American red squirrel (*Tamiasciurus hudsonicus*) abundance in spruce beetle-infested forests of Colorado

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Dedication

I dedicate this thesis to Julia Hicks, for without her mentorship throughout this research process, this thesis could not have been possible.

Abstract

My thesis project investigates how spruce bark beetle (*Dendroctonous rufipennis* Kirby) outbreaks in southern Colorado's coniferous forests are causing behavioral changes in the American red squirrel (*Tamiasciurus hudsonicus*), and how this could affect red squirrel and neighboring avian populations. This research uncovers how spruce bark beetle outbreaks are increasing individual tree mortality within spruce-fir forests of southern Colorado, leading to a decline in overall forest stand health. By analyzing individual tree statuses within vegetation plots, and conducting point-counts for both American red squirrels and cavity-nesting bird species, this study indicates how increasing mortality rates in spruce-fir forests, due to beetle outbreak, are decreasing red squirrel populations, as well as altering cavity-nesting bird populations at varying scales.

Introduction

Coniferous forests in southern Colorado are experiencing severe structural changes due to a spruce bark beetle (*Dendroctonous rufipennis* Kirby) epidemic. The spruce beetle is a bark beetle that affects Engelmann and blue spruce (*Picea engelmanni* and *Picea pungens*), and it is known to erupt and cause massive forest die off (Jenkins et al. 2013). This beetle has infested more than 180,000 ha of Engelmann spruce forests throughout the intermountain regions of the US Forest Service (Jenkins et al. 2013), and has infested over 161,065 ha of spruce forests in Colorado, compared to mountain pine beetle (*Dendroctonus ponderosae*) outbreaks which have infested 39,656 ha of limber pine (*Pinus flexilis*), ponderosa pine (*Pinus ponderosa*), and lodgepole pine (*Pinus contorta*) forests within Colorado (Colorado et al. 2013). While mountain pine beetle outbreaks have been declining in Colorado since 2013 (Colorado et al. 2013), spruce beetle outbreaks are not, but instead are expected to increase (DeRose et al. 2013). With the recent rise of temperatures over the past decade due to climate change, spruce beetle outbreaks throughout the western United States have been steadily increasing, as too have beetle brood survival rates at higher altitudes (DeRose et al. 2013). With increasing temperatures at higher elevations, not only are spruce forests becoming more susceptible to beetle outbreaks across larger elevation ranges, but also decreases in winter cold spikes, which are known to kill beetle populations, have lead to higher rates of survival for beetle brood during winter months (DeRose et al. 2013). This is further promoting the successful development of beetle larvae into adults, increasing beetle populations in infested forests come spring and summer, leading to the further spread of spruce beetle outbreaks in coniferous forests. Because of this, conifer tree density is greatly decreasing, which is affecting those species, such as the American red squirrel (*Tamiasciurus hudsonicus*), that rely on conifer trees for population success. In addition to habitat alterations, the structural changes occurring in forests consisting predominately of Engelmann spruce and Subalpine fir (*Abies lasiocarpa*), brought on by spruce beetle outbreak, are influencing behavioral changes in many species. As beetle outbreaks increase and Engelmann spruce, as well as other conifer tree species, continue to decrease in density, the American red squirrel is being forced to adapt to extreme changes in its natural environment. The American Red squirrel is common to spruce-fir forests throughout the western United States and can play an important role in the dispersal of mycorrhiza-forming fungi spores, which benefit the reproduction of conifer trees (Sullivan et al. 1995), therefore it is important to study how red squirrel populations are being affected by beetle outbreaks found within their natural environment. Though the American red squirrel depends upon the cone crop of spruce trees for its main source of food, it has recently been documented feeding upon spruce bark beetle larvae in infested spruce forests of Canada’s Kluane region (Pretzlaw et al. 2006). This adaptation could not only affect red squirrel populations, but could also have an effect on neighboring species that experience red squirrel predation, particularly avian communities. Although evidence of this new behavior has been documented in Canada, there have been no further published accounts of this behavior, nor evidence of larvae predation by red squirrels in Colorado, or within the continental United States. Because of this and the lack of research concerning broad scale forest disturbances on mammalian communities, this thesis aims to answer the following research questions:

1) Are American red squirrel populations being affected by spruce bark beetle outbreaks in Engelmann spruce forests?

2) Are American red squirrels feeding on spruce beetle larvae, and does this affect squirrel population density?

3) Do fluctuations in squirrel density in beetle-infested and uninfested conifer forests have any effect on neighboring cavity-nesting bird populations?

This study will provide the scientific community and land managers with further insight into American red squirrel ecology within spruce beetle outbreaks. This study is needed in order to assess the impacts of broad-scale bark beetle outbreaks on other forest-dependent species.

Background

Spruce Beetle Ecology and Outbreaks

Adult spruce bark beetles measure at 4.4 to 7 mm long (Schmid et al. 1977), and are black to dark brown in color, with reddish brown to black colored wing covers (Forest et al. 2011). Their primary host trees within Colorado and the Rocky Mountains are the Engelmann spruce and the blue spruce (Forest et al. 2011), while instances of attack on lodgepole pine have been recorded when small pine stands or individual trees are intermixed with infested spruce-fir forests (Schmid et al. 1977). From May to early August is when the majority of spruce beetle attacks occur (Schmid et al. 1977), in which adult beetles burrow through the bark found at the base of spruce trees, in order to reach the inner phloem of the tree. Spruce beetles prefer attacking downed, matured spruce trees, but also attack the lower 30 ft of the trunk of matured standing spruce trees (Forest et al. 2011). The majority of major outbreaks that have occurred and or are occurring in the western United States started in forest stands that experienced either logging or severe blow down (Schmid et al. 1977). Once adult beetles burrow into the trunks of standing or downed spruce trees, females begin constructing egg galleries less than a week after initial attack by burrowing grooves through the tree's xylem, which are then used for storing the eggs (Schmid et al. 1977). Spruce beetle eggs, which measure from .75 to 1 mm, are oblong in shape and pearly white in color, and take 3 to 4 weeks before hatching into white, legless, cylindrical larvae, measuring 6 to 7 mm at maturity (Schmid et al. 1977). As the larvae feed upon the host tree's phloem, they slowly develop into pupa, and then into an adult beetle over the course of a 1 to 4 year life cycle, depending on the surrounding environment's temperature and conditions.

A 2-year life cycle is most common, in which beetles attack during the summer, eggs are laid, hatch and then develop throughout the fall, winter, spring, and into the following summer. Once the newly developed adults diapause and overwinter in their host tree through the second winter of the cycle, they begin emerging in late spring and early summer to fly and attack new spruce stands (Schmid et al. 1977). Depending on the temperature of the environment surrounding the tree in which the eggs were laid, egg to adult development can occur within 1 year of the eggs being laid, and or can take up to 3 or 4 years on rare occasions. Higher minimum temperatures occurring in lower elevations have been found to progress larvae development into adult beetles within 1 year, where larvae develop and overwinter as adults and emerge to attack come the following summer (Schmid et al. 1977). Although this is unlikely to occur in the Rocky Mountains, due to Engelmann spruce occurring above 8,000 ft, where colder temperatures are known to stunt such rapid development, current trends in rising temperatures could possibly affect life cycle development rates of spruce beetles found in the Rockies in the near future. While a 3-year cycle occurs rarely, they occur more often then 1-year cycles and are usually caused by outbreaks occurring in areas of high elevation within Colorado, where cold temperatures during summer months may stunt larvae development, causing beetles to emerge after 3 years of slow maturation (Schmid et al. 1977). Though proposals have been made for the possibility of 4-year life cycles occurring in extreme environmental conditions, evidence of larvae taking up to 4 years to fully develop into adult beetles has yet to be documented (Schmid et al. 1977). Once adult beetles emerge from hibernation and or development, they fly out to further attack host material found in the vicinity of their original host tree, or will attack either un-infested stands or un-infested downed spruce. Spruce beetles primarily attack spruce trees with a diameter at breast height (DBH) of 7 to 14 inches because of the tree's increased height, while attacking less often those with a DBH of less than 7 to 8 inches (Schmid et al. 1977). This means that in major outbreaks, the majority of mature spruce trees are killed off, while it is more likely that younger spruce trees will be less affected.

