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Some Aspects of Woodpecker Predation on the Spruce Beetle in Colorado

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Master of Science Project in Entomology

University of Nebraska - Lincoln

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Contents

<u>Page</u>	<u>Topic</u>
1	Abstract
2	Introduction
4	Analysis of Historic Data
4	Introduction
5	Project Background
8	Methods
9	Results
11	Discussion and Conclusions
19	References Cited
21	Appendix - Statistical Code and Results in R

Figures

<u>Page</u>	<u>Figure (with abbreviated title)</u>
12	1. Median numbers of spruce beetles in woodpecker stomachs (by woodpecker sex and beetle stage).
15	2. Median numbers of spruce beetles in woodpecker stomachs (by season and beetle stage).
16	3. Median area of bark infested with spruce beetles.
16	4. Mean percent bark removed by woodpeckers.

Abstract

Historic data on predation by woodpeckers, primarily the American three-toed woodpecker (*Picoides dorsalis*), on epidemic levels of the spruce beetle (*Dendroctonus rufipennis*) in Engelmann spruce (*Picea engelmannii*) forests of Colorado are analyzed in this report. Significant differences in beetle consumption by male and female woodpeckers as well as seasonal differences in beetle consumption by woodpeckers in general were discovered through statistical analyses. Potential ecological explanations for observed differences are discussed.

Introduction

The spruce beetle (*Dendroctonus rufipennis*) is classified in the Coleoptera, the most specious order of insects, and is one of many destructive bark beetles formerly in the family Scolytidae, but now considered in the subfamily Scolytinae of the family Curculionidae. The spruce beetle and other species of bark beetles have received much attention in the literature because of their destructive impacts to forests and horticultural trees and shrubs.

The spruce beetle has a vast range in North America occurring from Alaska to Maine, through much of Canada, the Appalachian Mountains, the Rocky Mountains, and other mountainous areas of the western United States (Holsten et al. 1999). Engelmann spruce (*Picea engelmannii*), used mainly in construction of homes, is the primary host of the spruce beetle and perhaps of greatest concern with respect to damage. It is native to western North America with two small populations in northern Mexico (Little Jr. 1971). The spruce beetle was formerly referred to as the "Engelmann spruce beetle" and likely occurs throughout the range of Engelmann spruce (Massey and Wygant 1954), but apparently not in Mexico. In addition to its primary host, spruce beetles attack other commercially important spruces including white spruce (*P. glauca*), Sitka spruce (*P. sitchensis*), and the hybrid Lutz spruce (*P. x lutzii*) (Holsten et al. 1999).

Descriptions of the life history and ecology of the spruce beetle are provided in such works as Furniss and Carolin (1977), Massey and Wygant (1954), and Schmid and Frye (1977) and are described here in

general terms. In the Rocky Mountains of Colorado, a two-year life cycle is typical, but up to four years is possible. Adults, which are about 6 mm in length, attack trees usually in early summer by boring through the bark and tunneling between the bark and wood while forming galleries, where eggs are laid. Adults bore out through the bark creating "shothole" patterning and relocate to the bases of trees where they overwinter before re-emerging in early summer. Eggs hatch usually by early fall and the larvae overwinter in diapause in the galleries before resuming development in spring. Larvae go through four instars, attaining a length of about 6 mm, and pupate in late spring and early summer and then emerge from trees as adults. With this semivoltine life cycle, larvae and adults are present together.

Major contributors to spruce beetle attack include blowdown events, long-term drought, warm temperatures, fire, and the presence of older and denser stands, all of which increase tree susceptibility to insect attack (Colorado State Forest Service 2017). Spruce beetles typically maintain endemic population levels that can quickly become epidemic when forest conditions permit. With respect to insect infestation, "endemic" refers to resident populations below epidemic levels, a meaning different than its use in other areas of ecology. As examples of their capacity to devastate forests, in Colorado from 1996 to 2017, spruce beetle outbreaks caused forest tree mortality on more than 1.7 million acres, or 2,656 square miles of land (Colorado State Forest Service 2017). In Colorado from 1942 to 1948, spruce beetles accounted for loss of nearly 4 billion board feet of timber (Wygant and Nelson 1949). Various control measures are employed to combat

epidemic populations including insecticide treatments, management using aggregation pheromones and trap trees, timber thinning, removal of downed or damaged trees, and bucking of downed trees followed by exposure to sunlight (Holsten et al. 1999).

Three woodpecker species are predators on the spruce beetle in the Rocky Mountains. The American three-toed woodpecker (*Picoides dorsalis*) is considered by far the most important, taking beetles mainly from tree trunks and responding most aggressively to infestations. The hairy woodpecker (*P. villosus*) takes beetles from trunks, snags, and branches and the downy woodpecker (*P. pubescens*) feeds mainly by working branches and has the least pronounced response to infestations (Imbeau and Desrochers 2002; Koplín 1969; Schmid and Frye 1977). In the past, effects of vertebrate predators on bark beetle populations have not been considered great but Fayt et al. (2005) in their review of many studies provide evidence that the role of woodpeckers, especially the American three-toed woodpecker, could be greater than previously thought.

This project aims to shed additional light on the ecology of woodpecker predation on the spruce beetle via analysis of some historic data that was taken following vast damage to Engelmann spruce in Colorado resulting in epidemic beetle infestation.

