka wilderness of the Shoshone National Forest. The area is situated within the Yellowstone Grizzly Bear Recovery Zone (USFWS 1993).

2.2 Physiography

The area has a typical intercontinental high-elevation climate and terrain. It consists of steep mountain peaks up to 3477 m and valley bottoms at 2427 m, surrounded by a mosaic of forests, open slopes, and alluvial meadows (Tyers et al. *in prep.*). At higher elevations the forests consist of stunted whitebark pine and subalpine fur. Mature to old-growth stands of whitebark pine, subalpine fur, Engelmann spruce, and lodgepole pine (*Pinus contorta*) occur at mid- and lower elevations. In 1988 the forests at lower elevations burned north and northeast of Cooke City (Reinhart and Mattson 1992).

The forest contains several types of openings, such as talus slopes, high elevation plateaus, alluvial meadows, and avalanche chutes. Talus slopes have sparse or no vegetation. Higher elevation plateaus have subalpine grass-forb meadows and alpine turf. Wet meadows occur in stream drainages and seeps. At mid- and lower elevations, the riparian zones are covered by alluvial meadows with willow (*Salix* spp.) and grass-forb communities (Reinhart and Mattson 1992).

2.3 Climate

Cooke City has a climate typical for the whitebark pine zone, with cold winters and cool summers (Weaver 1990). In January, Cooke City has an average minimum temperature of -15 C° and an average maximum temperature of -4 C°. The average snowfall is 5268 mm each year. In July the average maximum temperature is 23 C° and the minimum temperature is 3 C°. The average precipitation is 655 mm each year (based on weather data collected 1967-2005). The highest amount of precipitation falls in May and June. Precipitation increases and temperature decreases with increasing elevation (Western Regional Climate Center 2009).

2.4 Animals

The study area supports several large carnivores, as the grizzly bear, black bear (*Ursus americanus)*, coyote (*Canis latrans*), mountain lion (*Felis concolor*), gray wolf (*Canis lupus*), Canada lynx (*Lynx canadensis*), and bobcat (*Lynx rufus*). Smaller carnivores, as red fox (*Vulpes vulpes*), pine marten (*Martes americana*), and weasels (*Mustela* spp.), are common. Ungulates normal to the area are mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*). Less common are moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus*). Common rodents are yellow-bellied marmot (*Marmota flaviventris*), Uinta chipmunk (*Neotamias umbrinus*), American pika (*Ochotona princeps*), and American red squirrel.

2.5 Settlements

Three settlements, Cooke City, Silver Gate, and Colter Pass, lie within, or close to, the study area. Highway 212, a National Scenic Highway, bisects the Cooke City Basin. This road is the northeastern entrance to YNP. The study area has an extensive road system of county, private, and Forest Service roads, mostly stemming from the mining activity between 1864 and 1954 (USDA 2009). Two maintained county roads (Miller Creek and Fisher Creek) are connected and form a well-used vehicle loop route. Some primitive roads, as the Lake Abundance and Goose Lake jeep trails, access the edge of the Absaroka-Beartooth Wilderness. Most traffic with wheeled vehicles occurs from July to mid-September (USDA 2009). There are also several four-wheel drive roads, and horse and foot trails in the area (Reinhart and Mattson 1992).

2.6 Human activities

While I collected my data in September and October 2009, the area was used extensively for hiking, four-wheel driving, horseback riding, hunting, fishing, and camping. Roadwork occurred on Highway 212 until October.

2.7 Mud Lake study area

The Mud Lake study area (Fig. 1) was situated northeast of Fisher Creek, near Mud and Round lakes. Four transect lines were placed across the Mud Lake Bench, on a north-south line. The sloping bench included a nearly pure whitebark pine forest at the higher edge, an area of mixed conifers, whitebark pine, Engelmann spruce, and subalpine fir at the lower edge, and the associated ecotone. These transect lines totaled 13,094 meters in length, each one between 2 and 3 km, and were spaced 0.5 km apart. The lines were designated ML1, ML2, ML3, and ML4, from west to east.

Figure 1 Mud Lake study area, picture taken at ML1, 15 October 2009.

3. Methods

3.1 Field methods

Field work to document conifers and midden density at the Mud Lake study site was conducted between 20 September and 4 October 2009. The bear sign data in the Cooke City area were collected between June-October in 1990-1991 and between July-October in 1996, 1997, 2003, 2004, and 2007-2009.

Bear sign data were sampled by walking the four line transects close to Mud Lake. These are part of originally 27 transects in a larger study area (Reinhart and Mattson 1992). Transect lines were laid out on USGS 15-minute topographic maps and 1:30,000 color aerial photographs. Transects were placed 0.5 km apart and oriented perpendicular to or parallel to topographic contours. The placement was dictated by landscape attributes. There was no attempt to exclude or include special habitats. Three persons walked each transect, all recording bear sign. One walked the center line and the other two zigzagged on each side, totally about 500 meters in width. Everyone had a GPS with coordinates for the transect. Bear sign included midden diggings, mushroom and root diggings, scats, tracks, sightings, daybeds, torn logs, turned stones, carcasses and vegetation with evidence of feeding of bears, and tree markings. When the sign was clearly defined, its size was measured. Information recorded when bear sign was detected was: UTM coordinates, cover type, slope, aspect, age and size of the sign, and, if possible, which species, grizzly or black bear, had made the sign. Scats (Fig. 10) and hear samples were sent to a laboratory for DNA analysis, but we could also sometimes determine species by tracks and size of scat. For more information about methods used in the collection of bear sign data, see Reinhart and Mattson (1992) and Yonge (2001).