Compared to past outbreaks, which were limited in both range and severity due to colder climates in the northern regions of the United States and decreasing temperatures brought on by seasonal change, increasing temperatures initiated by climate change over the past decade have increased the overall severity of outbreaks. Though spruce forests at high elevations are known to be less susceptible to beetle attack due to low temperatures, rising temperatures throughout North American have begun increasing minimum temperatures in higher elevations, increasing the range in which spruce beetles can successfully establish outbreaks (DeRose et al. 2013). Not only occurring at high elevations, climate change and rising temperatures have been found to be factors in increasing spruce beetle outbreaks throughout the American west (Bentz et al. 2010), at many different elevations. Just as the survival of beetle populations in forests can be dependent on the intensity of cold temperatures during winter months, warm temperatures too have an effect on beetle success, increasing both survival and development rates (Bentz et al. 2010). With increasing temperatures, especially during summer months, it has been found that larvae are more likely to skip pre-pupil diapause, leading to the full development of spruce beetle larvae into adults within one full year, which can result in exponential growths in beetle populations (Bentz et al. 2010). Not only is larvae development more proficient in warmer climates, but warmer temperatures in high elevation conifer forests are leading to decreased rates in beetle larvae mortality during winter months, which further promotes drastic increases in emerging adult beetles come summer (DeRose et al. 2013). Increasing temperatures in Colorado, Utah, and Alaska have also led to increases in overall lifespan and flight time for adult spruce beetles (Bentz et al. 2010). As the elevation range of the beetle increases, due to increasing temperatures, more conifer forests will become susceptible to infestation, leading to larger and more severe outbreaks. With increases in overall longevity and development, as well as decreases in beetle mortality, increasing temperatures will ultimately lead to more beetle outbreaks in the coming decades, further impacting conifer tree density in the western United States.

Effects of Outbreak on Forest Structure

Although it seems that outbreaks could potentially regulate spruce tree density, allowing young spruce trees to establish new stands once mature spruce have been killed off, the killing of mature spruce allows for other species of tree and ground vegetation to encroach into the once infested region, creating further competition for young spruce and spruce seedling establishment (Schmid et al. 1977). This usually results in a shift of forest structure and vegetation composition. Once a massive outbreak within a spruce-fir forest has subsided and most of the mature spruce have been killed, the overall diameter at breast height (DBH) of the stand decreases, and if encroachment of herbaceous vegetation does not kill the spruce seedlings, it has been found that logging used to remove the dead, standing, mature spruce will (Schmid et al. 1977). Infested forests are also known to experience drastic changes in the forest structure after an outbreak, primarily due to the establishment of vegetation and tree species that were suppressed by mature spruce prior to outbreak. In the mid 1870s, in the White River National Forest of Colorado, 10-

25% of mature spruce trees were killed because of a spruce bark beetle outbreak, while 24-40% of mature spruce trees found in Grand Mesa, Colorado were also killed off (Schmid et al. 1977). Before the White River outbreak, the forest overstory consisted of 90% spruce and only 10% fir, but after the outbreak the overstory fluctuated to 80% fir and only 20% spruce. When the White River National Forest experienced another major beetle attack in the 1940s, there were substantially more fir trees with a DBH greater than 3 inches than there were spruce, and more fir seedlings were found compared to spruce seedlings (Schmid et al. 1977). Although fir outnumber spruce in forests after initial infestation, due to the spruce's low shade tolerant nature and longer life range compared to the fir's high shade tolerance and shorter life range, the young spruce were able to grow larger and live longer, allowing them to compete with surrounding fir seedlings (Schmid et al. 1977). Over time, this leads to spruce trees dominating the overstory, but immediately after outbreak, fir density is more likely to be higher than that of spruce.

American Red Squirrel

American red squirrel populations span across much of the United States, beginning in the conifer forests along the U.S/Canadian divide, down into the northern and northeastern United States, as well as into the Rocky and Appalachian Mountains (Saunders et al. 1988). The red squirrel can be found in most coniferous and mixed forests located in the western and southwestern parts of Colorado. The appearance of the red squirrel can vary based on the season. During summer months, red squirrels tend to have reddish to olive gray coats with black lines running down either side of their torso, and a creamy white underbelly (Saunders et al. 1988). During winter, their ears grow reddish brown tufts of hair, and their coats gain a bright red stripe down the center of their back, while their underbelly remains white and or turns into a shade of gray or silver (Saunders et al. 1988). Red squirrels also have a distinguishable white ring that encircles each eye. This species of squirrel can measure an average of 30 cm long (12 in), with its tail measuring around 1/3 the length of its entire body, and can weigh up to 240 g (8.4 oz), (Saunders et al. 1988) making the red squirrel one of the smallest tree dwelling squirrel species found in North America.

When in estrous, female red squirrels tend to copulate with many males before insemination is complete. Gestation for females can range from 36 to 40 days, in which the female will give birth to an average of 3 to 5 young per litter (Saunders et al. 1988), but red squirrel litters have been known to range from 1 to 8 young per litter. Females usually produce one litter annually during the months of April and August, but some produce one litter for each month. At birth, a young red squirrel emerges from its mother womb pink, blind, and naked, and they tend not to open their eyes until they have reached 27 days of age (Saunders et al. 1988). After day 30, young red squirrels are fully furred and begin both venturing from the nest, as well as weaning. Once they reach 9 to 11 weeks old, young squirrels will begin traveling in and around their natal territories in order to secure their own. Due to the extreme territorial nature of the red squirrel, each individual takes control of a single territory (Larsen et al. 1994). Red squirrel territories generally do not overlap one another, but instances of overlap occur only when a squirrel's territory overlaps its original natal territory. Juvenile mortality is at its highest during periods where red squirrels are leaving their natal territory in search for unclaimed patches of forest. If juvenile squirrels fail to settle in a territory of their own and or do not return to their natal territory, it is unlikely individuals will survive their first winter alone.

American red squirrels build nests on conifer tree branches, inside natural tree cavities, as well as in abandoned woodpecker nests. Each nest can range from 3 to 18 m above ground and can have a diameter of 20 to 50 cm (Saunders et al. 1988). Red squirrels have also been found to nest up to 30 cm underground (Saunders et al. 1988). When underground, these squirrels will build a maze of tunnels connecting various sized chambers. These chambers are typically used for shelter and or to store conifer seed caches. Red squirrels depend upon the seed caches, which they gather throughout the warmer months, in order to survive the winter, when conifer seed supply is at its lowest. Evidence of red squirrel activity can be determined by finding middens, or piles of cone debris and or winter food caches dropped by red squirrels over a period of weeks, months, and or years. Middens can measure from 10 to 20 m in diameter (Willson et al. 2003), and tend to be present in areas with high red squirrel activity. If large or tall middens are present, surrounding squirrel populations will dig out tunnels and chambers within the midden in order to store their seed caches for winter retrieval.

The majority of the red squirrel's diet consists of conifer seeds produced by trees such as the Engelmann spruce. Red squirrels climb through branches and scavenge the forest floor in search of conifer cones, which hold the seeds that represent the majority of the squirrel's caloric and nutritional intake. Along with conifer seeds, red squirrels have been known to consume many natural nuts, plant buds, tree cambium, fungi, as well as insects, small birds, and bird eggs (Saunders et al. 1988). These includes cavity nesting bird eggs, nestlings, and as of recent years, spruce bark beetle larvae.

Squirrels as Avian Predators

When instances arise where conifer seeds are low in density due to beetle outbreak, habitat disturbance, and or seasonal change, the red squirrel is forced to target other food sources in order to maintain its required caloric intake needed to survive. In past studies where conifer seed density was low, there have been recorded observations of red squirrels both attacking and consuming avian eggs and nestlings (Pretzlaw et al. 2006). In fact, the American red squirrel is known to be a major avian nest predator in coniferous and mixed forested regions. A study on avian nest predation by red squirrels in Arizona concluded that when spruce beetle outbreaks spread throughout conifer forests and decrease conifer seed and cone density, avian egg and nestling predation by red squirrels can increase (Zugmeyer et al. 2007). Though avian predation by squirrels can increase in regions experiencing severe beetle outbreaks, predation by this squirrel species can also be brought on by either lactation, where females require higher caloric intake when raising young, and or the overall opportunistic nature of the red squirrel (Zugmeyer et al. 2007). Red squirrels are an opportunistic mammalian species, meaning they will hunt and consume prey that will present them with substantial nutritional sustenance when and if conifer seed density is low, in order to support their daily energy expenditure.

Therefore, a red squirrel preying upon avian nests and small birds isn't a rare occurrence, but can be quite common. In fact, a study conducted in parts of southeastern Alaska, northern British Columbia, and the southern Yukon used artificial nests and clay eggs in order to determine to what extent avian nests are at risk of predation by American red squirrels (Willson et al. 2003). Red squirrels were observed searching for bird nests, and once found they would steal the artificial eggs and at times destroy the nest before departing. When nest predation occurs, squirrels will either steal the eggs, or break and eat them within the nest itself, while the parent birds are absent. Out of the 92 nest predators recorded throughout the three study sites, 88% of the predators were either male or female red squirrels (Willson et al. 2003). Squirrel density increased and was positively correlated in areas with high Sitka spruce (*Picea sitchensis*) density, while risk of nest predation increased as squirrel density did (Willson et al. 2003). This study also found that while nest density remained constant in areas with relatively similar red squirrel densities, sites that were absent of red squirrels contained higher avian nest densities

(Willson et al. 2003). This suggests that avian species seek out nesting regions that experience lower nest predation rates, resulting in higher nest success rates. This evidence shows how red squirrel populations can have an effect on avian density, and may even regulate bird populations to some degree.