Analysis of Historic Data

Introduction

Historic data collected on woodpecker predation on the spruce beetle in Colorado from a Master of Science thesis written by the late

Frank T. Hutchison (1951), and available on the internet at <http://hdl.handle.net/10217/80199>, were analyzed with permission from Colorado State University. This data was published before widespread use of computers to quickly conduct statistical analysis. Methods and results of data analysis are presented in this section of the report with discussion of relevance integrated into the subsequent Discussion and Conclusions section.

Project Background

Hutchison (1951) collected a variety of data on woodpeckers and spruce beetles from November 1949 through June 1950 at Rabbit Ears Pass, Colorado following spruce beetle attack on Engelmann spruce in the region. Rabbit Ears Pass is in the northwest part of the state at elevations over 9,000 feet along Highway 40 between Steamboat Springs to the northwest and Kremmling to the southeast. The area was made susceptible to spruce beetle attack on Engelmann spruce following severe windstorms in western Colorado in 1939, resulting in extensive blowdown and weakening of trees. Spruce beetle populations became so great that even healthy trees were attacked. Some aspects of the study are discussed below but detailed fully in Hutchison (1951).

Hutchison (1951) established three study plots at Rabbit Ears Pass in 1949:

- 1) Plot 1 was characterized by infested trees primarily from beetle attack in 1949 with some from attack in 1948 (3:1 approximately).
- 2) Plot 2 was characterized by infested trees from beetle attacks in 1948 and 1949 (1:1 approximately).

3) Plot 3 was characterized by infested trees primarily from beetle attack in 1948 with some from attack in 1949 (3:1 approximately). Trees attacked in 1948 supported large numbers of adult beetles compared to larvae, while trees attacked in 1949 showed the opposite. Data on woodpecker predation on spruce beetles, however, were not shown by plot or by years of infestation in Hutchison (1951).

Of data presented in Hutchison (1951), the following are analyzed in this report:

- 1) Numbers of larval and adult spruce beetles consumed by male and female woodpeckers in areas similar to study plots.
- 2) Numbers of larval and adult spruce beetles consumed by woodpeckers in winter and spring in areas similar to study plots.
- 3) Area of bark of Engelmann spruce trees infested with spruce beetles within study plots.
- 4) Percent bark removed from Engelmann spruce trees by woodpeckers within study plots.

For each of the eight months of the study, ten woodpeckers were killed from areas with similar infestations to the three study plots.

Woodpeckers were not taken from the study plots themselves to avoid changing the nature of the plots with respect to such aspects as bark removal, for example. To assess predation on spruce beetles by woodpeckers, stomach contents were examined for each woodpecker killed and larval and adult spruce beetles counted. To assess woodpecker activity related to years of beetle attack, twenty Engelmann spruce trees were felled on each of the three study plots and data collected on area of beetle infestation and percent bark removed by woodpeckers

for each tree. Trees were felled after completion of other field work, presumably during summer 1950.

Three species of woodpeckers that preyed on spruce beetles at Rabbit Ears Pass were the American three-toed woodpecker, hairy woodpecker, and downy woodpecker. Hutchison (1951) considered woodpeckers as a group rather than by species because the great majority of the woodpecker feeding guild was of one species, the American three-toed woodpecker. This species, as noted earlier, is the most important predator of the spruce beetle.

Note that there are nomenclatural differences in Hutchison (1951) and the current literature: (1) The specific epithet of "*engelmanni*" was used for the spruce beetle, which is synonymous with "*rufipennis*" used currently and "*obesus*" present in literature from the 1960's (Wood 1982); (2) The specific epithet of "*tridactylus*" was used for the alpine three-toed woodpecker, a subspecies of the American three-toed woodpecker. The specific epithet currently used for the American three-toed woodpecker is "*dorsalis*"; (3) The hairy and downy woodpeckers were in the genus "*Dryobates*" but are currently considered in "*Picoides*" (Chesser et al. 2017).

Data available in Hutchison (1951) but not analyzed in this report include numbers of woodpecker pairs per plot; woodpecker consumption of spruce beetles on a daily basis in relation to temperature range, weather conditions, and time of day; inference of spruce beetle density per infested tree based on a previous study; and inference of amount and percent of spruce beetles consumed by woodpeckers based on beetle density estimates from a previous study.

These data provide important insight into woodpecker and spruce beetle ecology but were not analyzed because of my uncertainties about data collection methods and potential factors that could confound statistical analyses.

Methods

Statistical analyses and graphing were conducted in R (R Core Team 2017) and written code and numerical results, as well as the raw data, are presented in the Appendix. For each data set analyzed, the chosen alpha level of significance was 0.05, to which obtained p-values were compared. The Shapiro-Wilk Test was conducted on each data set to test for normality, thus establishing if data would be analyzed by parametric or non-parametric methods.

Based on the outcomes of the Shapiro-Wilk Tests, the non-parametric Wilcoxon Rank-sum Test, equivalent to the Mann-Whitney U Test, was used to compare male and female woodpecker consumption of spruce beetles and to compare woodpecker consumption of spruce beetles during winter and spring in areas similar to study plots.

The non-parametric Kruskal-Wallis Test was used to compare areas of bark infested with spruce beetles and, based on results, was followed by pairwise Wilcoxon Rank-sum Tests between study plots. For the three pairwise comparisons, a Bonferroni adjustment to the alpha level was necessary. This adjustment is the chosen alpha level divided by the number of pairwise comparisons; in this case $0.05/3=0.017$.

