

RED SQUIRREL (*TAMIASCIURUS HUDSONICUS*) MIDDEN SITE SELECTION
AND THE INFLUENCE OF CONIFER SPECIES COMPOSITIONS ON MIDDEN
OCCURRENCE IN THE COOKE CITY BASIN OF MONTANA

by

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DEDICATION

To my wife, Mandy, and son, Everest.

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ABSTRACT

Throughout the Greater Yellowstone Ecosystem (GYE), whitebark pine (WBP: *Pinus albicaulis*) seeds serve as an important fall food source for threatened Yellowstone grizzly bears (*Ursus arctos*). Grizzly bears depend on red squirrel (*Tamiasciurus hudsonicus*) midden sites to obtain WBP seeds. In light of recent WBP population declines, managers are concerned about the negative effects that loss of WBP may have on grizzly bears. Therefore, managing WBP for grizzly bears is facilitated by understanding red squirrel habitat requirements and identifying areas that are most likely to contain middens. Previous studies indicate that red squirrel middens are most prevalent in subalpine mixed conifer forests with interspersed WBP, but a critical gap remains in identifying a conifer species composition that is ideal for midden sites. We studied red squirrel habitat selection in the Cooke City Basin (CCB) of Montana to identify variables associated with midden sites and midden area. We also examined conifer species compositions to identify a composition where middens are most likely to occur. Habitat variables, midden counts, and midden area measurements were collected in 810, 30 meter diameter circular plots equally spaced along 27 transect lines in the CCB. General linear mixed models (GLMM) were used to assess variables associated with red squirrel midden site selection, and linear mixed models (LMM) were used to assess variables associated with midden area. Results of the GLMM indicated that red squirrel midden occurrence probability is positively associated with the amount of hillshade (light) and canopy cover in a conifer stand. Additionally, midden occurrence increased as the percent WBP in a stand increased up to 44 percent, but decreased thereafter. Results of the LMM indicated that midden area is positively associated with total canopy cover. We identified that a conifer species composition of approximately 44 percent WBP and a 56 percent mixture of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) is ideal for midden sites. We concluded that managing for areas within subalpine zone mixed conifer forests containing similar compositions should be a priority to ensure availability of prime habitat for midden sites and associated WBP seeds for grizzly bears.

LITERATURE REVIEW

Throughout the Greater Yellowstone Ecosystem (GYE), whitebark pine (WBP; *Pinus albicaulis*), a subalpine keystone conifer species (Tomback et al., 2001), has declined primarily due to mountain pine beetle (*Dendroctonus ponderosae*) infestations and whitebark pine blister rust (*Cronartium ribicola*) infections (Logan and Powell, 2001; Gibson et al., 2008; Logan et al., 2010; van Manen et al., 2013), but fire suppression management practices may also be contributing to the decline (Keane et al., 1990, Kean and Arno, 1993, Keane and Morgan, 1994). Blister rust infections and pine beetle infestations have reduced the number of cone-bearing WBP in excess of 90 percent in some areas (VanManen et al., 2013). Moreover, Macfarlane et al. (2013) estimated that mountain pine beetle outbreaks have resulted in moderate to severe WBP mortality in 82 percent of the WBP distribution in the GYE.

Managers are especially concerned, because WBP seeds serve as an important seasonal food source for federally protected GYE grizzly bears (*Ursus arctos*) (Mattson and Reinhart, 1994). However, although the importance of WBP seeds as a food source for grizzly bears is well established, recent research adds additional perspectives (van Manen et al., 2013; van Manen et al., 2016). In an extensive review of grizzly bear food habits and long-term population trends, van Manen et al. (2013) confirmed that GYE grizzly bears are opportunistic omnivores capable of diet-shifting. Additionally, the slowing of grizzly bear population growth over the last decade was more closely associated with increasing grizzly bear density than WBP declines (van Manen et al., 2016). These findings suggest that the availability of WBP seeds may not be as critical

for grizzly bear conservation as once perceived, but managers still acknowledge the importance of WBP seeds as a primary food source for grizzly bears. Although GYE grizzly bears have recovered and are likely at carrying capacity (Bjornlie et al., 2014; van Manen et al., 2016), management agencies have retained the federally protected status due to concerns over effects that WBP declines may have on the grizzly bear population. As a result, management priorities have shifted toward WBP research and conservation to ensure that WBP seeds are available to grizzly bears.

Whitebark pine is a long-living, slow growing high elevation conifer that has a life-span of over 500 years and can take up to 250 years or more to mature, depending upon site conditions (Arno and Hoff, 1990). It is considered a keystone species throughout the GYE, because it plays a disproportionately large role in its environment than its abundance would suggest (Primack, 1998). Whitebark pine help stabilize soils with deep root systems, slow snowmelt to increase moisture in the summer, reduce soil erosion by minimizing water surface run-off, and provide an important wildlife food source (Pitel and Wang, 1980). It is stress-tolerant and thrives in upper elevations of the GYE subalpine zone (2591m to 2896m) and at treeline (~3078m) where harsh conditions inhibit the growth of less stress-tolerant, competing conifer species. The upper subalpine zone (2743m to 2896m) is dominated by mature WBP stands below treeline and krumholtz WBP stands at treeline (Arno, 2001). Whitebark is also found in the lower subalpine zone (2591m to 2743m) where it primarily grows in association with subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) (Arno, 2001).

Fire disturbance affects the structure of many forest communities (Holling, 1992) and plays an important role in WBP ecology (Arno and Allison-Burnell, 2002).

Whitebark is considered a seral species of the lower subalpine zone where it is most commonly associated with subalpine fir and Engelmann spruce. At the uppermost limits of the subalpine zone, WBP is a climax species and dominates the landscape. Seral WBP sites follow a successional process in which WBP colonizes post-fire and reaches maturity but is eventually replaced by shade-tolerant Engelmann spruce and subalpine fir (Keane et al., 1994; Keane, 2001). Therefore, fire disturbance in seral WBP sites is considered important in the survival and regeneration of WBP, because WBP is susceptible to replacement by more shade-tolerant subalpine fir and Engelmann spruce in the absence of fire (Keane et al. 1994; Keane 2001b).

Since fire events are dynamic, the effects on WBP forests can be highly variable spatially and temporally (Holling, 1992). Fires range in size from a few trees or hectares, often ignited by lightning, to more unusual landscape-level events. Fire frequency is about every 60 to 300 years (Morgan et al., 1994) and intensity varies among and within events. Forest understories, canopies or both may be removed by fire.

Mixed-severity and stand-replacement fires are the most common WBP fire regimes (Arno and Allison-Burnell, 2002). Mixed severity-fires consist of either low-severity surface fires or high-severity crown or surface fires that are stand-replacing that occur separately or in combination (Morgan et al., 1994). Whitebark benefit from low-severity fires because they have thick bark, deep roots, and thinner crowns which enable them to survive while fire-intolerant fir and spruce are killed. This reduces competition

from fir and spruce that will eventually replace WBP in the absence of fire. It also enables WBP to persist and regenerate in these areas.

Stand-replacement fires occur every 300 to 450 years in WBP communities in the GYE (Barrett, 1994; Meyer and Pierce, 2003; Whitlock et al., 2003). They provide open burned areas for Clark's nutcrackers, the primary dispersal agents of WBP, to cache WBP seeds. WBP are able to regenerate more successfully on highly disturbed sites than other conifers present in the GYE (Tomback, 1982; Tomback et al., 1990).

Some studies indicate that modern-day fire exclusion management has hastened successional replacement of WBP by spruce and fir (Keane et al 1990, Kean and Arno 1993, Keane and Morgan 1994). However, even though fire suppression may have contributed WBP declines in some communities, it is not probable to conclude that all WBP communities have declined due to fire suppression. The effects are likely site-specific, and knowledge of fire interval history is necessary to draw appropriate conclusions. There is no conclusive evidence indicating that fire exclusion has changed fire return intervals in subalpine zones of the GYE (Romme and Despain, 1989).

Moreover, the progression of successional changes in WBP forests is measured in decades and centuries. Therefore, the forest structure associated with a given seral stage can change little over long periods of time. Generations of squirrels, and even bears, that select habitat based on forest stand characteristics may find WBP areas relatively unchanged.

While fire serves an important role in WBP ecology in the GYE, WBP serves an important role in red squirrel and grizzly bear ecology by providing seeds as a food

source. As a masting species, WBP has variable annual yields of seed production with good and poor seed production alternating every two to three years (Costello et al., 2014). Subalpine fir and Engelmann spruce have more consistent annual cone crops than WBP (Boe, 1954). In locations where WBP is found in association with fir and spruce, wildlife species, particularly grizzly bears and red squirrels, prefer to consume WBP seeds. Whitebark pine seeds serve as an important wildlife food source, because they are large and high in dietary fat content (52 percent: Lanner and Gilbert, 1994). Average WBP seed weight is 175 mg per seed which is over 13 times larger than seeds of other GYE conifers (subalpine fir: 13 mg/seed; Douglas fir: 11 mg/seed; Lodgepole pine: 4mg/seed; Engelmann spruce: 3 mg/seed) (McCaughey et al., 1986). Grizzly bears greatly benefit from WBP seed dietary fat because it provides energy and is efficiently converted to body fat (McDonald et al., 1988).

A unique relationship exists among WBP, grizzly bears, and red squirrels (*Tamiasciurus hudsonicus*) in the GYE. Whitebark pine cones are indehiscent, meaning that they do not open fully when ripe to release seeds. Grizzly bears rarely climb WBP to harvest seeds and depend on red squirrels to make seeds available by bringing cones to ground level (Hutchins and Lanner, 1982). From early August to the end of October, red squirrels gather WBP seeds and hide them in areas known as caches. Cache locations are easily identifiable by the presence of middens, which are large piles of cone debris left behind after a squirrel removes the seeds from cones. Midden sites are easily observable, nonmobile, fixed sites occupied by one squirrel (Kilham, 1954; Smith, 1968a; Wolff and Zasada, 1975; Vahle and Patton, 1983). Active middens are the best indicators of red

squirrel abundance (Mattson and Reinhart, 1996) and residency (McKinney and Fiedler, 2010). Therefore, active midden presence is a good indicator of red squirrel habitat selection.