When researching red squirrel predation on varying avian species, cavity-nesting bird species are prone to experiencing a great amount of nest predation by red squirrels. In some instances, nest success can depend on whether or not red squirrel predation occurs. A study conducted in Arizona, researching variations in nests and nest success in cavity-nesting bird species, found that the majority of failed nests were due to red squirrel predation, while observations were also noted of red squirrels leaving cavity-nests with bird young and or eggs (Li and Martin et al. 1991). Instances of nest failure due to predation were also primarily found in trees or snags in or located around large conifer trees (Li and Martin et al. 1991). Li and Martin found this to be due to the extensive activity of red squirrels in and around large conifer trees, leading to higher rates of predation by red squirrels on nests located closer to conifer trees. This supports the idea that red squirrels can largely affect nest success, species density, and the species diversity of cavity-nesting species found within regions with active squirrel populations. Because of the predator-prey relationship between red squirrels and cavity-nesting species, this study will focus on analyzing cavity-nesting bird abundance to see whether or not cavity-nesting avian species are being affected by squirrel populations found in both infested and un-infested conifer forests.

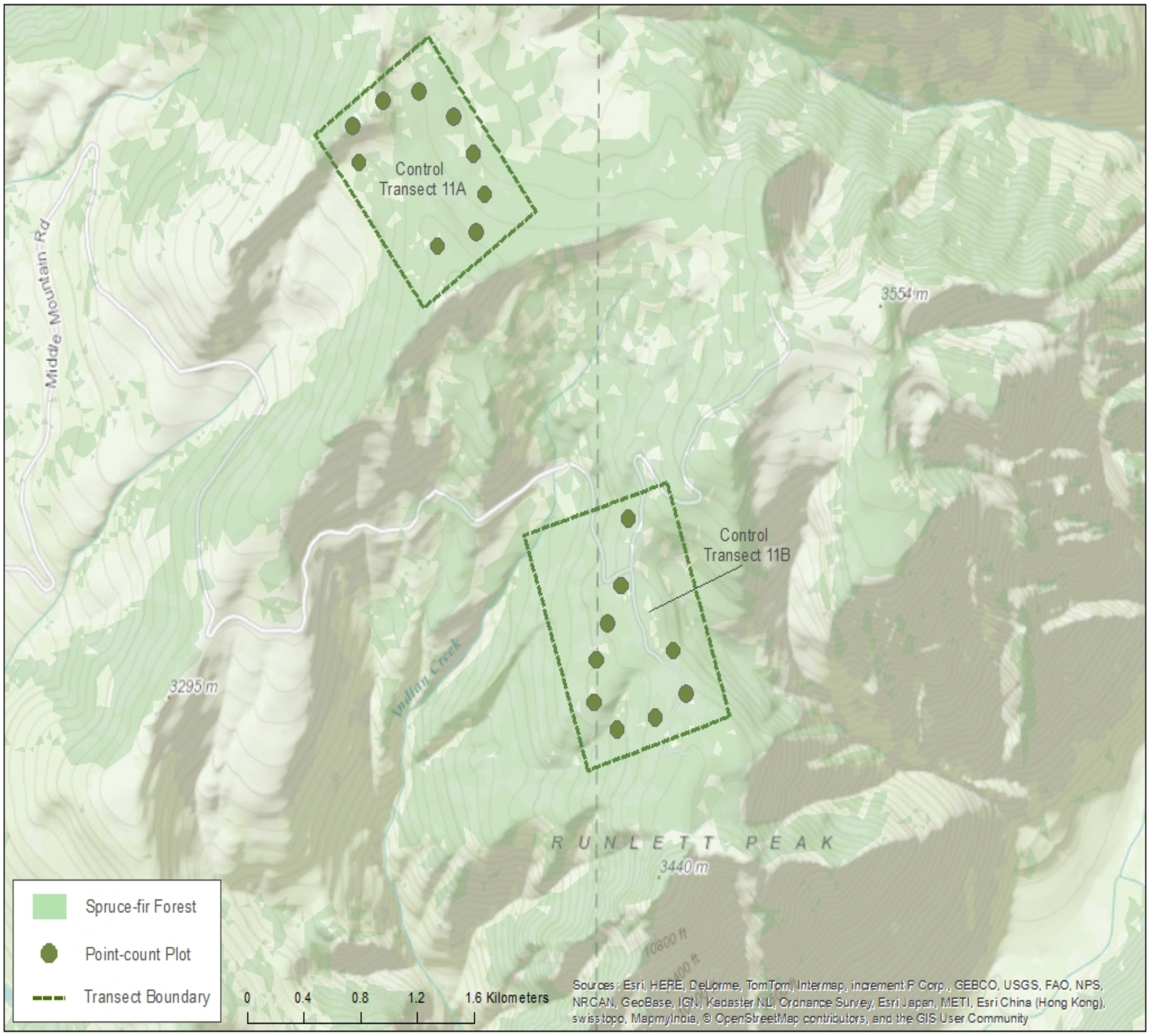
Behavioral Changes in Red Squirrels

While squirrels may regulate bird and nest density, spruce beetle outbreaks can and do promote fluctuations in squirrel density, depending on the severity of the outbreak in the specified region. This is primarily due to the high mortality of spruce trees when infested by spruce bark beetle. Large beetle outbreaks destroy most spruce trees found within infested stands, leaving little chance for red squirrel population success. Not only does decreased spruce density threaten red squirrel success rates, but spruce trees are unpredictable when it comes to seed crop produced each year (Gurnell et al. 1984), which means that infested spruce stands may also yield low seed density, leaving little for the squirrels to forage upon. Field studies in central-Alaska found that areas experiencing high spruce beetle severity tended to result in low red squirrel densities, compared to regions experiencing lower levels of beetle severity (Matsuoka et al. 2001).

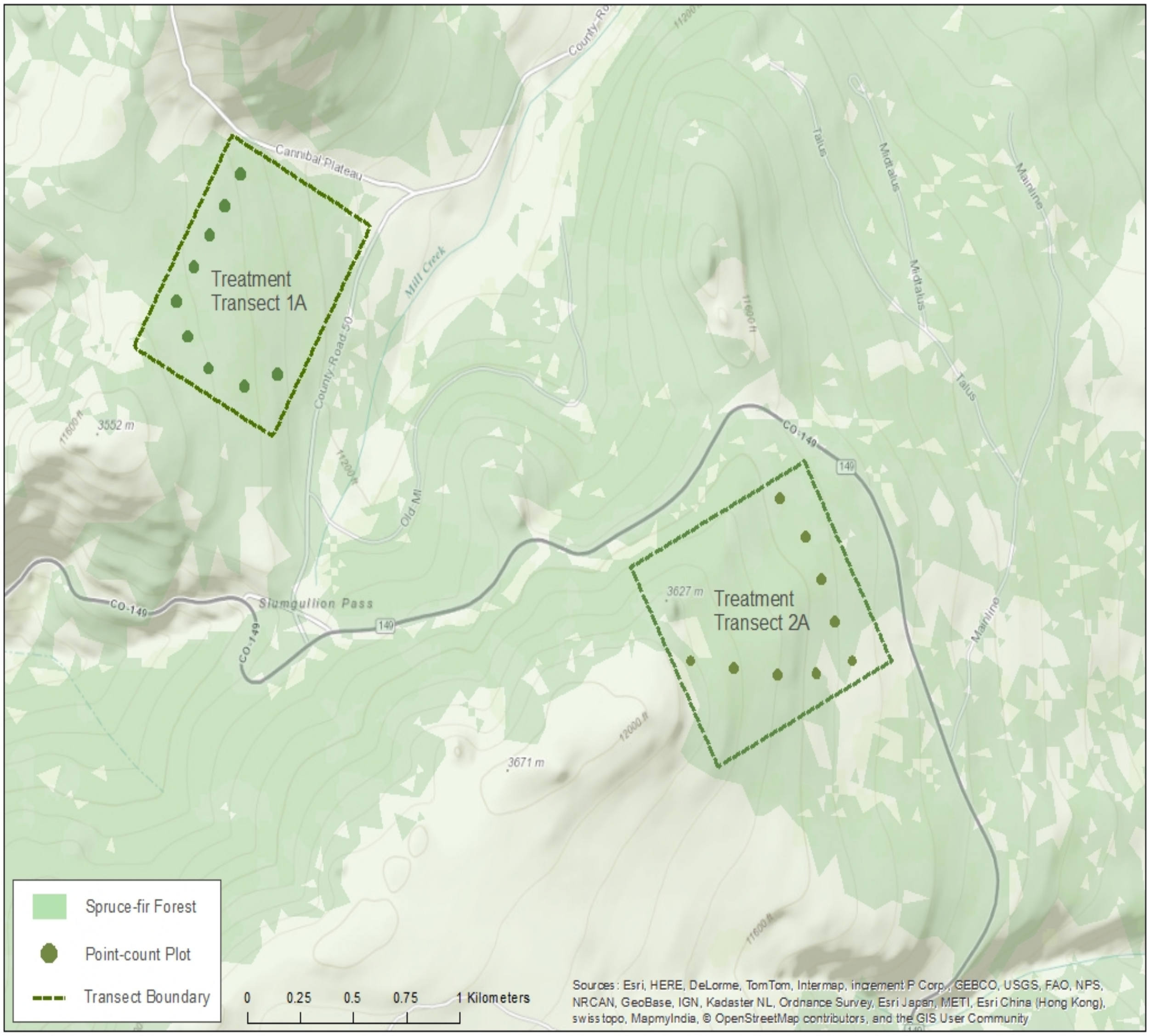
Although red squirrel populations are suffering from losses in spruce seed density, recent documentation has recorded the American red squirrel preying upon and consuming spruce bark beetle larvae in infested white spruce forests of Canada's Kluane region, found in the Yukon Territory (Pretzlaw et al. 2006). It is inferred that this behavioral change or adaptation in the red squirrel's diet is due to instances of low conifer seed density in regions experiencing spruce beetle outbreaks. Red squirrels were observed pealing sections of bark off of infested trees in order to locate and consume spruce beetle larvae (Pretzlaw et al. 2006). In this particular instance, the first onset of a spruce bark beetle outbreak began during the early 1990s, but beetle larvae predation by red squirrels did not begin in large quantities until 2002 to 2003. This extended period of time between the onset of the outbreak and the instances of beetle predation was most likely due to the increased severity of the effected forested region over time. The rapid increase of red squirrels consuming beetle larvae was said to be due to multiple years of low yielding conifer seed crops, leading to squirrels having to opt for other food sources. The initial occurrences of beetle larvae consumption could have been brought on by the red squirrel's cambium feeding behavior, in which the squirrels peel off the bark of conifer trees in order to gain access to the tree's cambium underneath (Pretzlaw et al. 2006). Although increased larvae predation may lead to sustaining red squirrel populations over short periods of time, spruce beetle larvae were found to yield significantly less nutritional value to red squirrels compared to the alternative food sources such as conifer seeds, avian nestlings, hare leverets, and other common food items (Pretzlaw et al. 2006). This means that future consumption of larvae by red squirrels may not lead to sustaining large squirrel populations in infested forests. These instances of beetle larvae predation by red squirrels has only been documented in Canada, and studies have yet to publish findings of the American red squirrel feeding on spruce beetle larvae within the United States. This gives little information as to whether American red squirrels are experiencing these behavioral adaptations in regions currently infested by beetle outbreak that are located within their species range, including Colorado.