A One-way Analysis of Variance (ANOVA) was used to compare bark removed by woodpeckers in areas attacked by spruce beetles among study

plots. F Tests were used to assess homogeneity of variances of percent bark removed among study plots; pairwise comparisons required adjustment of the chosen alpha level to 0.017, as was done above. Based on the results of the ANOVA, *post hoc* multiple comparisons were not warranted.

For clarity below, the interquartile range (IQR) calculated in R is quantile 3 minus quantile 1 (i.e. the 75th percentile minus the 25th percentile). Since non-parametric data are not well described by measures used for normally distributed data [e.g. mean and standard error (SE)], the IQR is reported here as a measure of dispersion for non-normal data, along with the median. The means and variances for all data analyzed, however, are available in the Appendix.

Results

The Shapiro-Wilk Test rejected null hypotheses of normality of data for male woodpecker predation on larval spruce beetles ($W=0.93$; $p=0.01$) and adult spruce beetles ($W=0.86$; $p=0.0001$) and for female woodpecker predation on larval spruce beetles ($W=0.85$; $p=0.0003$) and adult spruce beetles ($W=0.83$; $p=0.00009$). Median numbers of larval spruce beetles in stomachs were 55 per male woodpecker with $IQR=48$ and 31.5 per female woodpecker with $IQR=17.75$, while median numbers of adult spruce beetles in stomachs were 2 per male woodpecker with $IQR=5$ and 1 per female woodpecker with $IQR=3$. Male and female consumption of larval spruce beetles was significantly different ($W=1083$; $p=0.0003$), with males consuming more larvae. Male and female consumption of adult spruce beetles was not significantly different ($W=916$; $p=0.053$),

albeit nearly so at the chosen alpha level, with males consuming more adults in the samples taken.

Records of spruce beetles consumed by male and female woodpeckers combined (separate for larvae and adults) are presented by month in Hutchison (1951), from November 1949 through June 1950. For analysis of this data, mean number of spruce beetles consumed by woodpeckers during four winter months (November 1949 through February 1950) was compared to that consumed during four spring months (March 1950 through June 1950). The Shapiro-Wilk Test rejected null hypotheses of normality of data for woodpecker predation on larval spruce beetles during winter ($W=0.92$; $p=0.008$) and spring ($W=0.74$; $p=0.0000006$) and for woodpecker predation on adult spruce beetles during winter ($W=0.91$; $p=0.007$) and spring ($W=0.74$; $p=0.0000006$). Median numbers of larval spruce beetles consumed by woodpeckers during winter was 44 per bird with $IQR=46.75$, and during spring was 37 per bird with $IQR=25.5$. Median numbers of adult spruce beetles consumed by woodpeckers during winter was 2.5 per bird with $IQR=3$, and during spring was 1 per bird with $IQR=3$. Winter and spring consumption of spruce beetles by woodpeckers was significantly different for larvae ($W=993$; $p=0.01$) and adults ($W=938$; $p=0.04$), with winter consumption being greater in both cases.

The Shapiro-Wilk Test rejected null hypotheses of normality of data for area of bark infestation for Plot 1 ($W=0.89$; $p=0.002$), Plot 2 ($W=0.89$; $p=0.002$), and Plot 3 ($W=0.90$; $p=0.005$). Median areas (in square feet per tree) of bark infestation were 62.8 with $IQR=57.75$ in Plot 1, 69.1 with $IQR=34.05$ in Plot 2, and 94.2 with $IQR=76.55$ in Plot

3. The Kruskal-Wallis Test yielded statistical significance (chi-squared=6.1; p=0.05) but *post hoc* pairwise comparisons between plots using Wilcoxon Rank-sum Tests did not when p-values were compared against the adjusted alpha level of 0.017. Pairwise comparisons yielded W=565 and p=0.58 for Plot 1 versus Plot 2, W=428 and p=0.03 for Plot 1 versus Plot 3, and W=439 and p=0.04 for Plot 2 versus Plot 3.

The Shapiro-Wilk Test did not reject null hypotheses of normality of data for percent bark removed for Plot 1 (W=0.96; p=0.19), Plot 2 (W=0.95; p=0.10), and Plot 3 (W=0.95; p=0.12). Mean percent bark removed per tree was 53.7 ± 4.3 SE in Plot 1, 57.3 ± 3.6 SE in Plot 2, and 52.9 ± 3.4 SE in Plot 3. ANOVA yielded no significant differences in mean percent bark removed among Plots 1, 2, and 3 (F=0.39; p=0.68). The F Tests for homogeneity of variances yielded no significant differences at the adjusted alpha level of 0.017 for Plot 1 versus Plot 2 (F=1.4; p=0.33), Plot 1 versus Plot 3 (F=1.6; p=0.21), and Plot 2 versus Plot 3 (F=1.1; p=0.77), thus validating the assumption of equal variances.

Discussion and Conclusions

While Hutchison (1951) found a variety of arthropod species in woodpecker stomachs, approximately 99% were spruce beetles. Analysis of data from Hutchison (1951) quantifies the strong difference in larval spruce beetle consumption by male and female woodpeckers, with males consuming more beetles (Figure 1).