Middens and conifer trees were sampled by dividing every Mud Lake line, ML1 to ML4, into 30 segments, placing a 30-meter diameter circular plot at the end of each line segment, in total 120 plots. Middens were counted, their surface area was measured, and conifer trees were counted both by size and species. The trees were divided into two groups after measuring trunk diameter at breast height (≈1.4 m): poles between 5 to 9 inches (12.7 cm – 22.9 cm), and mature more than 9 inches (22.9 cm). Trees less than 5 inches (12.7 cm) were not counted.

The number of conifers infected by beetles and dead trees were counted and divided into groups. Dead trees were divided into two groups; red -newly dead, approximately within 3 years (D. Tyers, pers commun.), and silver –dead for a longer time. UTM coordinates and cover type were recorded for each circle.

3.2 Field analysis

For each circular plot (30 plots per 4 lines), the number of discrete squirrel middens (Fig. 2) was counted and each midden was measured. I treated both the midden count and total midden area per plot as response variables. I considered these response variables independently.

For each plot, the number of trees was counted according to the following categories:

- Mature whitebark pine (green)
- Mature whitebark pine (green but beetle-infected)
- Mature whitebark pine (red, newly dead)
- Mature whitebark pine (silver, old dead)
- Pole-sized whitebark pine (green)
- Pole-sized whitebark pine (green but beetle-infected)
- Pole-sized whitebark pine (red, newly dead)
- Pole-sized whitebark pine (silver, old dead)
- Mature and pole-sized spruce and fir (green)
- Mature and pole-sized spruce and fir (green but beetle-infected)
- Mature and pole-sized spruce and fir (red, newly dead)
- Mature and pole-sized spruce and fir (silver, old dead)

These constituted my explanatory variables. Cone-producing whitebark pine (CPWB) was defined as the total number of mature and pole-sized green whitebark, with or without beetle infection. Cone-producing spruce and fir (CPSF) was defined as the total number of mature and pole-sized green spruce and fir, with or without beetle infection. Pole-sized trees produce cones, but in lesser quantities than mature trees.

3.3 Functional analysis

First I examined the raw data, plotted the explanatory variables in graphs testet for normality and, when the data were not normally distributed, I tried two different transformations, one of the form ln(x + 1) and the other of the form sqrt(x + 0.5). I used the best transformation for each variable. Then I conducted a regression analysis to investigate if there were correlations between cone-producing whitebark and cone-producing spruce and fir.

3.4 Statistical analysis

To evaluate differences in midden distribution among transects, I simplified the midden data to frequency, by simply considering whether plots contained middens or not, and conducted a chi-squared test of independence. I then made a more detailed comparisons at the transect level using an ANOVA and a Tukey's HSD to examine all pair-wise differences between transects. I used the most normally distributed model or transformation for each variable. I used ANOVA for the midden counts and midden areas as well, because I assumed normality, although it was not as clear for these. The ANOVA test is robust and with the very low p-values I obtained, the test results should be reliable.

3.5 Multiple Linear Regression

Multiple linear regressions require continuous data and a generally normal distribution, which can be achieved through transformation. My study was designed as an analysis of variance with transects as the main effect, but the real variables of interest are cone-producing trees and midden number/size. If plots were spatially independent, I could ignore the transects and just analyze with plots. To determine whether the data were spatially independent (that individual plots could be considered not to influence each other), I regressed the values of each variable for each plot against the values associated with the adjacent plot. Given that the plot data show minimal spatial autocorrelation, multiple linear regressions were possible for both of my response variables. Also, for both midden counts and midden area, there was no evidence of three-way (Cone_WB*SF*transect) interaction, so these terms were removed. There was no evidence of any two-way interactions either, so in both cases, I used models without interactions.

3.6 Bear sign density in relation to middens occurrence

I simplified the forest structure and midden density to the transect level, using the relationship between the median midden area per plot and the average number of CPWB per plot, and regressed these with bear sign density. The results were statistically robust enough given the amount of variance within transects. However, the patterns were descriptive. It should be noted that I only have bear sign per kilometer on transect level and not on plot level.

3.7 Tree mortality

Trees were counted in several different groups. Live trees consist of both groups green and green with beetles. Recently dead or dying trees consist of both groups green with beetles and red -newly dead. The total of trees is the total for all groups, including silver trees.

Figure 2 A huge midden.
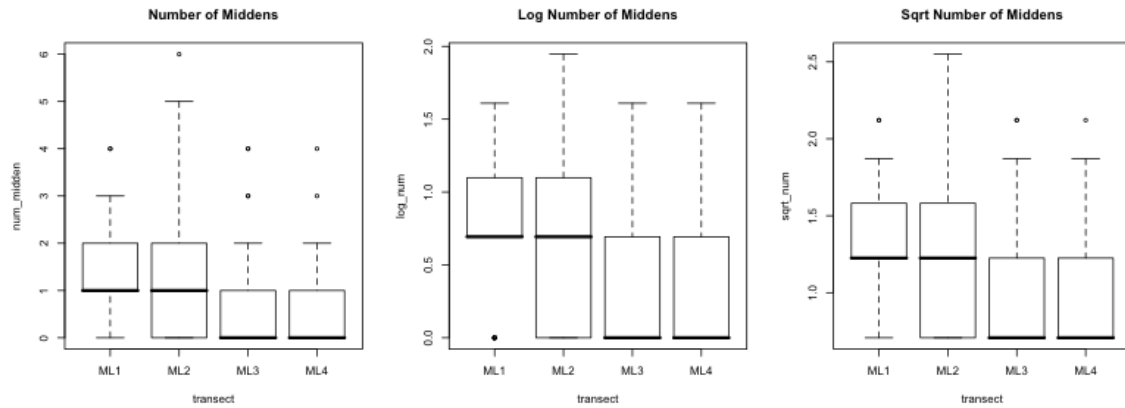
4. Results

4.1 Functional analysis

Figure 3 Number of red squirrel middens graphs in the four transects in the Mud Lake study area, south-central Montana 2009.