STUDY AREAS

The spruce-fir forests sampled in this study are located within southwestern Colorado's subalpine zone, which measures between 9,000 to 12,000 ft in elevation, and consists predominately of Engelmann spruce, with small patches of subalpine fir (*Abies lasiocarpa*), aspen (*Populus tremuloides*), and lodgepole pine (Whipple et al. 1979). Two study areas were chosen for data collection. The first (treatment) site was located in an area of active, high-severity spruce beetle infestation, located in the spruce-fir forests surrounding Slumgullion Pass campground, north of Slumgullion Pass, within Gunnison National Forest. The second (control) site was located in an area southwest of Slumgullion Pass with no evidence of active spruce beetle. This site was located in spruce-fir forests northeast of Vallecito campground, within the San Juan National Forest. The climate of spruce-fir forests is primarily moist and cool, with the majority of precipitation originating from snowfall. Alongside tree litter, snags, and fallen tree remnants, the understory of these forests consists of wildflowers, herbs, and low-growing shrubs that benefit from the moist forest floor. In order to conduct this field research and to best answer the listed research questions, areas experiencing both high severity and low severity spruce beetle infestations were chosen to conduct said research. Many spruce-fir forests located in the San Juan Mountains of southern Colorado have been labeled as experiencing moderate to severe spruce beetle infestations since 2002, and more recent outbreaks have occurred in the forests near Lake City, Colorado (Colorado et al. 2012). For this reason, two treatment transects were placed within the spruce-fir forests of the Slumgullion Pass sample area, south of Lake City, Colorado. Spruce-fir forests surrounding Middle Mountain Rd., located northeast of Vallecito Reservoir and east of the historical mining town of Tuckerville, was recorded experiencing little to no beetle activity or outbreak, which is why two control transects for this study were set up in this sample area. The two control transects, located in the Tuckerville site, were labeled as transects 11A and 11B. The two treatment transects, located in Slumgullion, were labeled as transects 1A and 2A.



Map 1. Locations of "Tuckerville" control transects 11A and 11B with no evidence of spruce beetles, near Lake Vallecito, Colorado.



Map 2. Locations of treatment transects 1A and 2A, located within the spruce beetle-infested "Slumgullion" site, south of Lake City, Colorado.

METHODS

Site Selection

Study sites were selected using USGS and Forest Service data, as well as ArcGIS maps explaining spruce beetle activity in the specified regions. Research sites were also visually observed before transect marking and data collection began in order to confirm evidence of spruce bark beetle outbreak, or lack thereof. By selecting a region with high severity and one with no evidence of beetle infestation, changes in squirrel and avian population patterns would be attributed to either the beetle severity of the given region and or red squirrel predation. The following methods were used in conducting beetle severity measurements in conifer stands, red squirrel point-count recordings, and point-count recordings for avian species.

Spruce Beetle Severity

In order to measure densities of squirrel and avian populations based on spruce beetle severity, four transects, measuring 2 km^2 each in size, and consisting predominantly of Engelmann spruce, were selected based on evidence of spruce beetle infestation. Two of the four transects, located in the Tuckerville site, were labeled as control survey transects, which contained little to no spruce beetle outbreak. The other two treatment transects located in the Slumgullion site had high levels of spruce beetle activity. A recommended minimum of at least two replicate treatment transects were used in order to best observe the affects of beetle outbreak (Dudley et al. 2003) on both red squirrel and avian species. Five 20m x 20m vegetation plots were also placed within each of the four transects in order to measure the varying tree species found within each transect, as well as the state of health for individual trees found within each plot. Vegetation plots were spaced at least 250 m away from one another. Within these vegetation plots, each tree was measured for diameter at breast height (DBH), and was labeled based on its status. Individual trees were labeled with one of the following statuses:

- Li (Live) – live/healthy standing trees.
- Gr (Green) – recently infected trees with green needles. Signs of beetle pitch tubes and frass may or may not be present.
- Ye (Yellow) – trees with yellow needles, as well as evidence of frass (beetle excrement), and pitch tubes.

- Nd (Needle Drop) – trees that retain more than 50% of their needles, due to infestation.
- Tw (Twig) – trees having 1-hr twigs, with no needles, and are in the grey color stage.
- Br (Branch) – trees that have less than 50% of twigs or no twigs, and have no needles.
- De (Dead) – Dead tree not killed by SB for other tree species.
- Sn (Snag) – a snag greater than 1.3m in height and has no branches.

Beetle severity was also measured by observing the number of fallen and dead standing spruce trees infested by the spruce beetle, as well as the state of decomposition due to spruce beetle infestation in live standing trees. Observing the number of dead standing trees killed by beetle infestation was used to indicate tree stand mortality (Veblen et al. 1991). The state of infestation for each tree was determined by observing the presence of adult beetles or larvae under the bark (Matsuoka et al. 2001) and or a pitch tube count.

Measuring Red Squirrel and Avian Population Densities

In order to accurately record red squirrel and avian abundance, 9 point-count stations were evenly placed within each transect site. A total of 36 point-count stations were used for data collection throughout all four transect sites (18 treatment and 18 control stations). Each count station had a radius of 25 m, and no station measured within 75 m away from the edge of each selected survey site (Hutto et al. 1986, Hutto et al. 1995). Point-count stations were spaced 250 m apart (Hanni et al. 2013). Each point-count station was marked by a center point-count tree, which was then wrapped with three lines of flagging tape and labeled with the point-count's unique ID and a compass bearing leading to next point-count station. Paths leading from one point-count station to another were marked with either flagging tape or stake flags. Compass bearings were also recorded in order to reach each point-count station in case of losses of flagging occurred between survey repetitions. Data collection for each survey site took place from 04:30 h to 10:30 h. Point-counts for red squirrels and avian species were recorded at each station for 6 minutes, before moving on to the next station. Due to the amount of noise made by surveyors when traveling from one point-count station to another, 1 to 2 minutes of silence and preparation were used before beginning each 6-minute point-count survey. Within each 6-minute count, surveyors recorded all red squirrels and avian species aurally and visually detected (Matsuoka et al. 2001, Hanni et al. 2013). Squirrel counts were recorded based on sightings and or hearing red squirrel territorial calls in and around the point-count station. Avian counts were recorded based on sightings, drumming, and or hearing the calls and songs of individual species. Professional birders were hired to assist surveyors in accurate avian species counts and identification. Data was collected from one transect site a day, and all four transects were each surveyed three times during the breeding season between June 25 and July 14, 2014. Point-count stations, within each transect, were surveyed three times in order to record the maximum occupancy of red squirrels and cavity-nesting species for each individual station. We then added the maximum counts recorded for each plot, per transect, in order to calculate the total amount of squirrels and or cavity nesters detected within each transect. Maximum counts were used in order to calculate the overall abundance of squirrels and cavity-nesters within each transect. This technique assures that no individuals are missed, within each plot, during breeding season. A time span of at least 24 hours was used in between the 1st, 2nd, and 3rd surveys for each transect site.