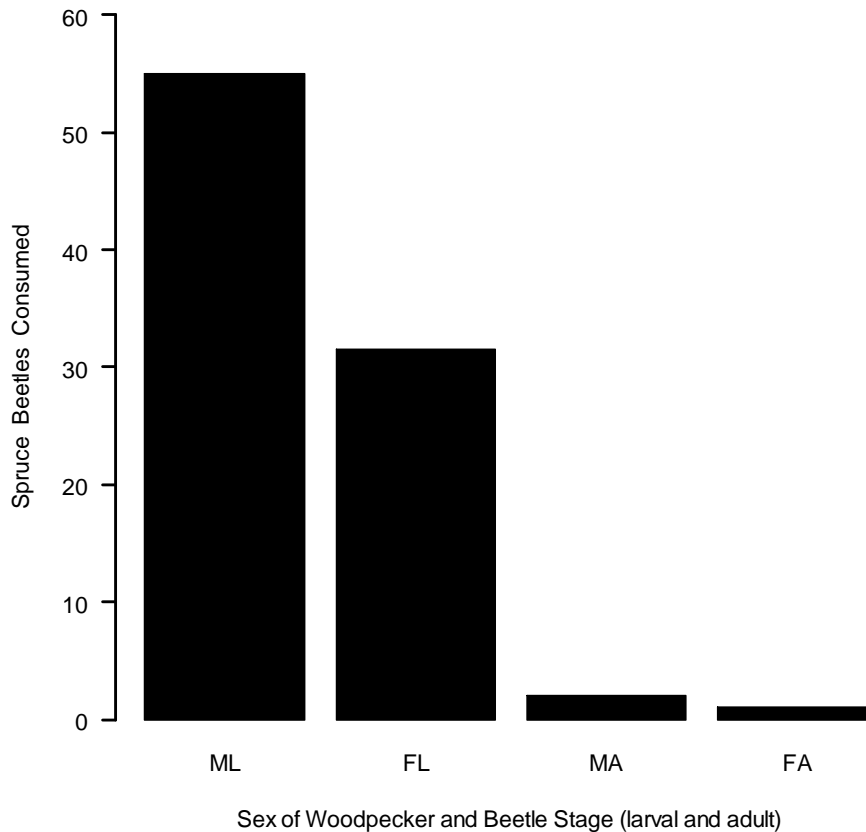


Figure 1. Median numbers of spruce beetles per woodpecker stomach in areas similar to study plots by woodpecker sex and beetle stage at Rabbit Ears Pass, Colorado from November 1949 through June 1950 (from data in Hutchison 1951). ML = male woodpeckers and larval beetles; FL = female woodpeckers and larval beetles; MA = male woodpeckers and adult beetles; FA = female woodpeckers and adult beetles.

Since there are no substantial sex-specific size differences in the American three-toed woodpecker, nor in the hairy or downy woodpeckers which were much less common during the study at Rabbit Ears Pass, other factors must account for observed differences in larval spruce beetle consumption by male and female woodpeckers. In high mountain country of such areas as Rabbit Ears Pass, egg dates range from late May to early July and fledging dates range from mid-to late July (Wiggins 2004). Female American three-toed woodpeckers spend more time in the nest and feed less during the nesting season

than males (Leonard Jr. 2001), which may contribute to the observed difference in larval spruce beetle consumption between male and female woodpeckers. American three-toed woodpeckers typically forage by working the trunks of trees and, to a much lesser extent, the branches (Koplin 1969; Imbeau and Desrochers 2002). There is evidence of resource partitioning with respect to foraging of male and female American three-toed woodpeckers. Females compared to males fed at higher locations on trees in Quebec, Canada (Imbeau and Desrochers 2002), on larger diameter trees in Alaska (Murphy and Lehnhausen 1998) and Manitoba, Canada (Villard 1994), and showed more of a tendency to forage in unburned areas in Alaska (Murphy and Lehnhausen 1998). On the White River National Forest in northwest Colorado, Massey and Wygant (1954) found that spruce beetles infested Engelmann spruce to an average height of 33 feet and that the average non-infested length of tree above the highest point of infestation was 54 feet. That female American three-toed woodpeckers forage more than males at higher locations on trees and in unburned areas, where less spruce beetles would occur, may contribute to explaining why less larval spruce beetles were found in the diets of females than males.

No statistically significant differences were detected in adult spruce beetle consumption between male and female woodpeckers at Rabbit Ears Pass, although nearly so with males consuming more adults than females in the samples taken. Lack of significance may have resulted from the inability to show differences at the chosen alpha level because of small numbers of adults consumed, and significant differences perhaps would have been seen with larger sample sizes.

Since adult spruce beetles are less available to woodpeckers during winter than in warmer months because of snow cover, the greater amount of spruce beetles in sample counts from male woodpeckers than from females may be explained by the typical situation of less foraging by female American three-toed woodpeckers than by males during the nesting season.

In northwest Colorado, adult spruce beetles emerge from about mid-June through mid-October. They overwinter in the bases of trees and re-emerge the following June and July (Massey and Wygant 1954). Hutchison (1951) noted that snow cover occurred at the bases of Engelmann spruce during winter at Rabbit Ears Pass. The overwintering locations of adults at bases of trees may provide excellent protection from woodpecker predation during winter as well as thermal refuge. This may explain the relatively small amount of woodpecker consumption of adult spruce beetles compared to larvae during the study at Rabbit Ears Pass.