The midden count data were strongly skewed. Transformations with $\ln(x + 1)$, and $\mathrm{sqrt}(x + 0.5)$ normalized the data somewhat, although neither transformation dealt with the radical zero-inflation. There was a high midden density on the transect Mud Lake (ML) 1 and it diminished towards ML4 (Fig. 3).
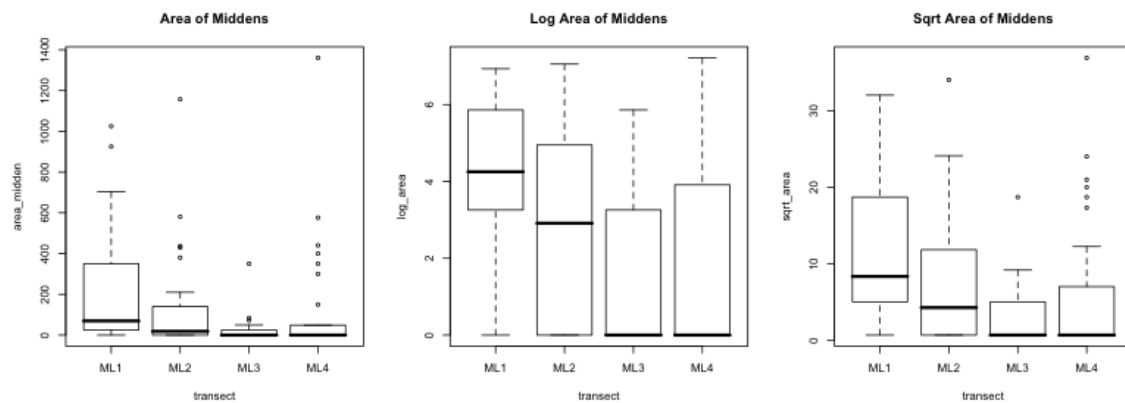

Figure 4 Area of red squirrel middens graphs in the four transects in the Mud Lake study area, south-central Montana, 2009.

Midden area showed a similar problem. The distribution was extremely skewed, with a high degree of zero-inflation. Log-scale and square root transformations helped to some degree, with the log transform being the best. The histogram and Q-Q plot of the log-scale transformation both showed a pattern of a radically large number of zero values, but a nearly

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normal distribution otherwise. Distributions at the transect level showed high midden area on ML1, decreasing towards ML4 (Fig. 4).
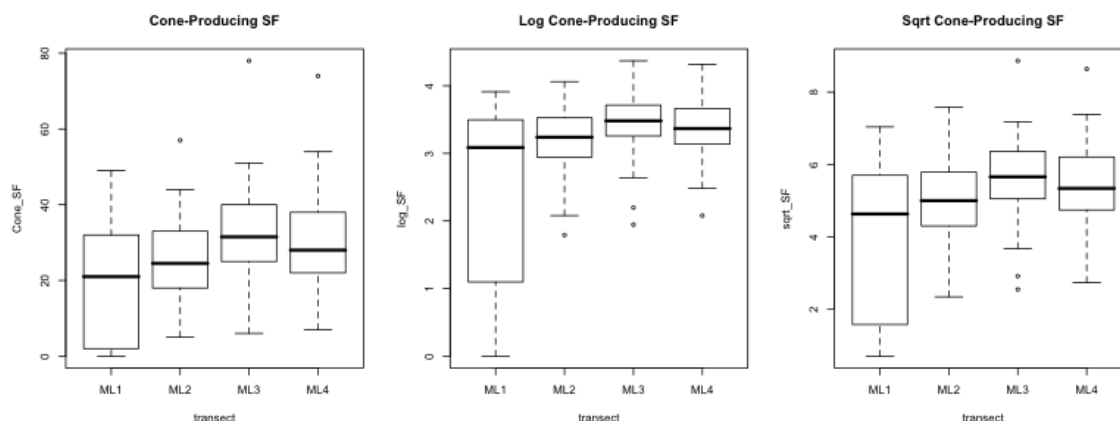

Figure 5 Cone-producing spruce and fir graphs in the four transects in the Mud Lake study area, south-central Montana, 2009.

The distribution of CPSF showed a surprising degree of normality, although somewhat positively skewed. Neither the log-scale nor square root transformation helped improve normality. There were relatively low densities of spruce and fir on ML1, increasing slightly towards ML4 (Fig. 5).

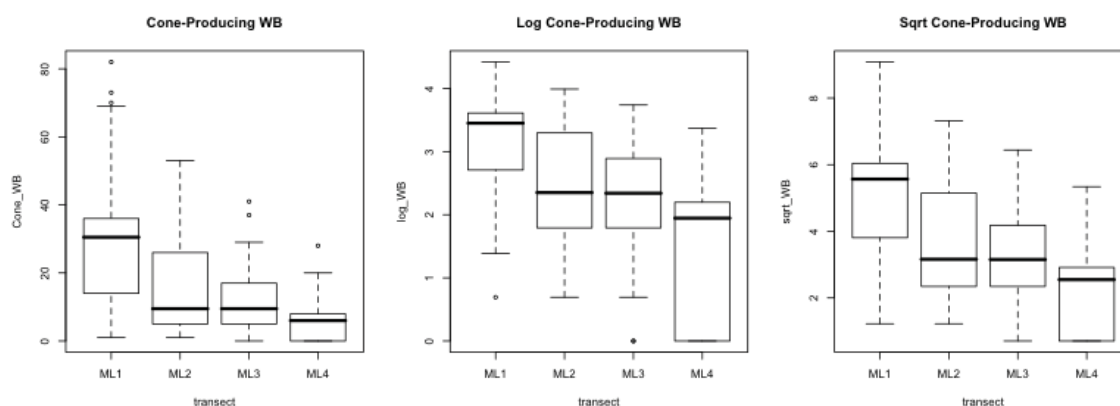**Figure 6 Cone-producing whitebark pine graphs in the four transects in the Mud Lake study area, south-central Montana, 2009.**