RESULTS

American Red Squirrel Populations

Preliminary preparations and transect flagging began on June 10, 2014, and data collection was initiated on June 25, 2014. All transects were surveyed three times each, and data collection for all four transects was completed by July 14, 2014.

American Red Squirrel Counts		
Treatment		
Transect	Total Counts	Count %
1A	16	21.05%
2A	11	14.47%
Control		
11A	29	38.16%
11B	20	26.32%
Total	**76**	**100%**

Table 1. Red squirrel abundance in treatment and control transects.

A total of 76 American red squirrels were detected over the four transects surveyed. Out of the 76 red squirrels recorded, 49 squirrels were detected within the two control transects, whereas only 27 red squirrels were detected within the two treatment (i.e. spruce beetle infested) transects. By adding the maximum detected squirrels for each point-count station, out of all three surveys, the total amount of detected squirrels for each transect was calculated. For example, if within transect 1A, 3 squirrels were detected in the first survey for station 1, 2 squirrels were detected in the second survey for station 1, and 4 squirrels were detected in the third survey for station 1, only the count of 4 squirrels would be added to the other maximum detected counts for the other 8 stations within that transect, in order to calculate total squirrel abundance.

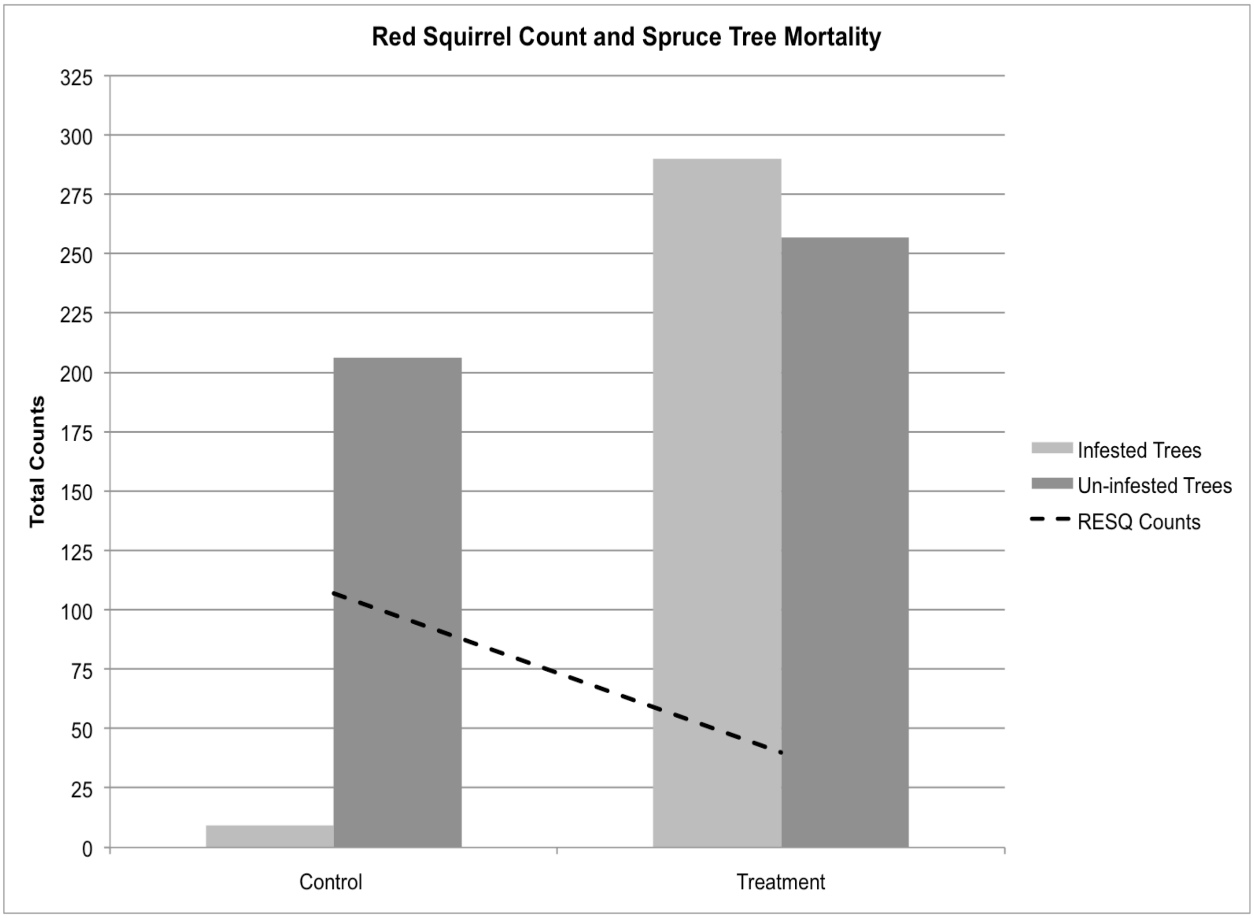


Figure 1. This figure compares the amount of infested and un-infested spruce found in the control and treatment transects, and depicts how red squirrel counts decrease as the number of infested spruce increase, creating a negative correlation between infested trees and squirrel counts. This negative correlation could be due to the decrease in seed availability accompanying increases in infected spruce trees.

By comparing total squirrel counts found in the control and treatment transects to the amount of infested and un-infested Engelmann spruce found within the control and treatment transects, we found a negative correlation between red squirrel counts and the number of infested Engelmann spruce. Red squirrel abundance was higher in the control transects and much lower in infested Engelmann spruce.

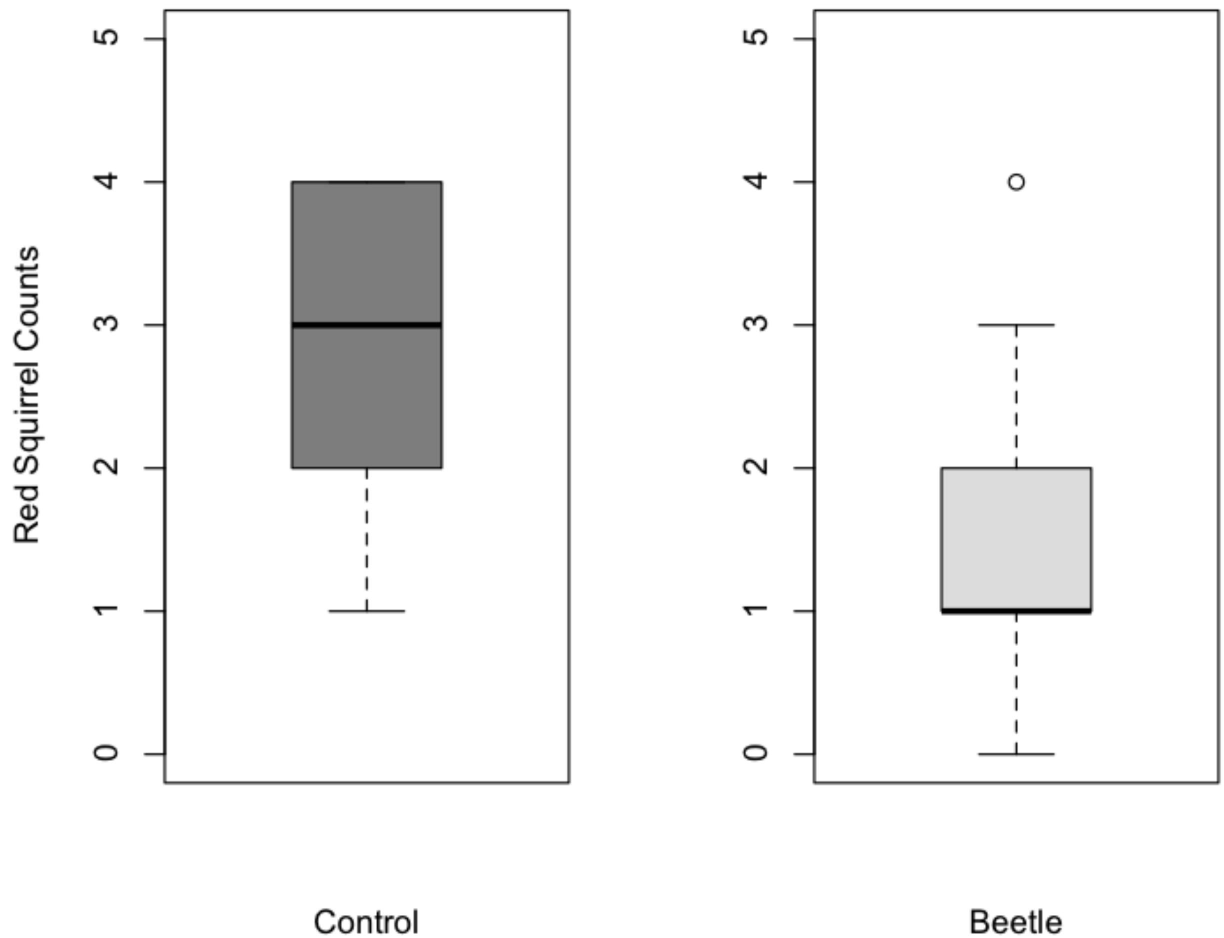


Figure 2. This box and whisker plot, produced through R programming software, was created to show the range in maximum occupancy counts found throughout all of the point-count plots within the treatment and control transects. Through this box plot, it is apparent that the 18 point-count plots found within the control transects had on average a higher maximum occupancy of red squirrels per plot, compared to the lower average maximum occupancy found throughout the treatment transect point-count plots. This shows how red squirrel abundance and activity is higher in spruce-fir stands that are not experiencing spruce beetle outbreak. The dashed whisker lines depict the maximum and minimum red squirrel counts detected throughout all of the point-count stations, the dark line within the boxes represent the median red squirrel counts for the control and treatment transects, and the boxes on either side of the median line represent the upper and lower ranges of recorded red squirrel counts. The circle depicted in the treatment box plot represents an outlier, or a count of 4 red squirrels detected at a single point-count station.