Hutchison (1951) did not indicate numbers of spruce beetles consumed by male and female woodpeckers separately with respect to month or season, but rather showed the data for males and females combined. A strong seasonal effect of woodpecker predation on spruce beetles at Rabbit Ears Pass was shown from analysis of data, with beetle consumption being greater during winter than spring (Figure 2). This may be explained by greater energetic needs of woodpeckers during the colder months and reduced female feeding during the nesting season. That woodpeckers feed on spruce beetles more during winter was also noted by Schmid and Frye (1977).

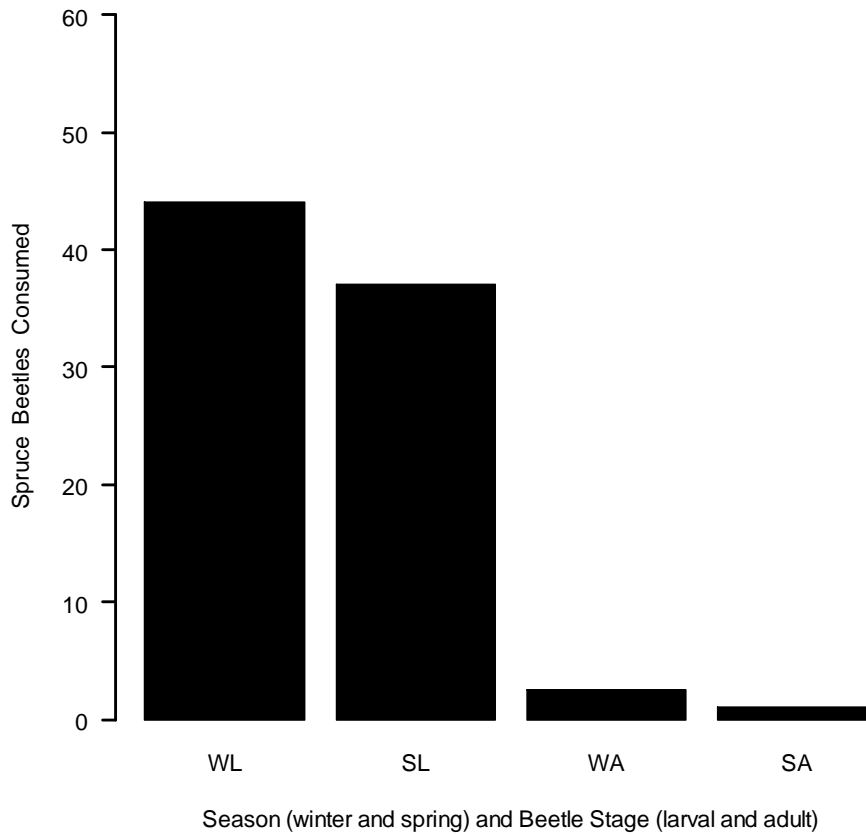


Figure 2. Median numbers of spruce beetles per woodpecker stomach in areas similar to study plots by season and beetle stage at Rabbit Ears Pass, Colorado from November 1949 through June 1950 (from data in Hutchison 1951). WL = winter/larval; SL = spring/larval; WA = winter/adult; SA = spring/adult.

Among study plots, no statistically significant differences were detected for area of bark infestation or percent bark removed by woodpeckers among trees felled in 1950 at Rabbit Ears Pass (Figures 3 and 4). That tree stands attacked primarily in 1949 had similar amounts of bark removed to those attacked in 1948 shows the quick response of woodpeckers to spruce beetle infestation.

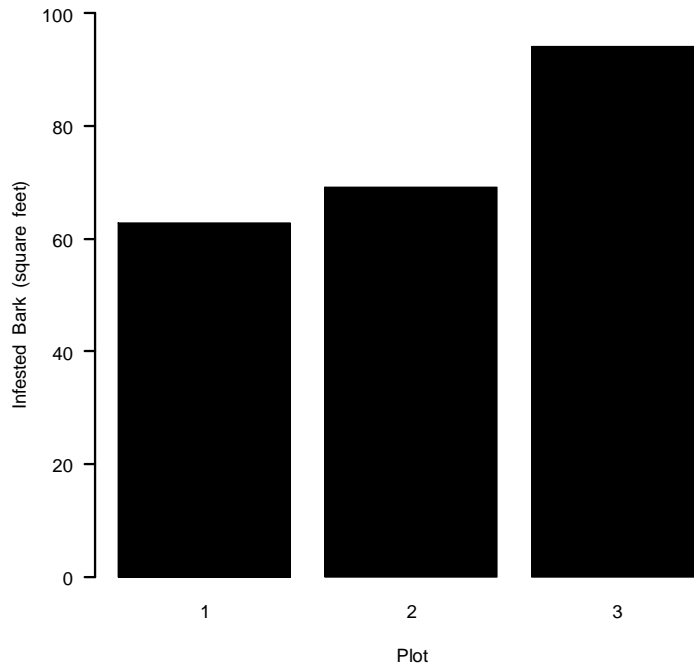


Figure 3. Median area of bark per Engelmann spruce tree infested with spruce beetles on three study plots at Rabbit Ears Pass, Colorado from November 1949 through June 1950 (from data in Hutchison 1951).