Red squirrels are a highly territorial granivorous species that actively protect middens from other seed predators year round (Carey, 1991; Hutchins and Lanner, 1982; Smith, 1968b; Torick, 1995). They do not hibernate and depend on cones stored in middens to survive winter. Each squirrel generally has one midden located in the center of its territory that serves as its primary activity center (Gurnell, 1984; McAdam et al., 2007). Red squirrels and grizzly bears directly compete for WBP seeds stored in middens, and nearly all conifer seeds that grizzly bears consume are obtained by raiding red squirrel middens (Mattson and Reinhart, 1994). Since grizzly bears depend on middens for WBP seeds, forest managers must manage red squirrel habitat to ensure that WBP seeds are available for grizzly bears. Effective management can be improved by understanding red squirrel habitat requirements for midden sites.

Various forest structure and site specific variables (total conifer stand basal area, canopy closure, conifer species composition, slope, aspect, and elevation are important factors associated with red squirrel midden sites (Vahle and Patton, 1983; Mattson and Reinhart, 1994; Mattson and Reinhart, 1997; Wood et al., 2007; Zugenmeyer and Koprowski, 2009). Squirrels favor habitat conditions that provide an abundant cone supply and adequate cover from predators (Rothwell, 1979; Steele, 1998). Previous studies indicate that red squirrel midden occurrence is positively related to total conifer stand basal area and canopy cover (Mattson and Jonkel, 1990; Zugenmeyer and

Koprowski, 2009). McKinney and Fiedler (2010) used active middens as indicators of red squirrel habitat selection and determined that total basal area of conifer species and percent canopy cover are important variables associated with red squirrel habitat selection in GYE forests ranging from Montana to Wyoming, as well as forests in northwestern Montana. Zugenmeyer and Koprowski (2009) observed that live tree basal area was higher at occupied middens compared to unoccupied middens and that midden sites have higher canopy cover, more large trees (>40cm DBH), and higher live tree total basal area than sites without middens. Midden sites are most abundant in areas with greater than 70 percent canopy closure in the Pinaleño Mountains of Arizona (Smith and Mannan, 1994). Red squirrels select areas within forests that have high conifer total basal area and percent canopy cover, thus meeting the aforementioned habitat needs of substantial cone supplies and protection from aerial predators.

Conifer species compositions are also important in red squirrel habitat selection (Mattson and Reinhart, 1990; 1997; Mattson, 2000). Red squirrels are restricted to mature forests because they rely on cover and tree seeds for survival and are generally found in most conifer and mixed woods forests containing high stem density and cover, regardless of human or natural disturbances (Koprowski, 2005). Optimal squirrel habitat in forests containing WBP (WBP zones) contain habitats with high over-story (canopy cover) and basal area of trees, as well as high diversity of tree species (Mattson and Reinhart, 1990; 1997). Red squirrels prefer to establish middens in mixed conifer forests over forests dominated by a single species, because annual cone crop sizes vary among conifer species (Mattson, 2000). Mixed forests provide more stable and predictable annual seed

supplies for red squirrels, because multiple conifer species are present. It is unlikely that all species in mixed forests will experience poor cone crops or cone crops failures in a given year, which ensures that red squirrels have dependable annual seed supplies. In contrast, cone production in pure WBP stands is annually variable, which would not support a squirrel population.

The number of cones stored in middens are positively correlated to midden area (Hurly and Lourie, 1997). Large middens can contain thousands of freshly cut cones each year (Finley, 1969) which can provide up to two years of cone resources for red squirrels (Gurnell, 1984). Storing such large numbers of cones in one place subjects red squirrels to direct competition from grizzly bears for seeds stored within middens. The probability that a grizzly bear will raid a midden site is influenced by midden area (Mattson and Reinhart, 1997). Grizzly bears were observed to raid large middens more frequently than small middens, because they were able to excavate more cones from larger middens (Mattson and Reinhart, 1997). Additionally, probability of a grizzly bear excavating a midden was positively related to annual WBP cone crop size (Mattson and Reinhart, 1997). The high energy content of WBP seeds (Tomback, 1982) makes them highly preferred by both red squirrels and grizzly bears. Years with large WBP cone crops provide more WBP seeds for grizzly bears to steal from middens.

Red squirrels are strategic foragers and harvest cones from conifer species with the highest cone energy content first (Smith, 1968a; Smith, 1970). In the GYE, red squirrels first select WBP cones, because WBP seeds have the highest energy content (27.7 kcal per cone) of all conifer species present: subalpine fir, Engelmann spruce,

lodgepole pine (*Pinus contorta*), and Douglas fir (*Pseudotsuga menziesii*) (Smith, 1970; Tomback, 1982). Subalpine fir yields the second highest cone energy content at 15.7 kcal per cone (Tomback, 1982; Smith, 1970) which is roughly half that of WBP. The conifer species most commonly associated with WBP in the subalpine zone (~2591 m to treeline around 3048m) are subalpine fir and Engelmann spruce (McCaughey and Schmidt, 1990). In nearly pure stands of WBP, squirrel population tends to be low compared to mixed conifer stands containing WBP (Mattson et al., 2001). McKinney and Fiedler (2010) observed a linear decrease in red squirrel cone predation as WBP abundance increased in forests. Even though red squirrels prefer WBP seeds, mixed conifer forests have more consistent annual cone crops than WBP dominated forests and provide squirrels with a more predictable annual food source (Reinhart and Mattson, 1990; Mattson, 2000).

Red squirrel densities in WBP zones also increase as exposure to prevailing winds and elevation decreases (Mattson and Reinhart, 1994). A negative relationship exists between WBP dominance and red squirrel density, because WBP basal area and dominance increases with wind exposure and elevation (Mattson and Reinhart, 1994). Active midden sites occur in locations with minor slopes and at lower elevations than inactive middens (Zugenmeyer and Koprowski, 2009). As slope increases, the probability of a midden occurring decreases (Wood et al., 2007), and red squirrel middens are more prevalent on north facing slopes than south facing slopes (Vahle and Patton, 1983). The difference between midden prevalence on north versus south facing slopes can be attributed to the hillshade values of site locations which indicate the amount of shade that

sites receive over the course of the year. As hillshade value increases, the amount of shade an area receives decreases. Middens require cool, moist conditions to keep stored cones from drying out, opening, and losing seeds (Finley, 1969). In the northern hemisphere, north facing slopes have lower hillshade values than south facing slopes which suggests that north facing slopes better support middens, because they are less exposed to direct sunlight and remain cooler.

As discussed, previous studies have identified variables most important for red squirrel habitat selection including: total conifer stand basal area, canopy closure, conifer species composition, slope, aspect, and elevation. It is important to further highlight the importance of conifer species compositions in red squirrel habitat selection. Forest structure composition of red squirrel habitats has been examined extensively indicating that red squirrels prefer mixed conifer habitats with a diversity of trees species (Mattson and Reinhart, 1990; Mattson and Reinhart, 1997; Mattson et al., 2001; Koprowski, 2005, McKinney and Fiedler, 2010). Red squirrel population residency tends to be low in WBP dominated stands (WBP comprises greater than 50 percent of total conifer species basal area) and high in mixed conifer forests with WBP constituting less than 50 percent of total conifer species basal area (McKinney and Fiedler, 2010). Conifer species compositions are diverse within mixed forests, and a critical research gap remains in understanding how conifer species abundances within mixed forests affect red squirrel habitat selection.

Red squirrel habitat selection within GYE mixed forests is best identified by active midden presence, because midden sites represent the center of red squirrel

territories (McAdam et al., 2007) and indicate current residency (McKinney and Fiedler, 2010). Even though red squirrel population residency is low in WBP dominated stands (McKinney and Fiedler, 2010), WBP seeds still serve as a preferred food source for red squirrels. This knowledge suggests that mixed conifer stands in GYE subalpine zones dominated by other conifer species (primarily subalpine fir and Engelmann spruce comprising greater than 50% of total tree species composition) with interspersed WBP is the most suitable habitat for red squirrels, but no studies, to our knowledge, have attempted to quantify a conifer species composition within mixed conifer forests that provides optimal red squirrel habitat for midden sites. Estimating optimal conifer species mixtures for red squirrel middens in the GYE has important management implications for grizzly bears.

Subalpine zone mixed forests provide the best habitat for red squirrels. However, they are also the focus areas for WBP conservation. For example, in response to recent WBP declines in the GYE, managers are targeting areas of mixed conifer forests that contain WBP for thinning and prescribed burn management in an effort to retain WBP (GYCC, 2011). Thinning and burning removes two species, subalpine fir and Engelmann spruce, that generally outcompete WBP for resources. Even though these procedures may benefit WBP, they could have near-term detrimental impacts on red squirrels and grizzly bears by decreasing available prime red squirrel habitat.

Therefore, the key to successful invasive WBP management methods depends on identifying areas within mixed forests that are most likely to contain red squirrel middens. Management in mixed forests must be strategic and focused on areas less likely

to contain red squirrel middens, but the problem remains in accurately identifying key areas within mixed forests where midden sites are most prevalent. Without this knowledge, managers risk reducing prime red squirrel habitat which will negatively impact grizzly bears. Results of this study will help managers identify areas within mixed conifer forests containing WBP that should be protected from thinning and burning to conserve prime red squirrel habitat and ensure WBP seeds are available to grizzly bears. Our findings could be incorporated into existing management plans to more strategically consider the effects of thinning and prescribed burns on grizzly bears.

In response to recent WBP population declines in the GYE, the Greater Yellowstone Coordinating Committee has published a strategy plan to ensure the long-term viability and function of WBP in the Greater Yellowstone Area (GYCC, 2011). The plan outlines specific goals including: 1) monitoring WBP condition, 2) protecting WBP from mountain pine beetle, blister rust, and fire through the use of verbenone, carbaryl, pruning, and fire suppression, 3) restoring WBP by planting blister rust resistant seedlings and implementing thinning and prescribed burns to remove competing conifers and create openings favorable for WBP regeneration, 4) Improve WBP by identifying potential blister rust resistant trees and propagating blister rust resistant seeds for planting. Although these strategies will benefit WBP, managers must consider how implementing these invasive techniques, specifically thinning and burning, will impact current WBP seed availability for grizzly bears at a local and landscape level.

Some primary goals of thinning and burning treatments in subalpine forests where WBP is seral are to reduce competition of shade-tolerant subalpine fir and Engelmann

spruce, reduce WBP pine beetle outbreak susceptibility, mimic mixed-severity fires, and create fuel breaks to decrease the chance of stand-replacing fires (GYCC, 2011).