Using the R statistical computing environment (R Core Team 2013), we conducted a Welch two sample t-test to determine whether or not red squirrel abundance was significantly different between the control and treatment sites. The abundance of red squirrels in the infested site was significantly lower than abundance in the control sites (p = 0.001855). Thus, there is a probability of .001855 that squirrel populations will increase in spruce-fir forests experiencing spruce bark beetle mortality. Because of this *p*-value we rejected the null hypothesis that squirrel abundance is higher in treatment transects. Therefore, it was more likely that within infested spruce-fir forest stands, compared to un-infested spruce-fir stands, squirrel abundance would have been significantly lower.

Cavity-Nesting Bird Species

After analyzing the avian count data, it was found that the control transects contained the largest species diversity with 36 different species of birds detected throughout the three surveys. Within the treatment transects, a total of 29 different species were detected over the course of all three surveys. Out of all the avian species detected in the control and treatment transects, only two cavity-nesting bird species were detected having significant numbers in both the treatment and control transects, which were the American three-toed woodpecker (*Picoides dorsalis*) and the mountain chickadee (*Poecile gambeli)*.

Cavity-nesting Bird Counts				
Transects	American three-toed woodpecker (ATTW)	ATTW Percentage	Mountain chickadee (MOCH)	MOCH Percentage
1A	31	42.47%	14	28%
2A	20	27.39%	11	22%
11A	6	8.22%	13	26%
11B	16	21.92%	12	24%
Total	73	100.00%	50	100.00%

Table 2. Abundance of two cavity nesters within treatment and control sites.

Cavity-nester counts showed that American three-toed woodpeckers were more abundant in infested spruce-fir stands, compared to mountain chickadee, but chickadee abundance was higher than American three-toed abundance in the control transects. American three-toed woodpeckers were more abundant in the treatment transects than they were in the control transects, but mountain chickadee abundance did not significantly change between the control and treatment transects.

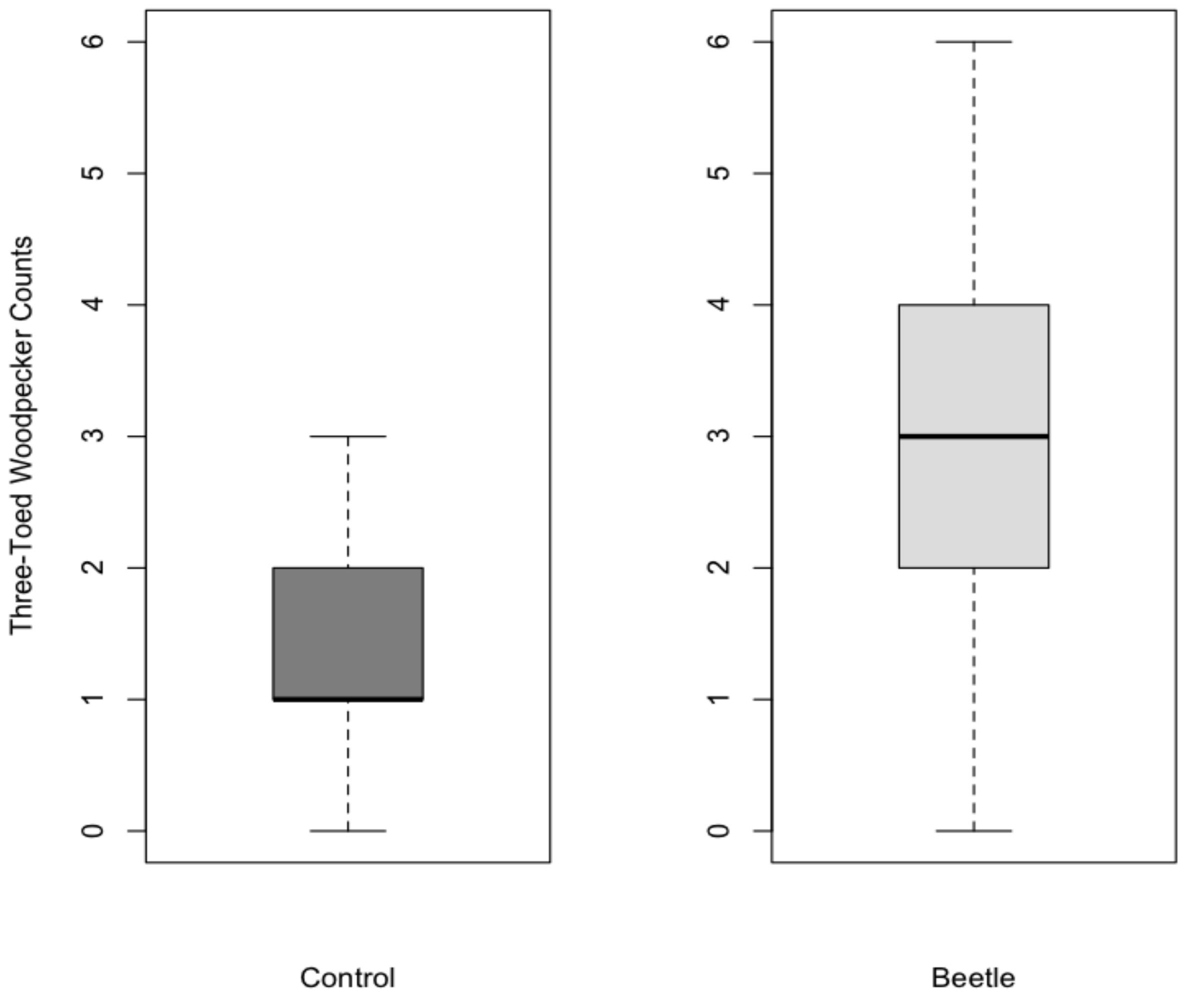


Figure 3. This box plot, produced through R programming software, was created to show the range in maximum occupancy counts for the American Three-toed woodpecker found throughout all of the point-count plots within the treatment and control transects. Through this box plot, it is apparent that the 18 point-count plots found within the treatment transects had on average a higher maximum occupancy of Three-toed woodpeckers per plot, compared to the lower average maximum occupancy found throughout the control transect point-count plots. This shows how woodpecker abundance and activity is higher in spruce-fir stands that are experiencing beetle outbreak, most likely due to the inclusion of larvae in the diet of this species of woodpecker. The dashed whisker lines depict the maximum and minimum American three-tied woodpecker counts detected throughout all of the point-count stations, the dark line within the boxes represent the median woodpecker counts for the control and treatment transects, and the

boxes on either side of the median line represent the upper and lower ranges of recorded woodpecker counts.

A Welch Two Sample t-test was then performed in R programming software, using the American three-toed woodpecker's maximum occupancy counts in control and treatment transects. The t-test produced a *p*-value of 0.0003026. This indicates that there is a probability of .0003026 that the null hypothesis of woodpecker counts being higher in the control transects would have been true. Due to the fact that this *p*-value is below 0.05, we rejected this null hypothesis, which indicated that it was more likely for American three-toed woodpecker abundance to be higher in beetle infested stands compared to un-infested sands. Because there was little variability between mountain chickadee counts in the control and treatment transects, a t-test was not performed for this cavity-nesting species.

Vegetation Plots

After collecting data from all 20 vegetation plots, it was found that the two primary tree species found in both the treatment and control transects were the Engelmann spruce and the subalpine fir. Within this study, Engelmann spruce were labeled with the vegetation code PIEN, and subalpine fir were labeled with the code ABLA. A total of 720 Engelmann spruce and 65 subalpine fir trees were recorded across all 20 vegetation plots, indicating that the four transects used for this study consisted predominantly of Engelmann spruce. A total of 50 subalpine fir and 181 Engelmann spruce were recorded in the 10 vegetation plots located within the two control transects, while only 15 subalpine fir and 539 Engelmann spruce were found in the 10 vegetation plots located within the two treatment transects (Table 3).

Tree Species Counts				
Site	ABLA	ABLA %	PIEN	PIEN %
Control	50	21.6%	181	78.4%
Treatment	15	0.03%	539	97.3%

Table 3. The total number and percentage of subalpine fir (ABLA) and Engelmann Spruce (PIEN) found in each site.