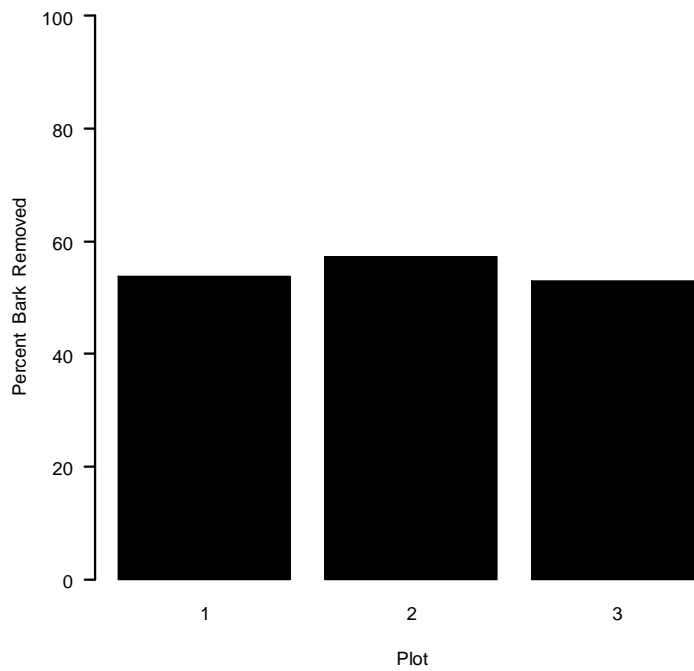


Figure 4. Mean percent bark removed by woodpeckers per Engelmann spruce tree on three study plots at Rabbit Ears Pass, Colorado from November 1949 through June 1950 (from data in Hutchison 1951).

Edworthy et al. (2011) found that woodpeckers in a study in British Columbia, including the three species present in the Hutchison (1951) study, were conservative with respect to reproductive investment. While greater food availability resulted in temporary increases in woodpecker abundance in beetle-infested forests, fecundity remained constant and it was concluded that change in woodpecker abundance was controlled mainly by variable survival and immigration rates. It is evident that woodpeckers do not follow the classic Lotka-Volterra or Nicholson-Bailey predator-prey models where fluctuation in abundance of predator respond to, but lags behind, that of prey. This could be an important trait in the ability of woodpeckers to provide some measure of control on spruce beetles, since their predatory response would not depend on a delayed population build-up of woodpeckers resulting from increased fecundity, but rather on presence of woodpeckers near areas of infestation and the ability to provide adequate numbers of immigrants. An example of a remarkable local population increase of American three-toed woodpeckers to epidemic levels of spruce beetles occurred at elevations over 10,000 feet at Deadman Lookout in north-central Colorado during summer 1964 where density changed from about 0.04 to 0.6 bird per acre in about one month, a 15-fold increase (Koplin 1967). Increases in woodpecker densities even substantially higher than this have been recorded (Fayt et al. 2005).

Perhaps woodpeckers serve as natural biocontrol agents by maintaining endemic spruce beetle populations below carrying capacity such that expansions may be somewhat slowed when forest conditions

become favorable to support epidemic infestations. If so, this may provide additional time for implementation of various control measures before spruce beetle populations become very high and more difficult to control. During epidemic infestations, woodpeckers may destroy up to 75% of the spruce beetle population (Massey and Wygant 1954) and, while woodpeckers certainly can't save a forest, perhaps they may aid in lowering beetle populations such that control measures may begin with more favorable prospects.

As noted in the Introduction section, major contributors to spruce beetle attack include blowdown events, long-term drought, warm temperatures, fire, and the presence of older and denser stands, all of which increase tree susceptibility to insect attack (Colorado State Forest Service 2017). Engelmann spruce forms nearly pure stands at timberline in the southern Rocky Mountains and is especially susceptible to fire because of its thin bark and persistence of dead lower limbs (Alexander and Shepperd 1990). While acknowledging considerable spatial and temporal variability in climate change, Bentz et al. (2010) predict that climate warming poses the potential of increased bark beetle outbreaks and resultant tree mortality in some areas over the next century in the western United States and Canada. If climate warms in the Rocky Mountains over a significant time period, the regional elevational bands suitable for Engelmann spruce may increase in elevation. With respect to geographic range, Engelmann spruce may be more susceptible to climate warming than many other species of forest trees because it occurs at such high elevations where relatively small areas of land occur above its current upper

elevational limits. This could perhaps result in increasingly disjunct stands of Engelmann spruce and fragmentation of populations of spruce beetles and American three-toed woodpeckers. The presence of disjunct stands of Engelmann spruce would likely become even more pronounced in southern portions of the species range, including Colorado, compared to forests of higher latitudes where the distribution of Engelmann spruce is currently more contiguous. Under conditions of increased susceptibility of Engelmann spruce to attack and isolation of stands, the availability of the American three-toed woodpecker and other woodpecker species as spruce beetle control agents could become increasingly important.