Additionally, interest in implementing thinning and burning in WBP zones is partially based on the idea that fire suppression practices over the last 60 plus years have suspended natural fire cycles in these WBP communities (Kean and Arno, 2001) resulting in fire intervals that have exceeded their historic range of variability. Yet, research in western North America suggests that many high-elevation forests fire regimes are functioning within their historic range of variation (Johnson et al., 1990; Sherriff et al., 2001; Buechling and Baker, 2004).

Although managers are focused on implementing thinning and burning treatments (GYCC, 2011), there are limited data that describe historic fire regimes in GYE WBP communities to guide these efforts. Romme and Walsh (2003) conducted a study to better understand historic fire regimes in WBP communities throughout the GYE and found little evidence of mixed fire regimes in WBP communities located in dense subalpine forests. This indicates that infrequent stand-replacing fires may be the main component responsible for current stand structures. The need to artificially simulate natural fire through thinning and burning in the GYE may be unnecessary because natural processes have maintained GYE forests throughout history and are still occurring naturally as evidenced by the Yellowstone fires of 1988.

It is estimated that approximately 27.5 percent of Yellowstone's WBP zone burned in the 1998 fires (Renkin and Despain, 1992). These fires were similar to historic fires during the 1700s (Schoennagel et al. 2004) which likely resulted in the

establishment of many present-day WBP stands (van Manen et al., 2013). Since over a quarter of the WBP zone burned and no conclusive evidence exists indicating that fire intervals have exceeded their historic range of variability, managers must assess whether it is beneficial to allocate resources to implement strategies such as thinning and burning to retain WBP. They must also consider the impacts these strategies may have on wildlife that utilize WBP zones, specifically red squirrels and grizzly bears, at a broader scale.

Podruzny et al. (1997) examined effects of the 1988 fire on red squirrel middens and bear use of middens in the Mt. Washburn region of Yellowstone. Their findings indicated that no middens were observed in burned areas and the number of active middens, midden area, and bear use of pine seeds decreased by 27 percent, 54 percent, and 64 percent, respectively, post-fire compared to pre-fire. The fires negatively impacted red squirrels and bears that utilize the area for conifer seed resources. After the fires, WBP seed availability for grizzly bears was reduced and not expected to increase for approximately 70 to 100 years, which is the time span it takes for newly established WBP to reach maturity and produce large numbers of cones (McCaughey and Schmidt, 1990). Podruzny et al. (1997) emphasize that managers should maintain large, secure areas with habitat that supports stable WBP and red squirrel numbers and re-evaluate implementing prescribed fires or timber harvesting that may result in further loss of seed producing conifers in the WBP zone. The CCB of Montana fits into this category and should be protected since it contains a healthy, intact WBP zone (Macfarlane et al., 2013) that supports red squirrels and grizzly bears.

Managers are currently targeting CCB subalpine mixed conifer forests containing

WBP for thinning and burning to prevent successional replacement of WBP and minimize the spread of mountain pine beetle outbreaks (GYCC, 2011). These forests are prime areas for red squirrels to establish midden sites (McKinney and Fiedler, 2010) which provide grizzly bears access to WBP seeds. Thinning and burning mimic fire disturbance, and fire disturbance has been documented to negatively alter prime red squirrel habitat for middens, thus decreasing availability of WBP seeds for grizzly bears (Podruzny et al., 1997). In addition, there is no conclusive evidence to suggest that fire regimes in GYE WBP zones are operating outside of their historical range of variation which undermines the need for thinning and burning management. We suggest that forests containing WBP in the CCB, or at least areas within these forests most likely to contain red squirrel middens, should be protected to ensure that grizzly bears have access to WBP seeds and that more research is needed to understand fire regimes specific to the Cooke City Basin of Montana before implementing invasive thinning and burning management. Our identification of a conifer species composition most likely to contain red squirrel middens will help managers identify areas most critical for grizzly bears to obtain WBP seeds which can be used to direct management in the CCB of Montana.

A counterargument which supports the need to thin and burn subalpine forests containing WBP in the GYE is related to the mountain pine beetle outbreak. Currently, mountain pine beetle are causing significant WBP declines in the GYE (Gibson, 2007). Mountain pine beetles are found in 95 percent of GYE forest stands containing WBP (MacFarlane et al., 2009) and have caused moderate to severe WBP mortality in 82 percent of the WBP distribution in the GYE (Macfarlane et al., 2013). Mountain pine

beetle outbreaks have periodically impacted the GYE over the past 300 years (Perkins and Swetnam, 1996) but have been relatively short in duration compared to the current outbreak, which is the most severe ever recorded (Gibson et al., 2008). In the past, the sustained cold temperatures of WBP ecosystems have limited distribution of mountain pine beetle into these areas (Logan et al., 2010) by killing beetles before they could complete their life cycles.

In order to reproduce, mountain pine beetles must kill their host species. It generally takes two years for mountain pine beetles to complete life cycles due to cold temperatures in WBP ecosystems, but recent uncharacteristically mild winters and warmer summers due to climate change have enabled mountain pine beetle to move into higher elevations and complete development in one year which increases the rate of beetle population growth and severity of outbreaks (Logan et al., 2010). Whitebark pine zone climate suitability for mountain pine beetles is projected to increase over the next century (Hicke et al., 2006; Bentz et al., 2010) which has managers concerned about the future of WBP in the GYE. However, aerial detection surveys have indicated that the peak of mountain pine beetle activity occurred in 2009 (U.S. Department of Agriculture 2012a, b, c). The combined effects of reduced seed production from WBP infected with blister rust and high WBP mortality caused by mountain pine beetles will reduce the likelihood of natural WBP seedling establishment in openings created by fire (GYCC, 2010). A potential solution is for managers to plant WBP seeds in openings created by thinning and burning management techniques (Keane and Parsons, 2010).

Additionally, protecting forested areas most likely to contain middens may help reduce grizzly bear-human interactions. The risk of negative grizzly bear-human interactions increases during years of poor WBP cone crops because grizzly bears move into lower elevational areas in search of alternate foods (Mattson et al., 1992). When WBP cone crops are large, grizzly bears generally remain in high elevation areas where WBP seeds are most abundant (Mattson et al., 1992). Pease and Mattson (1999) documented a doubling in death rate of bears during low cone crop years, and almost all mortalities were caused by humans. A recent study suggests increased bear-human conflict risks are not likely when WBP abundance is low because other food resources remain abundant in high elevations (Costello et al., 2014) which contradicts the findings of Pease and Mattson (1999). Middens can contain two years of cone resources (Gurnell, 1984) suggesting that WBP seeds can still be available to grizzly bears even in low WBP cone crop years. Protecting areas of mixed forests most likely to contain middens will not only ensure availability of WBP seeds for grizzly bears but may decrease the likelihood of bears moving to lower elevations in search of alternate foods where they are more likely to encounter humans.

INTRODUCTION

Throughout the Greater Yellowstone Ecosystem (GYE), whitebark pine (WBP; *Pinus albicaulis*), a subalpine keystone conifer species (Tomback et al., 2001), has primarily declined due to mountain pine beetle (*Dendroctonus ponderosae*) infestations and whitebark pine blister rust (*Cronartium ribicola*) infections (Logan and Powell, 2001; Gibson et al., 2008; Logan et al., 2010; van Manen et al., 2013), but fire suppression management practices may also be contributing to the decline (Keane et al., 1990, Kean and Arno, 1993, Keane and Morgan, 1994). Blister rust infections and pine beetle infestations have reduced the number of cone-bearing WBP in excess of 90 percent in some areas (van Manen et al., 2013). Managers are concerned because WBP seeds serve as an important seasonal food source for threatened GYE grizzly bears (*Ursus arctos*) (Mattson and Reinhart, 1994).

Currently, delisting the GYE grizzly bear is a priority for management agencies. In past years, grizzly bears have remained a threatened species in the GYE due to uncertainty of how they will cope with potential loss of WBP as a major food source despite evidence of a recovered grizzly population at carrying capacity (Bjornlie et al., 2014; van Manen et al., 2016). As a result, management priorities have shifted toward WBP research and conservation to ensure that WBP seeds are available to grizzly bears. The key to managing WBP for grizzly bears relies on preserving habitat for an unlikely counterpart, the red squirrel.

A unique relationship exists among WBP, grizzly bears, and red squirrels in the GYE. Whitebark pine seeds serve as an important food source for grizzly bears and red

squirrels (Primrack, 1998). Grizzly bears rely on WBP seeds as a fall food source (Mattson and Reinhart, 1994) to build up significant levels of fat crucial for survival over winter. Whitebark cones are indehiscent and not readily available to grizzly bears when ripe, because grizzly bears rarely climb WBP trees to harvest seeds. As a result, grizzly bears depend on red squirrels as intermediary agents to make WBP seeds available at ground level.

Red squirrels selectively harvest cones from conifer species with the highest cone energy content first (Smith, 1968a). In the GYE, red squirrels will first select WBP cones, because WBP seeds have the highest energy content (27.7 kcal per cone). It is not surprising that red squirrels prefer WBP seeds, because WBP cone energy content is nearly double that of subalpine fir which yields the second highest cone energy content at 15.7 kcal (Tomback, 1982; Smith, 1970). From early August to the end of October, red squirrels harvest WBP cones and hide them in areas known as caches. Grizzly bears can easily locate cache locations due to the presence of middens, which are large piles of cone debris left behind after a squirrel removes the seeds from cones. Each squirrel generally has one midden site located in the center of its territory that serves as its primary activity center (Gurnell, 1984; McAdam et al., 2007). Since grizzly bears depend on red squirrel middens to obtain WBP seeds, forest managers must understand red squirrel habitat requirements and actively protect areas within forests most likely to contain red squirrel middens.

Since active middens are located in the center of red squirrel territories (McAdam et al., 2007) and indicate residency (McKinney and Fiedler, 2010), they are very good

indicators of red squirrel habitat selection. Therefore, identifying variables associated with midden sites provides the greatest insight regarding red squirrel habitat requirements. Red squirrel habitat requirements have been extensively examined in the literature indicating that total conifer basal area and canopy cover (Mattson and Jonkel, 1990; Zugenmeyer and Koprowski, 2009; McKinney and Fiedler, 2010), slope (Zugenmeyer and Koprowski, 2009), aspect (Vahle and Patton, 1983), elevation (Mattson and Reinhart, 1994) and conifer species compositions (Koprowski, 2005; McKinney and Fiedler, 2010) are important variables associated with red squirrel midden site selection. Of these variables, understanding how conifer species compositions impact red squirrel midden site selection holds an instrumental role in WBP management for grizzly bears.