The distribution of CPWB was not quite as simple as CPSF. The whitebark data exhibited a strong degree of positive skew, although the square root transformation normalized it a great deal. There was a relatively high amount of whitebark on ML1, decreasing towards ML4 (Fig. 6).
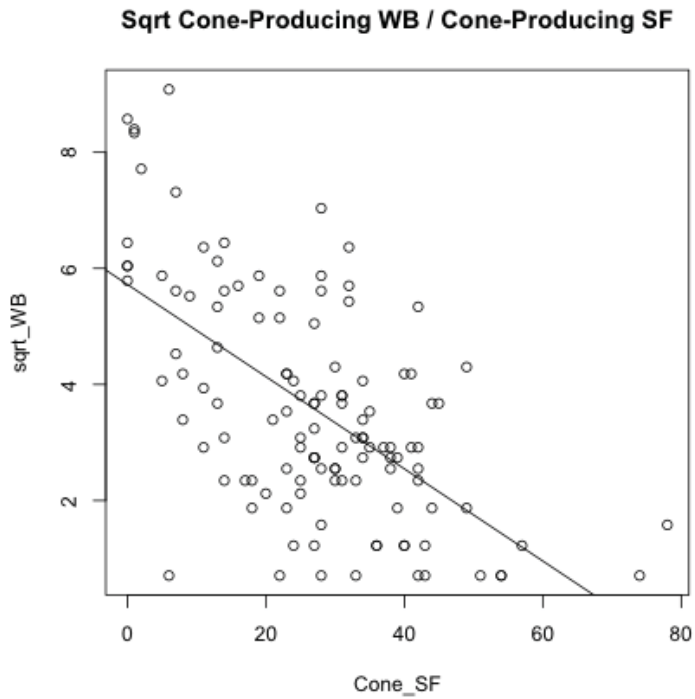
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Sqrt Cone-Producing WB / Cone-Producing SF

Figure 7 Regressing the cone-producing whitebark pine density against the cone-producing spruce and fir density show a strong evidence of a correlation.

I regressed the numbers of cone-producing whitebark trees against the numbers of cone-producing spruce and fir in each plot and found a strong inverse correlation ($r = 0.37$, $df = 118$, $p < 0.0001$) (Fig. 7). Because this correlation could be considered to be a confounding relationship, I simply summed the number of CPWB and CPSF as a single explanatory variable, the total of cone-producing trees (CPT) per transect.
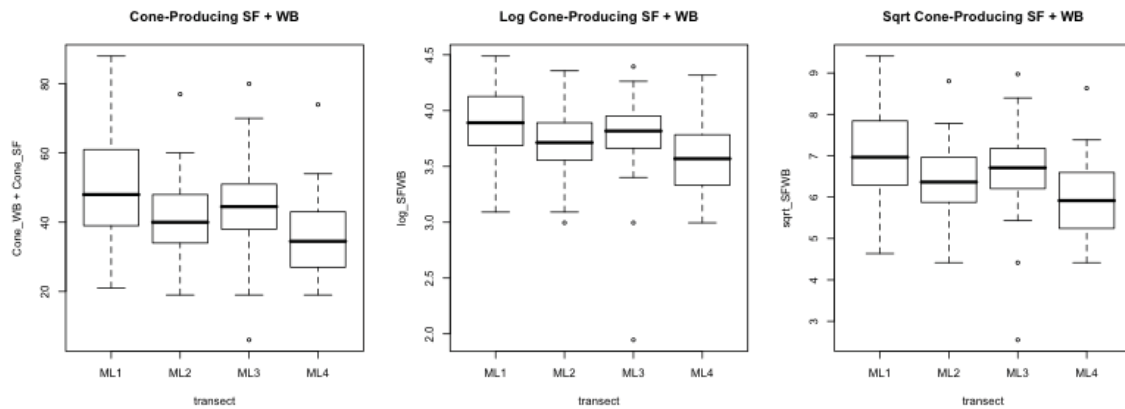
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Figure 8 Cone-producing trees in total graphs in the four transects in the Mud Lake study area, south-central Montana, 2009.

The square-root transform yielded the most symmetric distribution, as well as the cleanest variances for CPT. The highest numbers of CPT occurred on ML1 and the lowest on ML4 (Fig. 8).

4.2 Statistical analysis

I tested for differences in midden distribution among transects by simplifying the midden data to frequency and conducting a chi-squared test of independence. I found strong evidence for a difference in midden presence among transects (χ^2 = 15.62, df = 3, p = 0.00136). I inferred from Fig. 2 that midden frequency declined steadily from ML1 to ML4. There was also strong evidence for a difference in density of CPSF trees among transects (One-way ANOVA, F = 4.67, df = 3 and 116, p = 0.0041). As the one-way ANOVA showed a difference in CPSF among transects, I used a Tukey's HSD to identify the significant pair-wise differences. Significant differences occurred between the density of CPSF on ML1 and ML3 (p = 0.004) and between ML1 and ML4 (p = 0.026). No other combinations were significant (p values > 0.24).

There was also a significant difference in the density of CPWB among transects (one-way ANOVA, F = 16.28, df = 3 and 116, p < 0.0001). A Tukey's HSD procedure showed significant pair-wise differences occurring between ML1 and ML2 (p = 0.0036), between ML1 and ML3 (p = 0.00007), between ML1 and ML4 (p < 0.0001), and between ML2 and ML4 (p = 0.006). No other combinations were significant (p > 0.1), but between ML3 and

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ML4 there was a difference (p = 0.107). The last transect pair ML2 and ML3 showed no sign of difference (p > 0.714).