Within the treatment and control transects, in order to analyze how spruce beetle outbreak affected the overall health of spruce-fir stands, the status of each tree was recorded. Status codes were; Li (Live) – live/healthy standing trees, Gr (Green) – recently infected trees with green needles, signs of beetle pitchtubes and frass may or may not be present, Ye (Yellow) – trees with yellow needles, as well as evidence of frass (beetle excrement), and beetle pitchtubes, Nd (Needle Drop) – trees that retain more than 50% of their needles, due to infestation, Tw (Twig) – trees having 1-hr twigs, with no needles, and are in the grey color stage, Br (Branch) – trees that have less than 50% of twigs or no twigs, and have no needles, De (Dead) – Dead tree not killed by SB for other tree species, Sn (Snag) – an snag greater than 1.3 m in height and has no branches (Fig. 1 and 2, Table 4 and 5.)

Control Tree Status Counts								
Species	Live	Branch	Needle	Green	Yellow	Twig	Dead	Snag
ABLA	42	1	1	0	0	1	0	1
PIEN	156	7	0	0	3	12	0	2

Table 4. Total counts for each status category within control plots for subalpine fir and Engelmann spruce.

Treatment Tree Status Counts								
Species	Live	Branch	Needle	Green	Yellow	Twig	Dead	Snag
ABLA	14	1	0	0	0	0	0	0
PIEN	165	43	24	46	116	107	26	12

Table 5. Total counts for each status category within treatment plots for subalpine fir and Engelmann spruce.

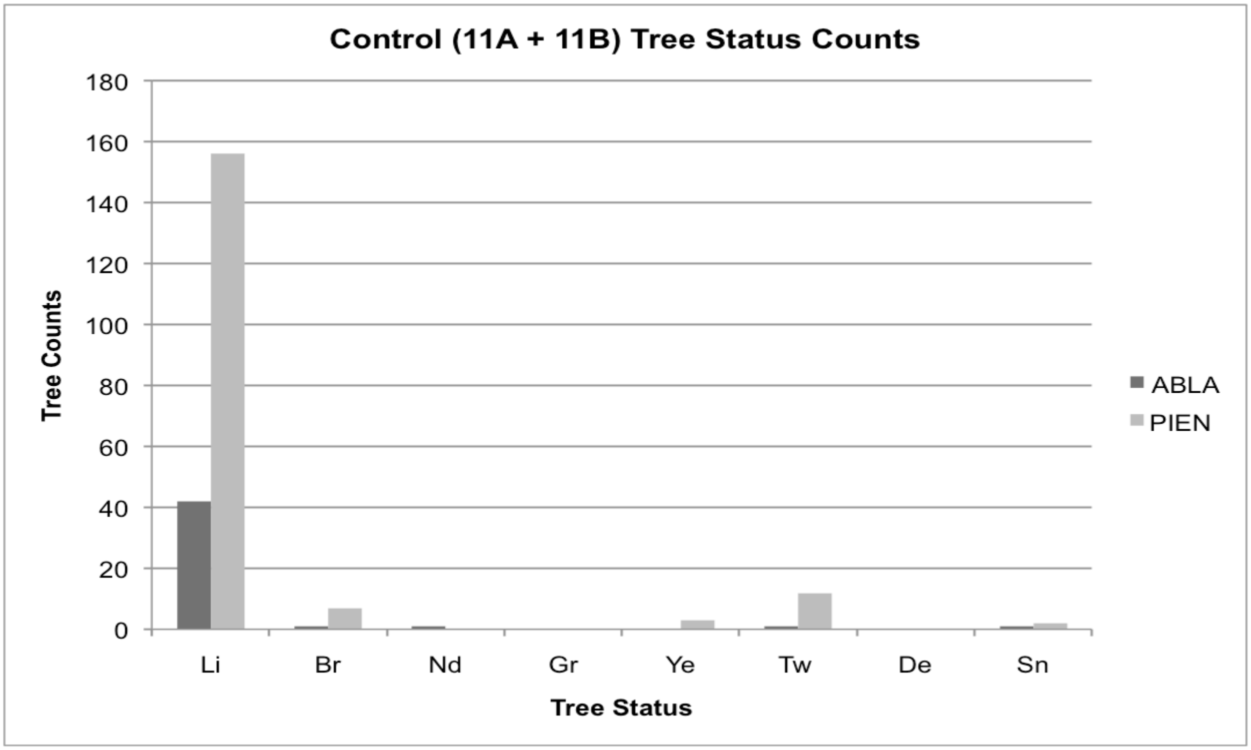


Figure 4. The number of trees counted in each status category within all control plots. Subalpine fir (ABLA) is shown in dark gray, and Engelmann Spruce (PIEN) is shown in light gray.

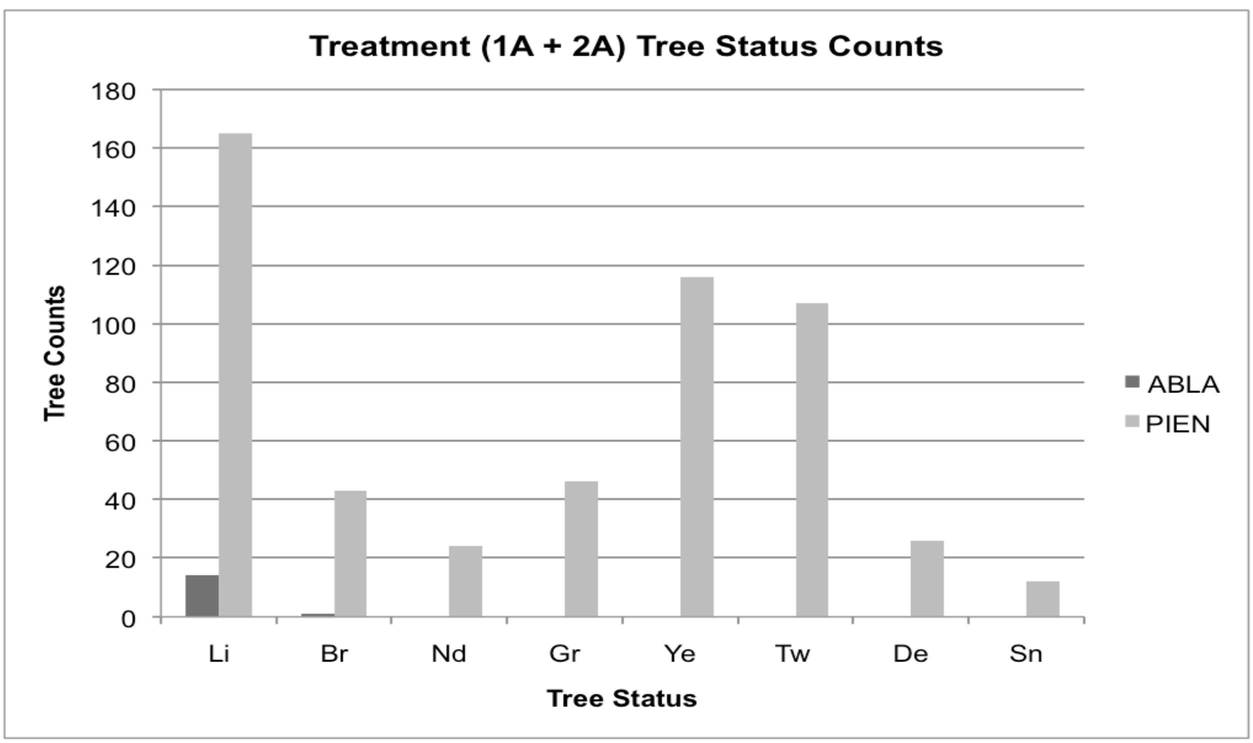


Figure 5. The number of trees counted in each status category within all treatment plots. Subalpine fir (ABLA) is shown in dark gray, and Engelmann Spruce (PIEN) is shown in light gray.

From the data tables and figures above, it is evident that within the treatment transects, the majority of Engelmann spruce were infested with beetles (Fig. 2), compared to control transects where very few trees were beetle infested (Fig 1.). Control transects had a similar number of live spruce as the treatment transects due to the high density of small diameter spruce in the treatment plots. Though the control transects had lower spruce tree density, the stand and the trees within it were healthier than those located within infested stands. Since the spruce beetle outbreak spanned such a large area in southern Colorado, it was impossible to find an un-infested control site close to the treatment site, with similar forest densities. Because of both the time constraints of this study and the inability to find an un-infested spruce-fir forest stand that matched in density to that of the infested sample area, this study is mainly comparing the presence of additional dead trees caused by spruce beetle outbreaks.

Spruce Mortality		
Site	Infested	Un-infested
Control	9	172
Treatment	288	251

Table 6. Amount of infested and un-infested Engelmann spruce found in control and treatment transects across all beetle status categories.

The vegetation plots within the control transects had very few instances of infested spruce out of the 181 trees recorded (Table 6). Comparing this to the treatment transects, which had a total of 539 recorded Engelmann spruce, of which more than half of those trees were seen experiencing varying stages of spruce beetle mortality. Instances of infestation for spruce varied from those trees that had been recently infested, to those trees that had been initially infested years prior to the survey, of which were experiencing the final stages of mortality before the death of the tree.