Red squirrel residency tends to be low in WBP dominated stands (WBP comprises greater than 50% of total conifer species basal area) and high in mixed conifer forests with WBP constituting less than 50% of total conifer species basal area (McKinney and Fiedler, 2010). Even though red squirrel residency is low in WBP dominated stands, WBP seeds are still preferred by red squirrels (Smith, 1968a). This knowledge suggests that mixed conifer stands in GYE subalpine zones dominated by other conifer species (primarily subalpine fir and Engelmann spruce comprising greater than 50% of total tree species composition) with interspersed WBP is the most suitable red squirrel habitat. Yet, no studies have attempted to quantify a conifer species composition within mixed conifer forests that provides optimal habitat for red squirrel middens. Estimating optimal conifer species mixtures for red squirrel middens in the GYE has important management implications for grizzly bears. Effective WBP

management for grizzly bears depends on identifying and protecting areas within mixed forests most likely to contain red squirrel middens.

Whitebark pine zones in the GYE are important foraging areas for grizzly bears to obtain WBP seeds. We studied red squirrel habitat selection in the WBP zone of the Cooke City Basin (CCB) of Montana. The CCB is an ideal study area to focus specifically on conifer species composition to examine how conifer species abundances affect red squirrel midden site selection. It contains one of the largest, healthy, intact WBP stands in the entire GYE that has remained greatly unaffected by the mountain pine beetle outbreak and recent fire (Macfarlane et al., 2013).

The upper subalpine zone (~2743 m to 2896 m) is dominated by pure mature WBP stands, and the lower subalpine zone (~ 2591 m to 2743 m) contains mixed conifer forest primarily dominated by subalpine fir and Engelmann spruce with interspersed WBP (Arno, 1979). The total elevational range of CCB forests spans from approximately 2316 m to treeline at 3078 m. At elevations below 2591 m, WBP is absent and mixed forests primarily dominated by subalpine fir and Engelmann spruce are abundant. The elevational gradient ensures that forest compositions range from 0 to 100 percent WBP which is crucial for assessing how conifer species compositions influence red squirrel midden occurrence. By collecting forest structure and site specific data (conifer species composition, canopy closure, slope, elevation, and aspect), midden counts, and midden area measurements along this elevational gradient, we were able to assess which variables were associated with red squirrel midden site selection and midden area, as well

as identify a conifer species composition optimal for red squirrel midden sites. The specific research objectives of this study were to:

- 1) estimate the forest structure and site characteristic factors (conifer species composition, total canopy cover, elevation, slope, and hillshade) that are associated with red squirrel midden site selection.
- 2) quantify a conifer species composition (mixture) at which active middens are most likely to occur.
- 3) estimate the forest structure and site characteristic factors (subalpine fir/Engelmann spruce basal area, WBP basal area, total canopy cover, slope, and hillshade) that are associated with red squirrel midden area.

Results of this study will help managers identify areas within mixed conifer forests containing WBP that should be protected from invasive management practices, such as thinning and burning, to protect prime red squirrel midden habitat and ensure WBP seeds are available to grizzly bears.

STUDY AREA

Cooke City Basin, MT

The study area encompasses approximately 91 km² in the Cook City Basin of Montana located 6 km from the northeast entrance of Yellowstone National Park (Mattson et al., 1992). The area is surrounded by designated wilderness areas and lies within the Yellowstone Grizzly Bear Recovery Zone established by the U.S. Fish and Wildlife Service in 1993. Annual average temperature is 1.55 C (34.8 F) with average high and low temperatures of 9.1 C and -6 C respectively. Annual precipitation averages include 628mm of rainfall and 513 cm of snowfall (U.S. Climate Data, 2016). Cool temperatures, steep, rugged mountains, and extensive valley floors are characteristic of intercontinental high elevation environments located along the 45th parallel (Yonge, 2001).

A variety of forest communities disjointed by avalanche chutes, talus slopes, alpine meadows, and nonforested openings are embodied throughout the study area. The most important aspect of the CCB is that it contains a subalpine zone with one of the largest, healthy, intact WBP populations in the GYE greatly unaffected by the mountain pine beetle outbreak (Macfarlane et al., 2013) and is utilized by grizzly bears despite high levels of human activity (Rossi, 2016). Forest communities are diverse in conifer species compositions with mixtures of WBP, Engelmann spruce, Rocky Mountain subalpine fir, lodgepole pine, and Douglas fir. The dominant tree species in the subalpine zone include WBP, Engelmann spruce, and Rocky Mountain subalpine fir. Lodgepole pine and

Douglas fir generally occur below the subalpine zone. Krumholtz forests of WBP, Engelmann Spruce, and subalpine fir are located at the highest elevations located at or near tree line. Mature forests dominated by single conifer species or mixed conifer species are found throughout the area with lodgepole pine and Douglas fir only present at the lowest elevational gradients.

METHODS

Study Design

In 1992, the Interagency Grizzly Bear Study Team (IGBST) and U.S. Forest Service systematically positioned 27 belt transects in 8 drainages in the CCB of Montana. Transects were originally designed to evaluate grizzly bear habitat use and distribution in response to human activity including mine reclamation and road construction in the CCB. Distance between transects is constant at 0.5 km, but length varies from 715 m to 5904 m. They were oriented perpendicular to topographic contours to cover elevational gradients which ensured that all forest cover types found throughout the CCB were represented. Transects covered the total elevational range of the study area from 2316 m to 3078 m at treeline. Slopes ranging from 0 degrees (flat ground) to 48 degrees (very steep mountain sides) and north, south, east and west facing aspects were found within transects.

Mixed forests and forests dominated by single conifer species occurred which were crucial for assessing how forest compositions impact red squirrel habitat selection. The conifer species most abundant in the area were Engelmann spruce, subalpine fir, and WBP. Elevations ranging from 2316 to 2591 m contained mixed forests devoid of WBP that were primarily composed of a mixture of subalpine fir and Engelmann spruce but occasionally contained interspersed lodgepole pine and Douglas fir. Forest composition gradually transitioned into mixed forests containing WBP at 2591 m with WBP abundance increasing to 100 percent of total conifer species composition as elevation

increased above 2591 m in some sites. Additionally, 0 to 100 percent mixtures of Engelmann spruce and subalpine fir were present. Engelmann spruce and subalpine fir were combined into one conifer group because they were always associated (McCaughey and Schmidt, 1990; Arno, 2001) throughout the study area. Red squirrel residency in forests decreases as WBP increases above 50 percent of total conifer species composition (McKinney and Fiedler, 2010), but an approximate conifer species composition ideal for red squirrel middens was not identified. The variety of conifer species compositions found in the CCB were perfect for estimating an ideal conifer composition for red squirrel midden sites.

Our study occurred from July to October of 2012 to ensure data were collected when red squirrels were actively caching conifer cones in middens. Red squirrel cone caching activity begins as early as July and is at its peak from mid-August to mid-September (Hutchins and Lanner, 1982). Variable radius circular plots are commonly used to assess squirrel habitat requirements (Merrick et al., 2007; Smith and Mannan, 1994). We implemented circular plots along the center line of the 27 original belt transects designed by the IGBST and U.S. Forest Service. Each transect line contained 30 evenly spaced 30 meter diameter circular plots resulting in a total of 810 plots with over 18,000 conifers surveyed. Vahle and Patton (1983) indicated that the best red squirrel habitat consists of mixed conifer forests that contain densely grouped conifer stands covering an area of 0.04 hectares (ha) or less. We assessed habitat characteristics within fifteen meter radius plots (total area of 0.071 ha) to ensure that conifer stands within plots were at least 0.04 ha in area.

Field Data

Data collected in 2012 included elevation, slope, aspect, tree counts by species, active midden counts, and midden area measurements for each plot. A Garmin eTrex GPS unit and compass were used to obtain elevation, slope, and aspect data. Active middens (n=201) were identified by the presence of freshly cut cones, cone scales, or chewed cone cores on or within larger multiple year accumulations of cone debris (Finley, 1969). Conifers were only included if they were of cone-bearing age ranging from pole trees (DBH of 12.7 cm to 22.9 cm) to mature trees (DBH of 22.9 cm or larger). Trees smaller than 12.7 cm DBH generally do not produce cones in the CCB (personal observation; LaMontagne et al., 2013).

In July of 2016, we revisited a subsample (n=85) of the 104 plots that contained middens to obtain conifer canopy cover percentages and basal area (BA) estimates. This subsample represents 82 percent of the 104 plots that contained middens. Canopy cover percentages were estimated using a convex forest densiometer in four cardinal directions (McKinney and Fiedler, 2010). The four percentages were averaged and converted into a total percent canopy cover for each plot. We also measured DBH of three trees that were best representative of average tree size for each conifer species. The three DBH measurements were averaged to obtain a final DBH estimate for each corresponding conifer species which were used to calculate the total BA in m² occupied by each species. Conifer species compositions for each plot were based on the percent BA of each species relative to the total conifer BA (McKinney and Fiedler, 2010).

GIS Data

Digital elevation maps (DEM) were used in the software ArcGIS (ESRI, 2011) to acquire canopy cover, slope, and hillshade values for each 30 meter diameter circular plot (n=810). Canopy cover is a numerical variable obtained from a 30m resolution DEM ArcGIS layer (<http://landfire.cr.usgs.gov/viewer>) that quantifies percent canopy cover in categories. The categories are either 0 percent or 15 to 95 percent by 10 percent increments. Slope is measured in degrees and was calculated by applying the ArcGIS function “Slope” to a 10m resolution DEM downloaded from viewer.nationalmap.gov. Hillshade estimates the amount of shade an area receives throughout the entire year (Ciarniello et al., 2007a). The ArcGIS spatial analyst tool “hillshade” was used to estimate a hillshade value for each plot by incorporating slope and aspect data from the DEM into the following expression:

$$\text{Hillshade} = 255.0 * ((\cos(\text{Zenith_rad}) * \cos(\text{Slope_rad})) + (\sin(\text{Zenith_rad}) * \sin(\text{Slope_rad}) * \cos(\text{Azimuth_rad} - \text{Aspect_rad})))$$

The hillshade tool calculates the hypothetical illumination of a surface based on an azimuth of 225 and sun angle equal to 45 degrees. This variable was transformed to the range 1 to 100% to facilitate interpretation using the following relationship:

$$\text{Hillshade \%} = \frac{\text{Hillshade} - \min(\text{Hillshade})}{\max(\text{Hillshade}) - \min(\text{Hillshade})} \times 100\%.$$

The gradient of 0 to 100% allows quantifying the amount of light the location receives as a function of topography. Lower values are associated with “cooler” locations while high values are associated with “warmer” locations (Ciarniello et al., 2007).