The density of CPT also differed significantly among transects (one-way ANOVA, F = 4.66 df = 3 and 116, p = 0.0041). A Tukey's HSD showed that the only significant pair-wise difference was between ML1 and ML4 (p = 0.002). No other combinations were significant (p > 0.12), but there were differences between ML1 and ML2 (p = 0.124) and ML3 and ML4 (p = 0.132). The rest of the transect pairs showed no sign of differences (p > 0.46).

There was also a significant difference in midden density among transects (one-way ANOVA F = 4.16, df = 3 and 116, p = 0.0077). A Tukey's HSD test provided evidence for significant pair-wise differences between midden density on ML1 and ML4 (p = 0.0148) and between ML2 and ML4 (p = 0.0488). No other combinations were significant (p > 0.13), but there was a difference between ML1 and ML3 (p = 0.132). The rest of the transect pairs showed no sign of differences (p > 0.3).

Additionally, there was a significant difference in the total midden areas among transects (one-way ANOVA, F = 5.97, df = 3 and 116, p = 0.0008). A Tukey's HSD approach showed significant pair-wise differences occurring between ML1 and ML3 (p = 0.0017) and between ML1 and ML4 (p = 0.0054). No other combinations were significant (p > 0.14), but there was a difference between ML2 and ML3 (p = 0.143). The rest of the transect pairs showed no sign of differences (p > 0.28).

4.3 Multiple Linear Regression

When accounting for transect effects on the midden counts, there was strong evidence that the density of discrete squirrel middens increased with increasing density of CPSF (R^2 = 0.1083, df = 114, p = 0.015) (Table 1). Additionally, there was suggestive evidence that the density of squirrel middens increased with increasing density of CPWB (p = 0.056) (Table 1). It should be noted that I would have obtained different p-values for the transect effect if I had used categorical variables. This would simply have compared each transect effect with the default reference level of ML1. Because ML1 had the highest response, we would see significant effects if any existed. Thus, there was evidence of a transect effect. Moreover, after accounting for a transect effect, there still was strong evidence of an effect of the density of CPT on density of middens (F = 3.891, df = 5 and 114, p = 0.0027).

Table 1 Results for a multiple regression testing for effects of the density of cone-producing spruce and fir trees and density of cone-producing whitebark pine trees on the density of red squirrel middens in the Mud Lake study area, south-central Montana, 2009. The density of discrete squirrel middens increases with increasing density of cone-producing spruce and fir trees (p = 0.015) and cone producing whitebark pine trees (p = 0.056).

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.8147	0.2270	3.589	0.0005
Cone_SF	**0.0089**	**0.0036**	**2.466**	**0.0151**
Cone_WB	**0.0606**	**0.0313**	**1.934**	**0.0556**
transectML2	-0.0136	0.1241	0.110	0.9129
transectML3	-0.2589	0.1285	-2.015	0.0463
transectML4	-0.2837	0.1404	-2.021	0.0457

After accounting for a transect effect, there was also strong evidence for a positive relationship between the total midden area and density of CPSF (R^2 = 0.16, df = 114, p = 0.004) (Table 2). Additionally, there was a positive relationship between the total midden area and density of CPWB (p = 0.026) (Table 2). After accounting for a transect effect, I found that the density of CPT positively influenced the total area of middens (F = 5.617, df = 5 and 114, p = 0.0001).

Table 2 Results for a multiple regression testing for effects on the total area of red squirrel middens with density of cone-producing spruce and fir trees and cone-producing whitebark pine trees in the Mud Lake study area, south-central Montana, 2009. The total area of red squirrel middens increases with increasing density of cone-producing spruce and fir trees (p = 0.004) and cone-producing whitebark pine trees (p = 0.026).

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.8316	1.1470	0.725	0.4699
Cone_SF	**0.0536**	**0.0183**	**2.930**	**0.0041**
Cone_WB	**0.3563**	**0.1583**	**2.251**	**0.0263**
transectML2	-0.7472	0.6269	-1.192	0.2358
transectML3	-2.2768	0.6493	-3.507	0.0007
transectML4	-1.5975	0.7094	-2.252	0.0263

Again, after accounting for a transect effect, there was a positive relationship between the density of middens and the density of CPT (R^2 = 0.115, df = 115, p = 0.013) (Table 3). There

was no evidence of an interaction between transect and CPT (F = 4.862, df = 4 and 115, p = 0.0012), so the non-interaction model was accepted.

Table 3 Results for a multiple regression testing for a relationship between the density of red squirrel middens and the total of cone-producing trees in the Mud Lake study area, south-central Montana, 2009. There is strong evidence for a positive relationship between the density of middens and the total of cone-producing trees (p = 0.013).

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.6036	0.2894	2.085	0.0393
Cone_SFWB	**0.0999**	**0.0396**	**2.527**	**0.0129**
transectML2	0.0089	0.1199	0.074	0.9410
transectML3	-0.2228	0.1185	-1.880	0.0627
transectML4	-0.2656	0.1240	-2.142	0.0343

The area model gave a similar result. There was a positive relationship between midden area and the total CPT ($R^2 = 0.161$, df = 115, p = 0.0059) (Table 4) when accounting for the transect effect.

Table 4 Results for a multiple regression testing for a relationship between midden area and the total of cone-producing trees in the Mud Lake study area, south-central Montana, 2009. This shows a positive relationship between red squirrel midden area and the total of cone-producing trees (p = 0.0059).