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Appendix - Statistical Code and Results in R

Male woodpecker consumption of larval spruce beetles:

```
> ML = c(112,91,38,31,117,87,75,33,76,127,127,72,36,72,70,19,71,40,
112,59,82,152,55,178,37,22,37,40,61,41,9,31,31,38,27,24,47,7,95,47,51,
62,102)
> mean(ML)
[1] 63.74419
> var(ML)
[1] 1522.814
> median(ML)
[1] 55
> IQR(ML)
[1] 48
> shapiro.test(ML)
W = 0.9284, p-value = 0.01025
```

Female woodpecker consumption of larval spruce beetles:

```
> FL = c(41,39,43,63,33,116,17,21,40,42,45,7,18,7,40,32,26,64,17,40,
24,51,11,27,51,50,30,17,24,37,31,29,31,24)
> mean(FL)
[1] 34.94118
> var(FL)
[1] 408.5419
> median(FL)
[1] 31.5
> IQR(FL)
[1] 17.75
> shapiro.test(FL)
W = 0.84969, p-value = 0.0002754
```

Comparison of male and female woodpecker consumption of larval spruce beetles:

```
> wilcox.test(ML,FL)
W = 1083, p-value = 0.0003092
```

Male woodpecker consumption of adult spruce beetles:

```
> MA = c(3,1,6,0,3,6,7,5,0,1,3,3,0,1,1,3,2,7,0,3,1,2,1,8,6,3,4,1,9,6,
0,8,0,1,0,0,7,0,8,3,0,0,1)
> mean(MA)
[1] 2.883721
> var(MA)
[1] 8.009967
> median(MA)
[1] 2
> IQR(MA)
[1] 5
> shapiro.test(MA)
W = 0.86087, p-value = 9.92e-05
```

Female woodpecker consumption of adult spruce beetles:

```
> FA = c(0,2,0,4,5,4,5,2,1,4,1,3,0,3,1,6,0,0,2,0,0,3,0,0,0,4,2,0,0,2,
0,1,0,0)
> mean(FA)
[1] 1.617647
> var(FA)
[1] 3.394831
> median(FA)
[1] 1
> IQR(FA)
[1] 3
> shapiro.test(FA)
W = 0.82602, p-value = 8.515e-05
```

Comparison of male and female woodpecker consumption of adult spruce beetles:

```
> wilcox.test(MA,FA)
W = 915.5, p-value = 0.05311
```

Woodpecker consumption of larval spruce beetles during winter:

```
> WL = c(112,91,41,38,39,31,43,117,87,64,75,33,76,33,127,127,116,72,
17,21,36,72,70,19,40,42,45,71,40,7,18,7,40,32,152,59,82,152)
> mean(WL)
[1] 61.68421
> var(WL)
[1] 1553.627
> median(WL)
[1] 44
```



```
> IQR(WL)
[1] 46.75
> shapiro.test(WL)
W = 0.91737, p-value = 0.008186
```

Woodpecker consumption of larval spruce beetles during spring:

```
> SL = c(26,62,102,55,178,64,17,37,22,40,37,40,24,51,61,11,41,9,27,31,
51,50,31,38,27,24,30,47,17,7,24,95,37,31,47,29,31,24,51)
> mean(SL)
[1] 41.69231
> var(SL)
[1] 907.7976
> median(SL)
[1] 37
> IQR(SL)
[1] 25.5
> shapiro.test(SL)
W = 0.74071, p-value = 6.202e-07
```

Comparison of woodpecker consumption of larval spruce beetles during winter and spring:

```
> wilcox.test(WL,SL)
W = 992.5, p-value = 0.01051
```

Woodpecker consumption of adult spruce beetles during winter:

```
> WA = c(3,1,0,6,2,1,0,3,6,4,7,5,0,5,1,3,4,3,5,2,0,1,1,3,1,4,1,2,7,3,
0,3,1,6,0,3,1,2)
> mean(WA)
[1] 2.631579
> var(WA)
[1] 4.401138
> median(WA)
[1] 2.5
> IQR(WA)
[1] 3
> shapiro.test(WA)
W = 0.91477, p-value = 0.00684
```

Woodpecker consumption of adult spruce beetles during spring:

```
> SA = c(0,0,1,1,8,0,2,6,3,0,4,1,0,3,9,0,6,0,0,8,0,4,0,1,0,0,2,7,0,0,
0,8,2,0,3,1,0,0,0)
> mean(SA)
[1] 2.051282
> var(SA)
[1] 8.049933
> median(SA)
[1] 1
> IQR(SA)
```

```
[1] 3
> shapiro.test(SA)
W = 0.74231, p-value = 6.622e-07
```

Comparison of woodpecker consumption of adult spruce beetles during winter and spring:

```
> wilcox.test(WA,SA)
W = 937.5, p-value = 0.04106
```

Plot 1: Infested area of trees (in square feet):

```
> P1 = c(28.3,172.8,130.9,52.4,150.8,150.8,80.6,37.7,29.3,28.3,44.5,
70.7,109.9,29.3,58.9,31.4,81.7,49.7,106.3,150.8,47.1,31.4,102.6,47.1,
78.5,75.4,87.9,213.1,40.3,62.8,56.5,97.7,62.8,78.5,26.7)
> mean(P1)
[1] 77.24286
> var(P1)
[1] 2187.903
> median(P1)
[1] 62.8
> IQR(P1)
[1] 57.75
> shapiro.test(P1)
W = 0.88542, p-value = 0.001641
```

Plot 2: Infested area of trees (in square feet):

```
> P2 = c(69.1,102.6,142.4,33,95.3,37.7,108.9,88.5,43.2,61.3,134,22,
62.8,88,36.7,56.5,81.7,102.6,53.4,78.5,40.3,164.9,75.4,55,65.5,65.6,
37.7,87.9,47.6,87.9,62.8,209.4,73.3,81.7,62.8)
> mean(P2)
[1] 77.6
> var(P2)
[1] 1519.162
> median(P2)
[1] 69.1
> IQR(P2)
[1] 34.05
> shapiro.test(P2)
W = 0.88699, p-value = 0.0018
```