Statistical Analyses

Red Squirrel Midden Site Selection

The goal of this analysis was to assess which measured environmental factors are associated with red squirrel midden site selection in the CCB. The conifer species composition variable was identified as the “percent of WBP trees” which indicates the percent WBP of overall conifer species composition based on tree counts. Conifer species compositions at midden sites were primarily composed of a mixture of WBP, subalpine fir, and Engelmann spruce. Fir and spruce were combined into one species category, because they were always associated with one another (McCaughey and Schmidt, 1990; Arno, 2001) throughout the study area. Therefore, assessing how conifer species composition impacted midden site selection only required incorporating the percent of WBP contained in the plot. Generalized linear mixed models (GLMM; Zuur et al., 2009) were used to complete the analysis. The response variable was coded as 1 for plots that contained an active red squirrel midden and 0 for plots where an active midden was absent. This response was assumed to follow binomial (Bernoulli) distribution with the logit link. A random intercept for the categorical variable of transects was included in all models. Variance inflator factors (VIF; Zuur et al., 2009) were used to assess collinearity among explanatory variables incorporated into the model (Table 1).

Table 1. Variables included in the red squirrel midden site selection model.

Explanatory Variable	Description
Percent of WBP	The conifer species composition variable is identified as the “percent of WBP” which indicates the percentage of trees in a plot that were identified as WBP based on tree counts. Conifer species compositions at midden sites were primarily composed of a mixture of WBP, subalpine fir, and Engelmann spruce. Fir and spruce were combined into one species category, because they always occurred in association with one another (McCaughey and Schmidt, 1990; Arno, 2001) throughout the study area. Therefore, assessing how conifer species composition impacts midden sites only required incorporating the percent of WBP trees in a conifer stand.
Slope	Slope measured in degrees, was obtained applying the ArcGIS function “Slope” to a Digital Elevation Model (DEM; 10m resolution) downloaded from viewer.nationalmap.gov.
Hillshade	Variable obtained using the tool Hillshade (Spatial Analyst) from the software ArcGIS (ESRI 2011; using azimuth 225 and sun angle equals 45°). This variable was transformed to the range 1 to 100% to facilitate interpretation using the following relationship: $\text{Hillshade \%} = \frac{\text{Hillshade} - \min(\text{Hillshade})}{\max(\text{Hillshade}) - \min(\text{Hillshade})} \times 100\%.$ The gradient of 0 to 100% allows quantifying the amount of light the location receives as a function of topography. Lower values are associated with “cooler” locations while high values are associated with “warmer” locations (Ciarniello et al., 2007).
Canopy Cover	A numerical variable obtained from a 30m resolution ArcGIS layer that quantifies percent canopy cover in categories. The categories are either 0% or 15% to 95% by 10% increments. Downloaded from the website http://landfire.cr.usgs.gov/viewer.

Four candidate models were developed using these predictors to test the hypotheses associated with red squirrel midden site selection (Table 2). These models were compared using Akaike Information Criterion (AIC), and the model with the lowest AIC was considered the most parsimonious model for red squirrel midden site selection in the CCB. After the model was selected, 85% confidence intervals (Arnold, 2010) were used to indicate which factors in the model were associated with probability of a red squirrel selecting a midden site. All models were fit using the package “lme4” (Bates et al. 2015) in R software (R Core Team, 2014). The Moran's I test of the R package “ape” (Paradis and Strimmer, 2004) was used to test for spatial autocorrelation in the residuals of the model.

Table 2. Competing models designed to test hypotheses about factors associated with red squirrel midden site selection in the Cooke City Basin, Montana.

Model	Variables/Tested hypothesis
M0	Intercept only Hypothesis: The measured variables, supported by the literature as good predictors of high quality red squirrel habitat, are not associated with red squirrel midden site selection.
M1	Slope + Hillshade + Canopy cover Hypothesis: Slope, hillshade, and canopy cover are associated with red squirrel midden site selection in the CCB but the percentage of WBP trees is not associated with midden site selection.
M2	Slope + Hillshade + Canopy cover + Percent of WBP* Hypothesis: Slope, hillshade, and canopy cover are associated with midden site selection in the CCB. In addition, the percentage of WB trees is associated with red squirrel midden site selection in a monotonic way.
M3	Slope + Hillshade + Canopy cover + Percent of WBP + Percent of WBP ² Hypothesis: Slope, hillshade, and canopy cover are associated with midden site selection in the CCB, and there is a quadratic association between percentage of WBP trees and probability of midden site selection.

Ten-fold cross validation assessed the predictive capability of the model (Boyce et al., 2002; Johnson et al., 2006) by dividing the data set into ten parts of equal size. The best model was then fit to nine tenths of the data and the remaining tenth was used as validation set. Ten resource selection probability function (RSPF) bins were created by predicting RSPF values using the fitted coefficients and the remaining tenth of the data. Predicted values were grouped using deciles (quantiles from 10% to 100% by 10% increments). Johnson et al. (2006) advise that bins should be created so that they have the same area. Since all plots in this study had the same area, organizing data into bins that contained the same number of locations produced bins of the equal area. The procedure was repeated using each of the ten parts of the data alternatively as a validation set. Midpoints of the RSPF bins were re-scaled to 0-1 and then regressed against the proportion of used location in each bin (Johnson et al., 2006). If the models have high predictive capability, the regression of proportion of used locations and RSPF bin midpoints should have high R^2 , intercept not different than zero, and slope not different than one (Johnson et al., 2006).

Red Squirrel Midden Area

The goal of this analysis was to assess which of the measured environmental factors are associated with midden area in the Cooke City Basin. The analysis was done using linear mixed models (LMM). The response variable considered in this analysis was total midden area (m^2) per plot. The response was log-transformed to meet assumptions of homogeneous variance and normality. A random intercept for the categorical variable of transects was included in all models. The explanatory variables included in the models

(Table 3) were tested for collinearity using variance inflator factors (VIF; Zuur et al., 2009).

Table 3. Variables included in the red squirrel midden area model.

Explanatory Variable	Description
Slope	Defined in Table 1.
Hillshade	Defined in Table 1.
Canopy Cover	Total percent conifer canopy cover in each plot measured with a convex forest densitometer . See Field Data subsection of the Methods section a more detailed description.
Total Basal Area SF	Total combined basal area (m ²) of Rocky Mountain subalpine fir and Engelmann fir in each plot.
Total Basal Area WBP	Total basal area (m ²) of WBP in each plot.

Four candidate models were developed to test hypotheses regarding the relationship between with red squirrel midden area and environmental factors (Table 4). These models were compared using AIC, and the model with the lowest AIC was considered the most parsimonious model for red squirrel midden area in the CCB among the candidate models. After the most parsimonious model was selected, 85% confidence intervals (Arnold, 2010) were used to indicate which factors in the model were associated with midden area. All models were fit using the package “lme4” (Bates et al. 2015) of the software R (R Core Team 2014). The Moran's I test of the R package “ape” (Paradis and Strimmer, 2004) was used to test for spatial autocorrelation in the residuals of the most

parsimonious model. Model fit was assessed using pseudo R^2 for mixed models implemented in the R package MuMIn (Barton, 2016).

Table 4. Competing models designed to test hypotheses about factors associated with midden area in the Cooke City Basin, Montana.

Model	Variables/Tested hypothesis
M0	Intercept only Hypothesis: The measured variables are not associated with midden area. Slope + Hillshade
M1	Hypothesis: Slope and hillshade are associated with midden area, but total canopy cover, total basal area of SF, and total basal area of WBP are not associated with midden area. Total Basal Area SF + Total Basal Area WB + Total Basal Area SF * Total Basal Area WBP
M2	Hypothesis: Total basal area of both SF and WBP are associated with midden area, but slope, hillshade, and total canopy cover are not associated with midden area. Total Canopy Cover (estimated in the field)
M3	Hypothesis: Total canopy cover is associated with midden area, but slope, hillshade, total basal area of SF, and total basal area of WBP are not associated with midden area.

* WBP = whitebark pine, SF = Rocky Mountain subalpine fir/ Engelmann spruce mixture

RESULTS

Red Squirrel Midden Site Selection

Results from the AIC model selection (Table 5) indicates model 3 (M3) is the most parsimonious model among the candidates, which suggests that red squirrel midden site selection in the Cooke City Basin might be associated with the factors: slope, hillshade, and canopy cover and a quadratic function of the percentage of WB pine trees in the site. Results from the most parsimonious model (M3; Table 6) provided evidence to support an association between probability of selection of midden sites and all variables included in the model, except for slope from which the 85% confidence interval did not include zero. The odds-ratio of selection of a site increased about 2% per 1% increase in canopy cover and decreased about 1.8% per 1% increase in hillshade. Results of this model also suggest that the probability of red squirrel midden site selection is maximized when plots contained 43.6 percent WBP (Figure 1). Results from the Moran's I test provided no evidence of spatial auto-correlation in the residuals (p-value = 0.69). Even though the estimated correlation between bin mid points and proportion of used locations in 10-fold cross validation was 0.93 and the R^2 of the regression was 0.98, the confidence intervals for the intercept and coefficient did not contain zero (95% C.I. = -0.06, -0.01) and one (95% C.I. = 1.25, 1.57) respectively (Figure 2). When the regression was repeated excluding the bins associated with locations of the 20% highest probability of use (points A and B of Figure 2) the intercept and coefficient were not different than zero (95% C.I. = -0.03, 0.01) and one (95% C.I. = 0.33, 1.07) respectively. These results

indicate that the model was good at predicting red squirrel midden site selection in areas of 80 percent lowest use, but it overestimated the probability of selection in areas of 20 percent highest use. The conditional modes of the random effects for transects (Figure 3) indicate there is relatively high variability in probability of use for the different transects, mainly for the transects ML1 and ML2. The odds of selecting a midden site was 32 times higher in ML1 and 7.6 times higher in ML2 than the estimated average (Figure 3). These results indicate that there could be factors associated with transects that were not accounted for in our analysis.