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.2141	1.469	0.146	0.8844
Cone_SFWB	**0.5627**	**0.2007**	**2.803**	**0.0059**
transectML2	-0.6240	0.6086	-1.025	0.3074
transectML3	-2.0607	0.6016	-3.426	0.0009
transectML4	-1.5048	0.6295	-2.390	0.0185

4.4 Bear sign density in relation to middens occurrence

Bear sign (Fig. 10) density, measured as number of sign per transect kilometer over all years of the study, was relatively high on ML1, and decreased continuously toward ML4 (Fig. 9).
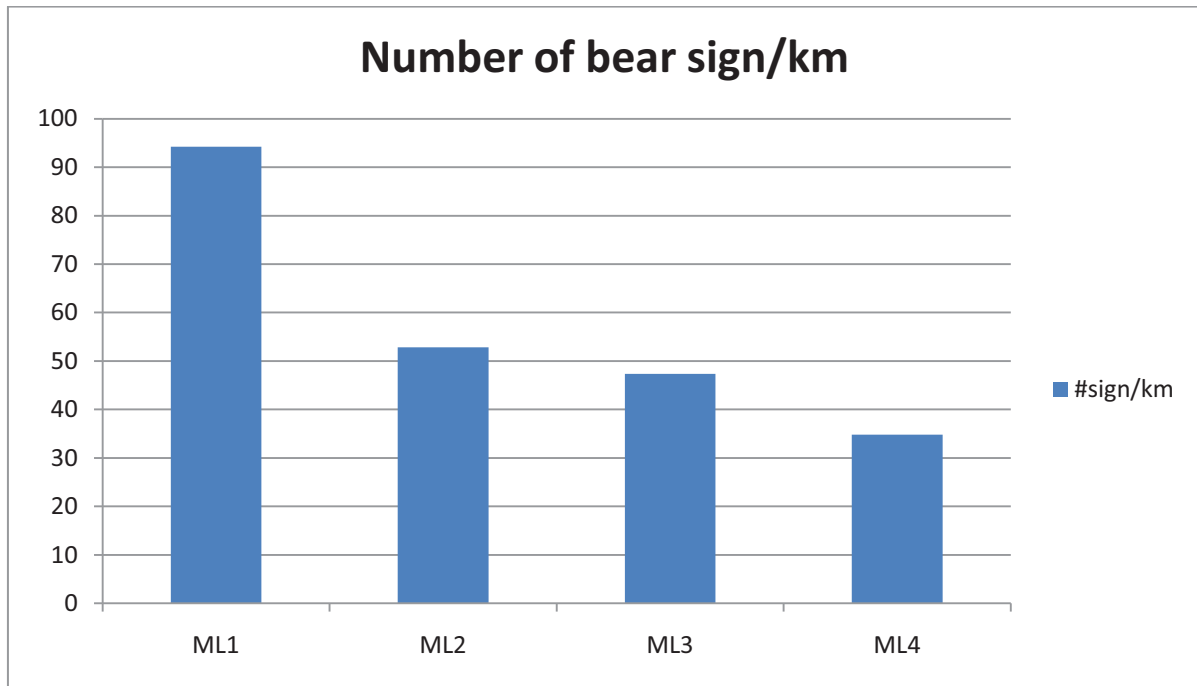

Figure 9 Bear sign density per kilometer at each transect in the Mud Lake study area, south-central Montana, 1990-2009.

Figure 10 Bear scat with lots of whitebark pine seeds, a typical bear sign in whitebark pine forests.

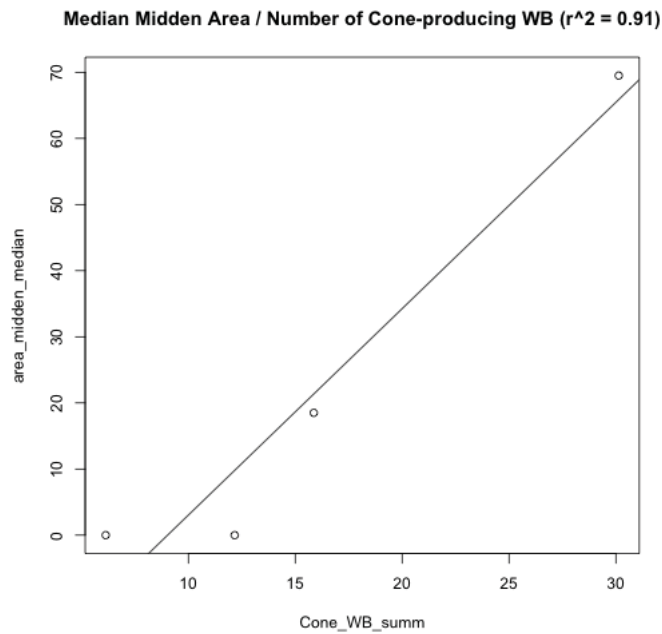**Median Midden Area / Number of Cone-producing WB (r^2 = 0.91)**

Figure 11 Regression of the median red squirrel midden area against the density of cone-producing whitebark pine trees per transect in the Mud Lake study area, south-central Montana, 2009.

Simplifying the forest structure/midden density project to the transect-level relationship between the median midden area per plot and the average density of CPWB per plot showed a strongly linear trend ($R^2 = 0.91$, $p = 0.03$) (Fig. 11). But because of the amount of variance within transects, it was not statistically robust enough to be considered other than descriptively.
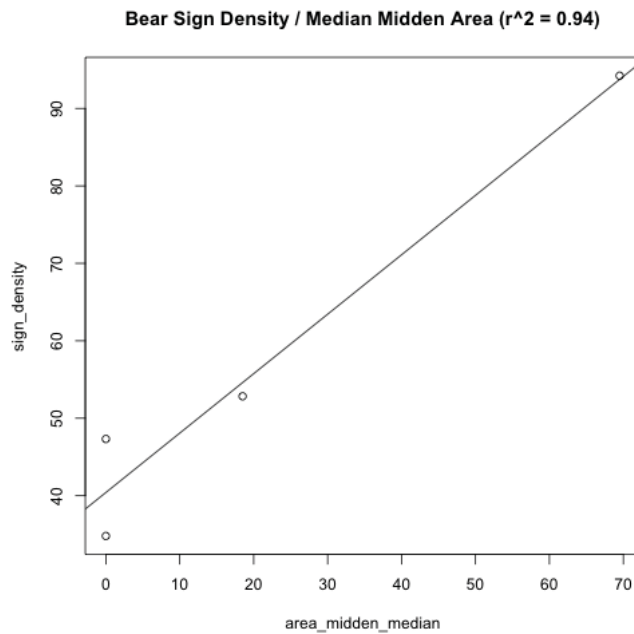
Figure 12 Regression of the bear sign density against the median red squirrel midden area in the Mud Lake study area, south-central Montana, 2009.