Table	Avg. ABLA D.B.H (cm)	Avg. PIEN D.B.H (cm)	% Live PIEN	% Beetle Infested PIEN	Total # of RESQ	Total # of MOCH	Total # of ATTW
Control	12.99	25.31	72.56%	0.04%	49	25	22
Treatment	11.27	17.58	30.16%	53.02%	27	25	51

Table 7. This table depicts the overall average DBH (measured in cm), for both tree species found within the treatment and control transects. It depicts the percentage of live and infested Engelmann spruce found in the control and treatment transects, as well as displaying the total counts for red squirrels, mountain chickadees, and American three-toed woodpeckers recorded within the control and treatment transects.

Count data for both cavity-nesting species and red squirrels was then compiled alongside the average DBH measurements for Engelmann spruce and subalpine fir, as well as the percentages of infested Engelmann spruce found in the control and treatment transects (Table 7.). This was done to better visualize possible correlations between avian counts and squirrel counts, as well as correlations between squirrel counts and tree DBH, and or squirrel counts and infested Engelmann spruce percentages for the control and treatment transects. American three-toed woodpecker counts positively correlated with increases in infested Engelmann spruce found in the treatment transects, while the counts negatively correlated with increasing percentages of live spruce in the control transects. American three-toed woodpecker counts also negatively correlated with increasing red squirrel counts in the two control transects, while red squirrel abundance positively correlated with the higher average DBH of Engelmann spruce found in the two control transects. Also, it is important to note the decrease in average DBH for Engelmann spruce from the control transects to the treatment transects. This is due to the beetles attacking more mature Engelmann spruce, while leaving the younger spruce with smaller DBH un-infested.

DISCUSSION

Red squirrel abundance was found to be higher in the control transects, of which had only a few instances of spruce beetle infestation found in Engelmann spruce. This means that increasing mortality rates found in Engelmann spruce within the treatment transects, brought on by beetle outbreak, leads to less suitable habitat for squirrel populations. This is most likely due to the decrease in overall conifer seed and cone crops produced by infested spruce (Pretzlaw et al. 2006). Due to the American red squirrel's reliance on conifer seeds for its primary source of nutritional intake, decreasing seed availability negatively affects squirrel populations inhabiting infested spruce-fir forests. Low conifer seed density will also push red squirrels into becoming more competitive with other individuals, which over time will increase either red squirrel mortality, and or increase squirrel migration rates out of the infested stand, further decreasing squirrel abundance within the outbreak region. Not only are decreasing seed crops in infested spruce-fir forests negatively affecting the caloric intake of the red squirrel, of which conifer seeds are vital in replenishing energy expenditures when foraging, but low cone and seed availability will further hinder winter food caches of the red squirrel. If competition for seeds during warmer months is higher among squirrels in stands experiencing outbreak, winter cone supply will be low, resulting an increase in red squirrel mortality during winter months. Due to adult and juvenile reliance on winter food caches for survival, especially during periods of snowfall where food sources are not accessible, deaths during winter will most likely increase, resulting in lower red squirrel abundance over time. Red squirrel abundance also positively correlated with the increasing average DBH of Engelmann spruce found within the control transects. This provides further evidence to past findings of red squirrel populations being more abundant and active in stands having larger and more mature Engelmann spruce (Li and Martin et al. 1991). This could possibly be due to the larger seed and cone crops produced by more mature spruce, compared to the smaller crops produced by smaller and younger spruce.

Low seed availability in infested conifer stands also pushes red squirrels to expand the range of food sources in which they have been known to consume. In past studies covering outbreaks in regions such as Canada's Yukon Territory, red squirrels have been seen feeding on spruce bark beetle larvae (Pretzlaw et al. 2006), but this behavior had not been documented within Colorado prior to this study. During this study, two instances were recorded of individual red squirrels pulling the bark off of infested Engelmann spruce in order to consume the larvae residing within the cambium of infested Engelmann spruce trees. These two occurrences are the first recorded instances of American red squirrels supplementing their diet with spruce bark beetle larvae. Although this proves that this new feeding behavior is prevalent within Colorado's spruce-fir forests experiencing outbreak, the fact that there were only two instances recorded of this behavior either means that this behavior is just now being introduced into this population of red squirrels, or that this behavior is being implemented by many red squirrels residing within the treatment transects, but the low nutritional value of spruce bark beetle larvae is not sustaining squirrel populations residing within the treatment transects. As found in past studies that documented this behavior, the consumption of larvae does not provide the red squirrel with equivalent caloric intake to that of the conifer seed (Pretzlaw et al. 2006). Over time, this will result in decreasing red squirrel populations in forests experiencing severe beetle outbreak and low conifer seed availability, which is likely to be equivalent to what is occurring to populations residing in the stands of the treatment transects.

Due to low seed availability and the inability of beetle larvae to support red squirrel populations, red squirrels in the treatment transects have to find more nutritional resources in order to replace their energy expenditures, such as cavity-nester eggs and nestlings. This could be a possible reason behind the negative correlation between American three-toed woodpecker counts and red squirrel counts in the control transects. American three-toed woodpecker counts were found to be lower in the control transects compared to the treatment transects, while red squirrel counts were higher in the control and lower in the treatment. Lower woodpecker abundance in the control could be due to the increase in nest predation rates by red squirrels, brought on by the increase in red squirrel abundance. Though the control transects would have higher conifer seed availability, which would support higher squirrel populations. The red squirrel is known for being an opportunist when it comes to preying upon and consuming nutritional food sources (Pretzlaw et al. 2006). Higher red squirrel abundance in the control transects could lead to higher rates of nest predation, ultimately resulting in lower woodpecker nest success rates, which would lead to a decrease in American three-toed woodpecker abundance within the control transects over time. This could also explain the higher American three-toed woodpecker counts found in the treatment transect. With lower red squirrel abundance in the treatment transects, nest predation by red squirrels would decrease, resulting in an increase in woodpecker nest success rates, leading to an increase in American three-toed woodpecker abundance. American three-toed woodpeckers are also known to feed upon spruce beetle larvae, which could also support larger populations of this woodpecker in spruce-fir forests experiencing spruce bark beetle outbreak, as seen in treatment transects 1A and 2A. Populations of American three-toed woodpeckers are known to increase during spruce beetle outbreaks (Hutchinson et al. 1951, Koplin et al. 1969). When speculating whether red squirrel abundance has any effect on mountain chickadee populations, it seems that they may not. Mountain chickadee counts were found to be the same in both the control and treatment transects, which leaves one to infer that neither the spruce beetle outbreak or red squirrel predation has any effect on mountain chickadee abundance. While conducting this study, no instances were recorded of red squirrels entering or exiting the nest of a cavity-nester, which means we can only speculate that the low abundance of American three-toed woodpeckers in the control transects can partially be attributed to red squirrel predation.

When referring to the differences in avian species diversity found in the control and treatment transects, this is most likely attributed to the differences in forest density, as well as the higher number of dead trees found in the treatment transects. The treatment transects were placed within a much denser forest stand, which can limit the amount of avian species that are more successful in open forest stands, such as that of the control transect. Also, the higher number of dead trees in the treatment transects, of which were killed by beetle outbreak, could also cause a decrease in overall avian species diversity. Many avian species rely upon seed foraging for their main source of caloric intake, and with decreases in seed availability brought on by beetle outbreak within the treatment transects, species diversity would be expected to decrease as avian species migrate to stands with higher seed availability.

Not only does this study prove that spruce beetle outbreaks in southern Colorado's coniferous forests are negatively impacting American red squirrel populations, but it also gives evidence to the behavioral changes occurring in this species of squirrel, brought on by the infestation of its native forests. Now that red squirrels have been documented consuming spruce bark beetles in multiple studies, the possibility of this new behavior occurring in squirrel populations residing in other infested forests across the western U.S is likely. If spruce bark beetle outbreaks continue to increase in both severity and range in the future, especially as spruce-fir forests become more susceptible to beetle attack because of the increasing temperatures of climate change, American red squirrel populations could continue to decrease throughout North America. Although this may prove to be beneficial for the success of avian species that experience predation by the red squirrel, such as the American three-toed woodpecker, other negative consequences within ecosystems infested by spruce bark beetle are likely. The results of this study can provide land managers with further insight as to how spruce bark beetle outbreaks are affecting mammalian and avian species residing within infested forests, as well as the importance of combating outbreaks in order to prevent further decline in American red squirrel populations.

Conclusion

The findings of this thesis study indicate that spruce bark beetle outbreaks in spruce-fir forests of southern Colorado are causing behavioral changes in American red squirrel feeding patterns, as well as causing fluctuations in red squirrel and American three-toed woodpecker populations. Although the adaptive behavior of red squirrels feeding upon spruce bark beetle larvae may not be impacting squirrel abundance in infested forests overall, the negative correlation between red squirrel populations and American three-toed woodpecker populations within infested forests indicates that red squirrel abundance can have an effect on avian abundance for some cavity-nesting bird species. Although larvae predation by red squirrels may continue within populations of southern Colorado's coniferous forests, it will unlikely result in any population stabilization, therefore beetle outbreaks will continue to lead to decreases in red squirrel abundance over time.

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