Table 5. Results from the Akaike Information Criterion (AIC) model selection of red squirrel midden site selection candidate models. Models are ranked from the most parsimonious (M3) to the least parsimonious (M0).

Model	d.f.	AIC	delta AIC	AIC weight
M3 = Slope + Hillshade + Canopy cover + Percent of WBP + Percent of WBP ²	7	497.59	0.00	0.86
M1 = Slope + Hillshade + Canopy cover	5	501.90	4.32	0.10
M2 = Slope + Hillshade + Canopy cover + Percent of WBP	6	503.81	6.23	0.04
M0 = Intercept only	2	519.10	21.51	0.00

Table 6. Results from the most parsimonious model (M3) for red squirrel midden site selection in the Cooke City Basin Montana.

Variable	Estimate	Std. Error	Exp. Estimate	Exp. Lower	Exp. Upper
(Intercept)	-2.3136	0.808	0.099	0.031	0.317
Percent WBP	0.0416	0.015	1.043	1.020	1.066
Percent WBP ²	-0.0005	0.000	1.000	0.999	1.000
Slope	-0.0216	0.018	0.979*	0.954	1.004
Hillshade	-0.0178	0.009	0.982*	0.970	0.995
Canopy cover	0.0196	0.005	1.020*	1.012	1.028

* These coefficients can be interpreted as the multiplicative effect for one unit change in the explanatory variable on the odds of midden site selection. The exponential estimate of 1.02 for canopy cover, for example, suggests that the odds of selection increased 2% for an increase of 1% in canopy cover.

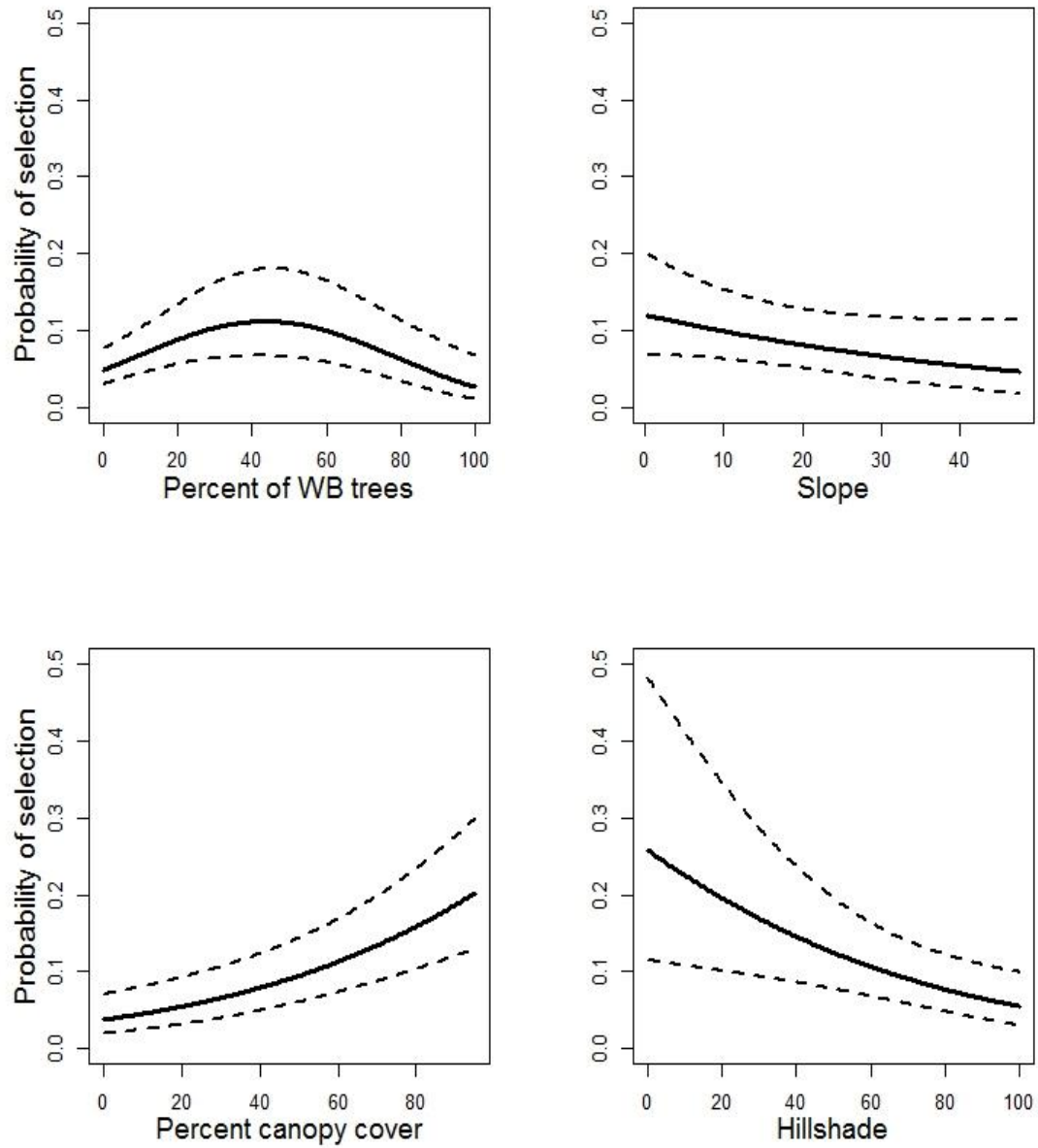


Figure 1. Estimated effect of the percent WBP trees in a plot, slope, percent canopy cover, and hillshade on probability of red squirrel midden site selection in the Cooke City Basin, MT.

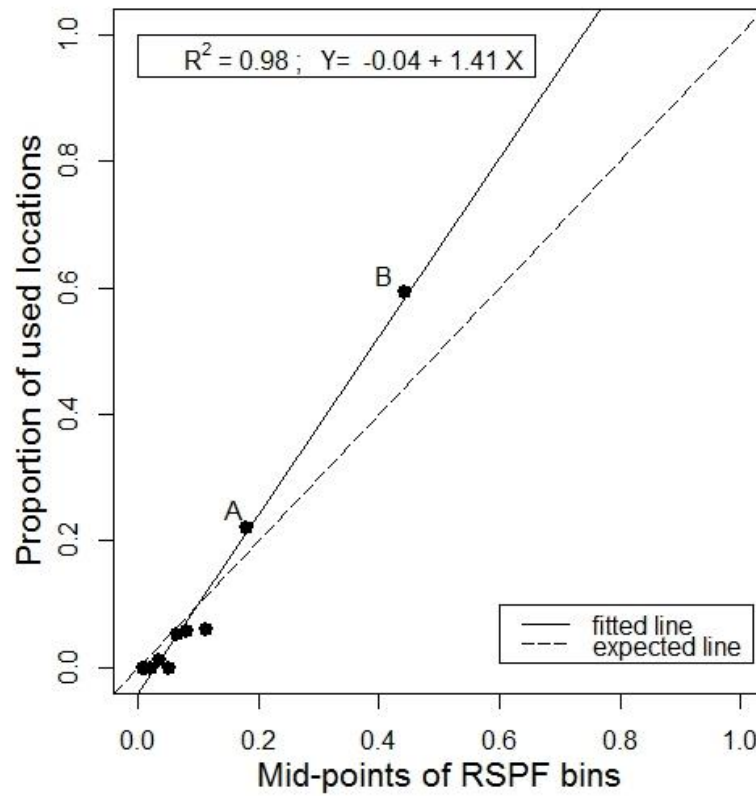


Figure 2. Mid-points of RSPF prediction bins plotted against proportion of used locations with fitted regression line and expected regression line. Models with high predictive capability yields regression lines with intercept not different than zero and coefficient no different than one (expected line). The fitted regression line indicates good prediction for the areas of lowest 80% use (excluding points A and B).