Bear sign density and median red squirrel midden area showed a very strongly linear trend (R^2 = 0.94, p = 0.02) (Fig. 12). High numbers of bear sign correlated positively with high area of middens, but as before this was just descriptive, because of the high amount of variance within midden area.
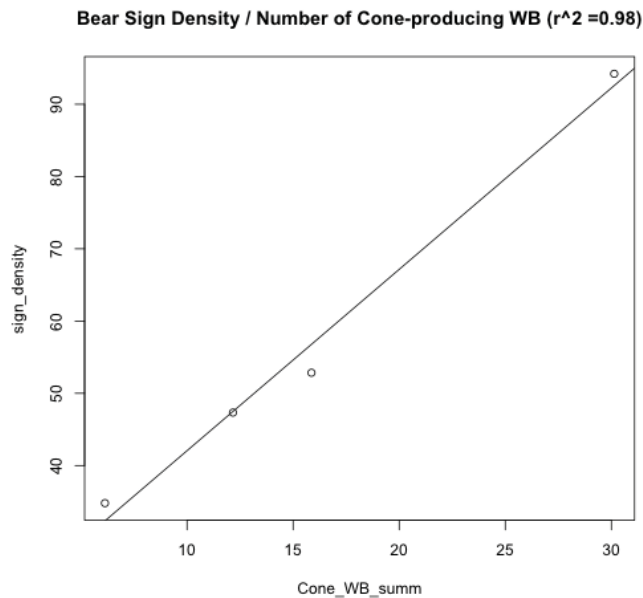
Figure 13 Regression of the bear sign density against the density of cone-producing whitebark pine trees in the Mud Lake study area, south-central Montana, 2009.

Regressing the bear sign density values against the average density of CPWB showed a strong linear trend ($R^2 = 0.98$, p = 0.006) (Fig. 13). This showed that bear sign density was directly associated with amounts of cone-producing whitebark pine trees, but because of the variance within transects it was just descriptive.

4.5 Tree mortality

On the Mud Lake study area in 2009, I found that 4.04 % of the 1,929 live CPWB were infected with beetles, 4.61% of the 1,042 mature trees, 3.38 % of the 887 pole-sized trees, and 3.12 % of 3235 live CPSF. I also found that 8.78 % of the 2,165 whitebark pines, 11.64 % of the 1,229 mature and 5.02 % of the 936 pole-sized whitebark pines were recently dead or dying, as were 6.78 % of the 3,657 spruce and fir.

5. Discussion

My first prediction, a higher density of red squirrel middens in mixed forest, was supported. I found more middens in mixed forest and the density increased with more CPT. My second prediction, a positive relationship between the density of red squirrel middens and the density of bear sign, was also supported. I found more bear sign in association to higher densities of middens. My third prediction, high densities of trees with beetle infection, was also supported. I found high densities of such trees in the Mud Lake study area.

Similar to the studies of Kendall (1983) and Mattson and Reinhart (1997), I found more middens in mixed forests, but with a high content of whitebark pine. Because whitebark pine is a masting species with fluctuating cone crops (Tomback et al. 2001), red squirrels are dependent upon other tree species' cone production during years with few whitebark pine cones (Mattson and Reinhart 1997). The Mud Lake transects cover an area with both pure whitebark forest at the higher elevation, an area of mixed conifers with whitebark, spruce, and subalpine fir at the lower elevation and the associated ecotone. I found that there were more middens at ML1, both in frequency and by area, and that this diminished towards ML4 (Figure 3 and 4). This can be explained by the amounts of CPT on ML1 decreasing towards ML4 (Fig 8 and Table 3). Because red squirrels mainly eat and cache conifer seeds, more cones means more food and therefore more middens.

The series of one-way ANOVA procedures gave strong evidence for a clinal change in forest composition and midden density across the study area. The number of CPSF increased from ML1 to ML4, the number of CPWB decreased from ML1 to ML4, and the area of middens decreased from ML1 to ML4. Since red squirrels are dependent on other conifers when whitebark pine has a bad cone crop (Tomback et al. 2001), it is common to have spruce and fir in some degree close to a midden. But because CPWB has a lot better potential as a food resource, because of large cones and good digestibility (Mattson et al. 1992 and Keane 2000), I expected that the decrease in midden density should be associated with the decrease in whitebark pine and an increase in spruce and fir. However, the driving factor for the decrease in midden density could be differences in elevation or shadow from mountains close by. The multiple linear regression models showed that both CPSF and CPWB were positively associated with squirrel middens (Table 1). Based on the model, the area with the strongest potential for middens would be an area with both whitebark pine and spruce and fir components. Thus, the diminishing midden density from ML1 to ML4 was reflective of the sharply diminishing whitebark pine density from ML1 to ML4, with the increase in spruce and fir density from ML1 to ML4 having less effect. The lack of red squirrel middens in pure whitebark pine stands was probably mainly due to whitebark pine's highly variable cone crops, but less total overstory, less species diversity, and the climate associated with these stands are also factors that might have contributed (Reinhart and Mattson 1988).