Plot 3: Infested area of trees (in square feet):

```
> P3 = c(36.7,137.4,94.2,141.4,80.6,128.3,104.7,208.9,127.2,50.3,37.7,
87.9,75.4,146.6,68,179,308.4,136.1,155.5,135.6,91.6,183.3,62.8,78.5,
36.7,50.3,53.4,56.5,144,25.1,125.7,75.4,94.2,57.6,94.2)
> mean(P3)
[1] 104.8343
> var(P3)
[1] 3406.694
> median(P3)
```

```
[1] 94.2
> IQR(P3)
[1] 76.55
W = 0.9039, p-value = 0.005043
```

Comparisons of infested area of trees (Plot 1, Plot 2, Plot 3):

```
> x = c(P1,P2,P3)
> g = factor(rep(1:3, c(35,35,35)))
> kruskal.test(x,g)
Kruskal-Wallis chi-squared = 6.1018, df = 2, p-value = 0.04732
> wilcox.test(P1,P2)
W = 564.5, p-value = 0.5767
> wilcox.test(P1,P3)
W = 428, p-value = 0.03063
> wilcox.test(P2,P3)
W = 439, p-value = 0.04208
```

Plot 1: Percent bark removed from trees by woodpeckers:

```
> P1 = c(85,50,50,70,85,80,70,70,65,20,40,50,40,5,95,75,20,20,75,60,
65,30,50,50,40,60,5,40,70,40,25,90,90,20,80)
> mean(P1)
[1] 53.71429
> var(P1)
[1] 637.2689
> median(P1)
[1] 50
> IQR(P1)
[1] 32.5
> shapiro.test(P1)
W = 0.95757, p-value = 0.1931
```

Plot 2: Percent bark removed from trees by woodpeckers:

```
> P2 = c(50,50,75,80,70,70,80,70,35,35,75,80,50,60,30,40,60,15,50,75,
50,90,50,60,70,20,60,65,20,60,90,45,90,15,70)
> mean(P2)
[1] 57.28571
> var(P2)
[1] 454.916
> median(P2)
[1] 60
> IQR(P2)
[1] 25
> shapiro.test(P2)
W = 0.94855, p-value = 0.1022
```

Plot 3: Percent bark removed from trees by woodpeckers:

```
> P3 = c(30,35,60,60,70,40,50,60,70,90,40,70,90,75,40,50,60,60,50,90,
30,25,60,65,40,50,25,90,50,20,50,30,20,40,65)
> mean(P3)
```

```

[1] 52.85714
> var(P3)
[1] 410.7143
> median(P3)
[1] 50
> IQR(P3)
[1] 25
> shapiro.test(P3)
W = 0.95091, p-value = 0.1208

```

Comparisons of percent bark removed from trees by woodpeckers (Plot 1, Plot 2, Plot 3):

```

> x = c(P1,P2,P3)
> g = factor(rep(1:3, c(35,35,35)))
> data.aov = aov(x ~ g)
> summary(data.aov)

```

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
g	2	386	193.1	0.385	0.681
Residuals	102	51099	501.0		

Test for homogeneity of variances of percent bark removed from trees by woodpeckers (Plot 1, Plot 2, Plot 3):

```

> var.test(P1,P2)
F = 1.4008, num df = 34, denom df = 34, p-value = 0.3304
95 percent confidence interval:
 0.7071001 2.7752504
sample estimates:
ratio of variances
 1.40085
> var.test(P1,P3)
F = 1.5516, num df = 34, denom df = 34, p-value = 0.2054
95 percent confidence interval:
 0.7831993 3.0739270
sample estimates:
ratio of variances
 1.551611
> var.test(P2,P3)
F = 1.1076, num df = 34, denom df = 34, p-value = 0.7674
95 percent confidence interval:
 0.5590887 2.1943303
sample estimates:
ratio of variances
 1.107621

```

Figure 1:

```

> C = c(55,31.5,2,1)
> barplot(C, xlab="Sex of Woodpecker and Beetle Stage (larval and
adult)",ylab="Spruce Beetles Consumed", ylim=c(0,60), las=1, lwd=2,
names.arg=c("ML","FL","MA","FA"), border="black", col="black")

```

Figure 2:

```
> S = c(44,37,2.5,1)
> barplot(S, xlab="Season (winter and spring) and Beetle Stage (larval
and adult)",ylab="Spruce Beetles Consumed", ylim=c(0,60), las=1,
lwd=2, names.arg=c("WL","SL","WA","SA"), border="black", col="black")
```

Figure 3:

```
> B = c(62.8,69.1,94.2)
> barplot(B, xlab="Plot",ylab="Infested Bark (square feet)",
ylim=c(0,100), las=1, lwd=2, names.arg=c("1","2","3"), border="black",
col="black")
```

Figure 4:

```
> P = c(53.71,57.29,52.86)
> barplot(P, xlab="Plot", ylab="Percent Bark Removed",
ylim=c(0,100), las=1, lwd=2, names.arg=c("1","2","3"), border="black",
col="black")
```