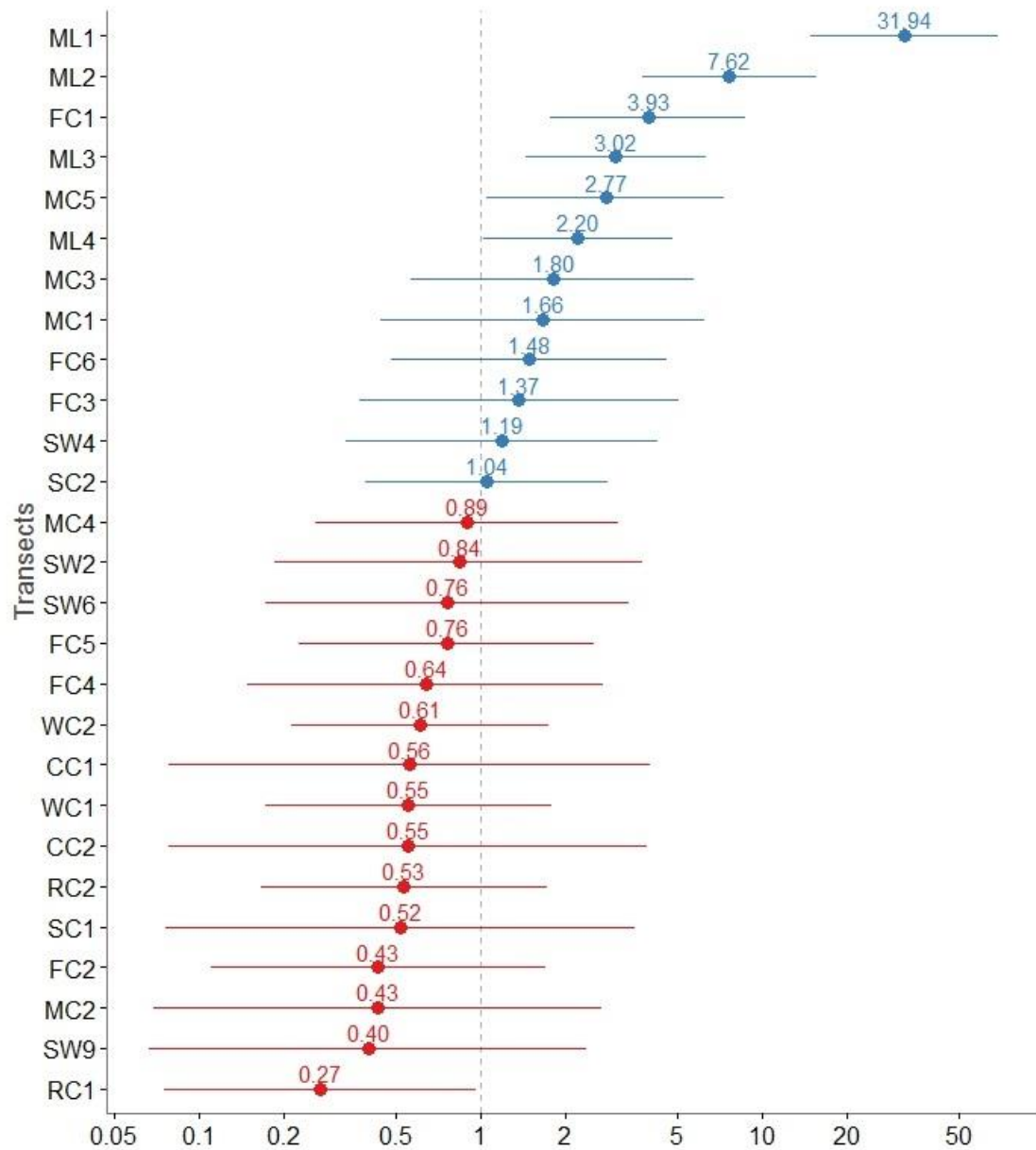


Figure 3. Exponentiated conditional modes (with 95% confidence bands) estimated for the transects of Cooke City Basin of Montana regarding midden site selection. The estimated values can be interpreted as the multiplicative effect on odd-ratios of red squirrel midden site selection. For example, the estimate of 1.66 for the transect MC1 suggests that the odds of a location having an active red-squirrel midden site in MC1 was 66% higher than the average.

Red Squirrel Midden Area

Results from the AIC model selection indicate M3 as the most parsimonious model for midden area (Table 7). In this model, the estimated coefficient for total canopy cover predicts an increase of about 33% in midden area for a 10% increment in canopy cover (Table 8, Figure 4). The estimated pseudo R^2 for this model was equal to 0.237 indicating that this model only explains 23% of the observed variability in the response. The conditional modes of the random effects for transects indicate there is moderate variability in midden area for the different transects (Figure 5). In addition to canopy cover, other factors not accounted for in the model are responsible for the observed variation. Results from the Moran's I test results showed no evidence of spatial autocorrelation in the residuals (p-value = 0.20).

Table 7. Results from the Akaike Information Criterion (AIC) model selection for red squirrel midden area. Models are ranked from the most parsimonious (M3) to the least parsimonious (M0).

Model	d.f.	AIC	delta AIC	AIC weight
M3 = Total cover	4	497.59	0.00	0.93
M0 = Intercept only	3	501.90	5.69	0.05
M1 = Slope + Hillshade	5	503.81	8.95	0.01
M2 = Total Basal Area SF + Total Basal Area WBP + Total Basal Area SF *				
Total Basal Area WBP	6	519.10	9.41	0.01

Table 8. Results from the most parsimonious model (M3) for red squirrel midden area in the Cooke City Basin Montana.

Variable	Estimate	Std. Error	Lower	Upper
(Intercept)	1.3343	0.503	0.610	2.058
Total cover	2.8706	1.005	1.424	4.318

* These coefficients can be interpreted as the increase in the log (midden area) for one unit (percent) change in the total cover.

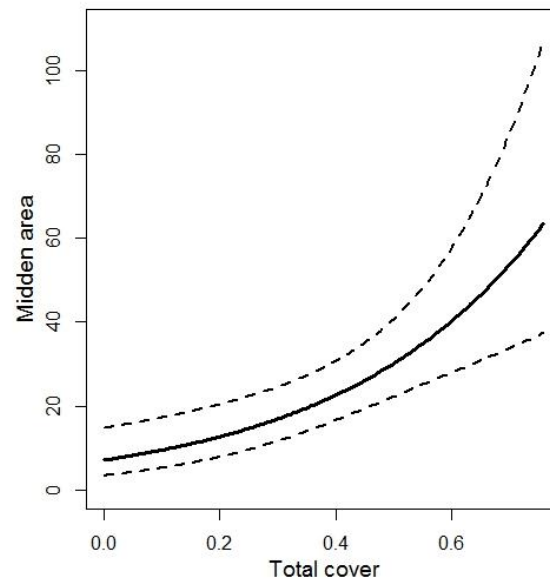


Figure 4: Estimated effect of total cover on total red squirrel midden area in the Cooke City Basin of Montana.

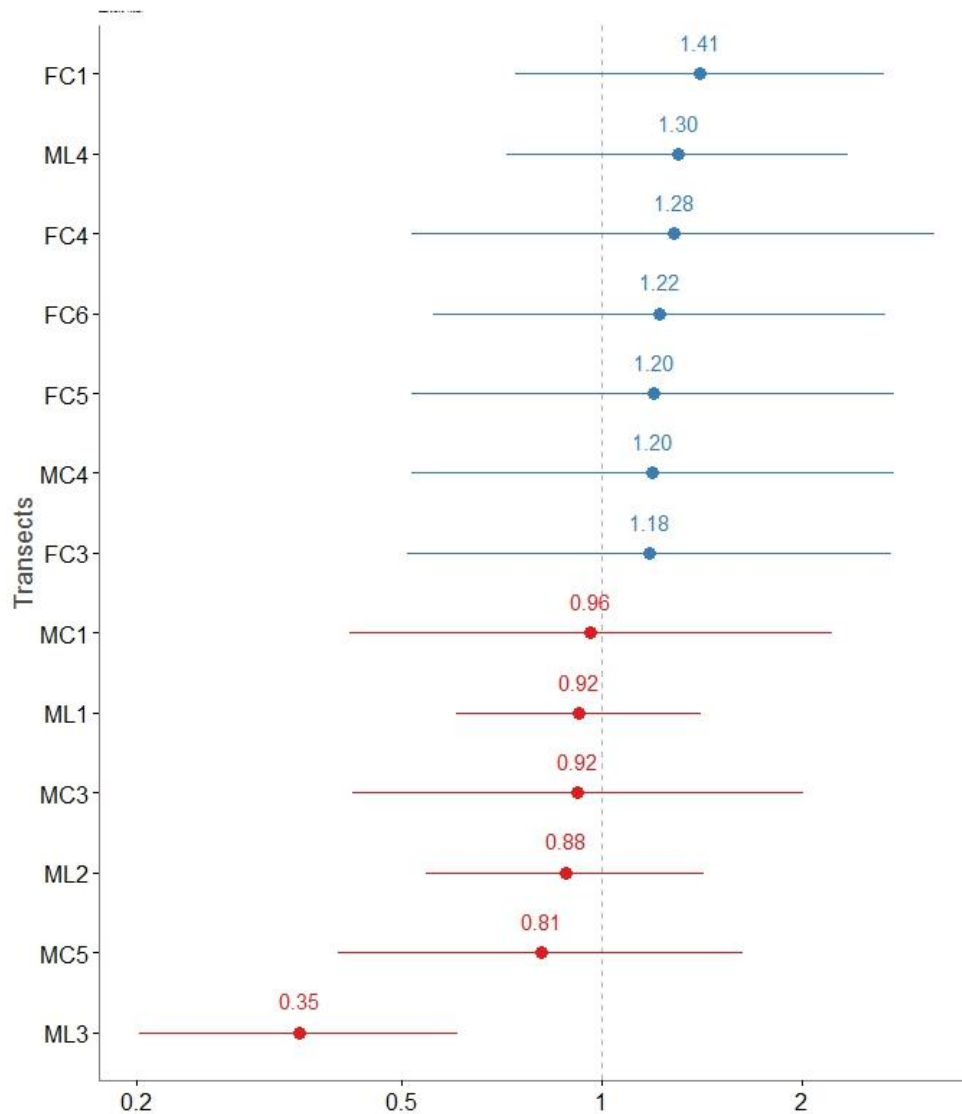


Figure 5. Exponentiated conditional modes (with 95% confidence bands) estimated for transects in the Cooke City Basin of Montana regarding midden area. The estimated values can be interpreted as the multiplicative effect on odd-ratios of red squirrel midden area.

DISCUSSION

Active middens are located in the center of red squirrel territories (Gurnell, 1984; McAdam et al., 2007) and indicate residency (McKinney and Fiedler, 2010). Therefore, they are very good indicators of red squirrel habitat selection. Conclusions about red squirrel habitat selection can be made by assessing forest structure and site specific variables associated with midden sites.

Results of our study support the hypothesis that red squirrel midden site selection is associated with the amount of hillshade, canopy cover, and WBP present in a conifer stand. The probability of an active midden site occurring increased as canopy cover increased but decreased as hillshade values increased. This suggests that cool, shaded areas with dense canopy cover are preferred red squirrel habitat. Conditions at these sites may be favorable for preserving cones stored within middens, providing greater protection from predators, and providing a more abundant conifer seed food source. The increased probability of an active midden occurring at a site as hillshade value decreased is supported by the findings of Finley (1969) who reported that middens require cool, moist conditions to keep stored cones from drying out, opening, and losing seeds. Previous studies also report that midden occurrence increases as canopy cover increases (Mattson and Jonkel, 1990; Zugenmeyer and Koprowski, 2009; McKinney and Fiedler, 2010). Red squirrels depend on cones stored within middens to survive winter, and shaded areas with high canopy cover may provide optimal cone storing conditions, maximize cone availability, and offer increased protection from overhead predators.

Midden occurrence probability was highly variable among transects which indicates that other factors not accounted for in our analysis may be responsible for the observed variations. While other factors may be at play, we suggest that variations observed may be due to the fact that middens did not always occur in plots along transects that the model predicted should contain middens. The explanation could be attributed to our study design. Our transects were oriented perpendicular to topographic contours to cover elevational gradients. This ensured that all forest compositions found throughout the CCB were represented among the 810, 30-meter diameter circular plots contained within transects, but we were restricted to surveying for middens in areas only contained within plots. Even though some plots that the model predicted should have middens were devoid of middens, it is possible that middens were present in adjacent areas surrounding our plots but were not accounted for in our sampling.