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The relationship between the median midden area per plot and the average density of CPWB per plot showed a strongly linear trend (Fig.11), which I expected. Higher density of middens is associated with higher density of CPWB, as Klenner and Krebs (1991) and Ulvund (2007) also found in their studies. I regressed the CPWB against the CPSF and found a correlation that the density of CPWB decrease as the density of CPSF increases (Fig. 7). This showed that the balance with regeneration of the forest is an important issue. With fire suppression the last 80 years, the more shade tolerant species, spruce, and fir, have become dominant over whitebark pine in many areas (Keane 2000).

Midden density and bear sign density showed a very strong positive relationship (Fig. 12). Higher density of bear sign is indeed associated with higher density of red squirrel middens as Kendall (1983), Reinhart and Mattson (1992) and Ulvund (2007) also found. Regressing the bear sign density against the average density of CPWB showed a startlingly linear trend (Fig. 13). This shows that bear sign density is directly associated with amounts of cone-producing whitebark pine as Mattson and Reinhart (1997) and Blanchard and Knight (1991) also found in their studies.

Studies like Mattson and Reinhart (1997) and Ulvund (2007) documented which cover types are important for bears when raiding red squirrel middens. My study showed which forest structure is important for midden density, and therefore to bears that raid middens. My results showed that it is the increase in cone-producing whitebark pine that probably is the driving factor in red squirrel midden density, but as mentioned before, red squirrels are dependent on other conifers as well, because of the fluctuating crops of whitebark pines. Therefore middens are rarer in pure whitebark pine stands than in mixed forest. For bears in the GYA, ungulates and whitebark pine seeds are considered to be the two most important foods for grizzly bears (Mattson et al. 1992). My study showed a positive relationship between bear sign and midden density, which means that bears use mixed forest with high content of whitebark pine to a high degree. To secure the grizzly bear population in the GYA, it is very important to secure whitebark pine as a food source.

In 2009 whitebark pines had a good to excellent cone production year. The Interagency Grizzly Bear Study team found a mean at 46.5 cones per tree, and a maximum of 630 cones on one tree in transects in the Greater Yellowstone Ecosystem (Haroldson et al. 2010),

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compared with the poor crop in 2010, with a mean at 5.2 cones per tree and a maximum of 65 cones on one tree (Haroldson et al. 2011). The Cook City Basin is an area with high levels of human activity, as well as being an important bear habitat. Karterud (2010) found a high density of middens around daybeds in the Cook City Basin. This may indicate that, as long as the bears have adequate cover for protection and shelter, they are willingly to tolerate disturbances like human activity and roads to access a rich food supply provided by whitebark pine cones. The Cook City Basin can be considered to be a "hot spot", with very important habitat including a high density of the keystone species whitebark pine and therefore a good food production habitat for bears and other species (Tyers et al. *in prep.*). Whitebark pine communities support a large biodiversity. Whitebark pines often have a species rich understory of plants and it supports many fungus, microorganism, lichens, and mosses. The trees provide shelter, food, nesting sites, tree holes, and other habitat features both for vertebrates and invertebrates (Tomback et al. 2001).

Prior to 1930 the succession, where whitebark pine is replaced by the more shade tolerant spruce and fir, was interrupted by naturally occurring fires (Keane and Morgan 1993). Fire exclusion, together with mountain pine beetle and blister rust, has accelerated this succession and spruce and fir has become dominant in many forests historically dominated by whitebark pine (Keane 2000). Whitebark pine is quite fire tolerant, because of its thick bark, deep roots and small crown, and it has a huge advantage after fires, because its seeds are dispersed by animals. Clark's nutcrackers (*Nucifraga columbiana*) can disperse whitebark pine seeds up to 100 times further than wind disperses seeds from Engelmann spruce and subalpine fir (Tomback et al. 1993).

Blister rust is an introduced disease that first came to the eastern United States around 1898 (Kinloch 2003). The combination of blister rust with mountain pine beetle epidemics has killed over 50 % of all whitebark pine in some areas (Kendall and Keane 2001). Trees that are genetically resistant to blister rust may be infected by pine beetles and killed, young trees and seedlings that regenerate in a burned area may be killed by blister rust. There are also problems with sick trees not able to produce enough cones to support a good regeneration, which also affects the animals that are so dependent on the seeds (Tomback et al. 1995). When loosing whitebark pine, the carrying capacity of the subalpine zone probably will

decrease dramatically for pine seed-eating birds and mammals, especially for those harvesting seeds for later use or those who raid such catches (Tomback and Kendall 2001). Without the opportunity to raid red squirrel middens, bears might wander far for food in summer and fall and an increase in human contact will surely lead to many bears being killed (Tomback et al. 2001).

6. Conclusion

In this study I found more red squirrel middens in mixed forest with a high content of whitebark pine. This supports my prediction (i) and are the same as Mattson and Reinhart (1997) and Ulvund (2007) found in their studies. Whitebark pine is a highly valuable food source for many species. It is considered a keystone species and increases community biodiversity (Tomback et al. 2001). More biodiversity results in more red squirrels, because they can rely on other food sources when the highly variable whitebark pine cone crop is low.

I found that more cone-producing trees resulted in more middens, as did whitebark pine trees. Whitebark pine seeds cached in middens have been considered an important food source for bears (Kendall 1983, Mattson et al. 1992 and Keane 2000). I found more bear sign in association with high density of middens, this supports my prediction (ii).

My third prediction (iii) was also supported by the high percentages of dying and newly dead trees in the Mud Lake study area. High numbers of dying and newly dead trees can infer a coming epidemic with mountain pine beetle and blister rust. This can have enormous consequences for the animals that are so dependent on the food supply whitebark pine offers. The decrease of whitebark pine will probably lead to less biodiversity.

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