Furthermore, others have identified mixed conifer habitats with a diversity of conifer species as red squirrel preferred habitat (Mattson and Reinhart, 1990; Mattson and Reinhart, 1997; Mattson et al., 2001; Koprowski, 2005; McKinney and Fiedler, 2010). Our results similarly indicate that red squirrels preferentially selected habitats in mixed conifer forests to establish middens, and midden occurrence was maximized in mixed forests comprised of approximately 44 percent WBP and a 56 percent mix of subalpine fir and Engelmann spruce. We identified a quadratic relationship between midden occurrence and the percent WBP of overall conifer species composition in our plots. Probability of a midden occurring increased as the percent WBP in overall composition increased up to 44 percent but decreased after this threshold was surpassed.

These findings indicate that red squirrel habitat conditions become less hospitable as WBP abundance in stands increases above 44 percent. Similar conclusions were made by McKinney and Fiedler (2010) who indicated that red squirrel population residency tends to be low in WBP dominated stands (WBP comprises greater than 50% of total conifer species basal area) and high in mixed conifer forests with WBP comprising less than 50% of total conifer species basal area (McKinney and Fiedler, 2010). Mattson and Reinhart (1997) also concluded that red squirrels prefer mixed conifer habitats but indicated that midden occurrence was positively associated with lodgepole pine basal area. Our results differ from Mattson and Reinhart (1997) due to differences in subalpine zone conifer species compositions between our study areas. Lodgepole pine was most commonly associated with WBP at midden locations in the Mount Washburn study area of Mattson and Reinhart (1997), but lodgepole only occurred in 5 percent of our 104 midden locations in the CCB. The remaining 95 percent of our middens were established in mixed forests comprised only of subalpine fir, Engelmann spruce, and WBP. Even with our differences in findings of Mattson and Reinhart (1997), the concept that red squirrels prefer mixed conifer habitats is still justified.

Differences in habitat conditions between CCB mixed forests containing WBP and WBP dominate forests provide one possible explanation for the observed decrease in midden occurrence as WBP abundance increased above 44 percent in conifer stands. Whitebark is stress-tolerant and dominates the upper subalpine zone at (2743m to 2896m at treeline) where harsh conditions inhibit the growth of less tolerant, competing conifer species (Arno, 2001). As wind exposure and elevation increase, WBP pine dominance

increases (Mattson and Reinhart, 1994). Mature WBP stands grow in clumps, often described as tree islands, and are widely disconnected (Tomback et al., 2014) which greatly increases exposure to prevailing winds and provides less overhead protection for red squirrels. Alternatively, mixed forests containing WBP are located in the lower subalpine zone (2591m to 2743m) where conditions are not as harsh enabling less stress tolerant subalpine fir and Engelmann spruce to persist with WBP (Arno, 2001). Forests in this area are dense and highly connected (Pfister et al., 1977) providing red squirrels with greater protection from wind and overhead predators. As a result, middens were more likely to occur in mixed conifer forests containing WBP over WBP dominant forests in our study area. Our findings are supported by those of Mattson and Reinhart (1994) which indicate that a negative relationship exists between WBP dominance and red squirrel density.

Additionally, differences in seed energy content and annual cone crops among GYE conifer species may also explain why midden sites were primarily found in mixed forests containing WBP, subalpine fir, and Engelmann spruce. Red squirrels are strategic foragers and harvest cones from conifer species with the highest cone energy content first (Smith, 1968a; Smith, 1970). In the GYE, WBP seeds have the highest energy content (27.7 kcal per cone) of all conifer species present: Rocky Mountain subalpine fir, Engelmann spruce, lodgepole pine, and Douglas fir (Smith, 1970; Tomback, 1982). Subalpine fir yields the second highest cone energy content at 15.7 kcal per cone (Smith, 1970; Tomback, 1982) which is roughly half that of WBP. We observed an increase in midden occurrence as WBP abundance increased to 44 percent of overall composition in

conifer stands which suggests that red squirrels prefer to consume WBP seeds when available.

The decrease in midden occurrence as WBP increased above 44 percent may be explained by the inconsistency of WBP annual cone crops. Whitebark is a masting species and has variable annual yields of seed production with good and poor seed production alternating every two to three years (Costello et al., 2014). Subalpine fir and Engelmann spruce have more consistent annual cone crops than WBP (Boe, 1954), thus, providing red squirrels with a more stable food supply. In our study area, red squirrels maximized survival by establishing middens in mixed forests containing a slightly larger abundance of subalpine fir and Engelmann spruce than WBP to ensure that they would still have an adequate cone supply to survive winter even in years of WBP cone crop failure.

The number of cones stored in middens are positively correlated to midden area (Hurly and Lourie, 1997). We observed a positive relationship between midden area and conifer stand total canopy cover. Stands with high canopy cover likely provide red squirrels with more cones to harvest and store in middens than stands with low canopy cover, which may explain why midden area increased as canopy cover increased in our study area. Yet, we cannot conclude that total canopy cover was the only factor associated with midden area, because we observed variability in midden area among the transects. This indicates that there are other factors associated with midden area that were not accounted for in our study. It is possible that the observed variability in midden area can be attributed to midden age, or the amount of time a midden site has been

consistently used by red squirrels. Midden sites may be used by several successive generations of red squirrels. Finley (1969) suggests that large middens could be decades old with cone debris accumulations representative of use by many red squirrel generations. As a result, middens will only increase in area if they are consistently occupied by red squirrels for consecutive years. Therefore, in addition to canopy cover, it is probable that midden area is also positively associated with midden age in our study area.

Large middens can contain thousands of freshly cut cones each year (Finley, 1969) which can provide up to two years of cone resources for red squirrels (Gurnell, 1984). Consequently, red squirrels subject themselves to competition by storing such large quantities of a valuable food resource in one area. Red squirrels and grizzly bears directly compete for WBP seeds stored in middens, and the probability that a grizzly bear will raid a midden site is influenced by midden area (Mattson and Reinhart, 1997). Grizzly bears were observed to raid large middens more frequently than small middens, because they were able to excavate more cones from larger middens (Mattson and Reinhart, 1997). Additionally, probability of a grizzly bear excavating a midden is positively related to annual WBP cone crop size (Mattson and Reinhart, 1997). The high energy content of WBP seeds (Tomback, 1982) makes them highly preferred by both red squirrels and grizzly bears. In the GYE, threatened Yellowstone grizzly bears depend on WBP seeds as an important fall food source, and nearly all WBP seeds (>90 percent) they consume are obtained by raiding red squirrel middens (Mattson and Reinhart, 1994). Therefore, WBP zone conifer stands containing middens can be identified as prime

habitat for grizzly bears to obtain WBP seeds.

In conclusion, red squirrels in the GYE are critical intermediary agents that make WBP seeds available to threatened GYE grizzly bears by storing WBP cones in middens. Managing WBP for grizzly bears is enhanced by identifying which areas within mixed conifer forests are most likely to contain red squirrel middens. While previous studies indicate that red squirrels prefer to establish midden sites in mixed conifer forests (see above), no studies, to our knowledge, have identified an approximate conifer species composition within mixed forests that are optimal for midden sites. We have filled this critical gap in the literature by identifying that midden sites are most likely to be found in mixed forest conifer stands comprised approximately of a 44 percent WBP and 56 percent mixture of subalpine fir and Engelmann spruce. We conclude that areas within subalpine zone mixed forests in the CCB containing similar conifer species compositions should be protected to ensure that WBP seeds are available for grizzly bears.

MANAGEMENT IMPLICATIONS

In response to recent WBP population declines in the GYE, the Greater Yellowstone Coordinating Committee has published a strategy plan to ensure the long-term viability and function of WBP in the Greater Yellowstone Area (GYCC, 2011). The plan outlines specific goals including: 1) monitoring WBP condition, 2) protecting WBP from mountain pine beetle, blister rust, and fire through the use of verbenone, carbaryl, pruning, and fire suppression, 3) restoring WBP by planting blister rust resistant seedlings and implementing thinning and prescribed burns to remove competing conifers and create openings favorable for WBP regeneration, 4) Improving WBP by identifying potential blister rust resistant trees and propagating blister rust resistant seeds for planting. Although these strategies will benefit WBP, managers must consider how invasive techniques, specifically thinning and burning, will impact WBP seed availability for grizzly bears.

Subalpine zone mixed forests provide the most suitable habitat for red squirrels (McKinney and Fiedler, 2010) and are also key areas of WBP conservation. Managers are targeting areas of mixed conifer forests that contain WBP for thinning and prescribed burn management (GYCC, 2011). Thinning and burning mimic fire disturbance, and fire disturbance has been documented to negatively alter prime red squirrel habitat for middens, thus decreasing availability of WBP seeds for grizzly bears (Podrutzny et al., 1997). In addition, studies suggest that fire regimes in GYE WBP subalpine zones are operating within their historical range of variation (Meyer and Peirce, 2003; Whitlock et al., 2003) which may undermine the need for thinning and burning management to retain

WBP. At the least, such management prescriptions should consider WBP forests as an ecosystem-wide resource rather than focusing only on site-specific projects.

Therefore, we suggest that management in these mixed forests must be strategic and focus on areas less likely to contain red squirrel middens. Areas that contain middens should not be treated. Prior to our study, managers had not been presented with data that could help them identify specific areas within mixed forests where midden sites are most prevalent. Without this knowledge, managers risk impacting prime red squirrel habitat which will negatively impact grizzly bears.

Our study is the first to identify that the ideal conifer species composition for red squirrel middens is a mixture of approximately 44 percent WBP and 56 percent subalpine fir/Engelmann spruce. This finding can help managers identify areas most critical for grizzly bears to obtain WBP seeds which can be used to direct management in the CCB of Montana and similar environments. Managers could use our study as a model to identify areas in WBP forests with these characteristics and proactively protect them. They should avoid thinning and burning in areas of subalpine mixed conifer forests that contain similar compositions in the CCB, because protecting these areas will help ensure grizzly bears have access to WBP seeds in middens.

However, we recommend caution when developing management strategies based on our findings for areas outside of the CCB, because the conifer composition we identified as optimal for red squirrel midden sites was based on conifer counts rather than basal area which is the more common approach. Conifer species compositions derived from these two methods will differ because basal area compositions account for the

overall area occupied by each species relative to the overall area occupied by all conifer species in a stand, while tree count compositions only account for the proportion of each species relative to the overall number of trees in a stand.

Our study could be used as a model for conducting research in other subalpine zones containing WBP. If future studies in subalpine zones outside of the CCB also identify a composition ideal for midden sites similar to the composition presented in our study, managers can use our results to help direct WBP thinning and burning management in other forests.

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