Spring 1-1-2016

Influences of Anthropogenic and Bark Beetle Disturbances on Breeding Bird Populations in the U.S. Rocky Mountains: Lessons from the American Three-Toed Woodpecker

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INFLUENCES OF ANTHROPOGENIC AND BARK BEETLE DISTURBANCES ON BREEDING BIRD POPULATIONS IN THE U.S. ROCKY MOUNTAINS: LESSONS FROM THE AMERICAN THREE-TOED WOODPECKER

by

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A thesis submitted to the
Faculty of the Graduate School of the
University of Colorado in partial fulfillment
of the requirement for the degree of
Doctor of Philosophy
Department of Geography
2016
This thesis entitled:

Influences of anthropogenic and bark beetles disturbances on breeding bird populations in the U.S. Rocky Mountains: Lessons from the American three-toed woodpecker

written by Julia Jean Kelly

has been approved for the Department of Geography

_________________________
(Thomas T. Veblen)

_________________________
(Victoria A. Saab)

Date______________________

The final copy of this thesis has been examined by the signatories, and we find that both the content and the form meet acceptable presentation standards of scholarly work in the above mentioned discipline.

IACUC protocol # ___ 1408.02___
ABSTRACT

Kelly, Julia Jean (Ph.D., Geography)

Influences of anthropogenic and bark beetles disturbances on breeding bird populations in the U.S. Rocky Mountains: Lessons from the American three-toed woodpecker

Thesis directed by Professor Thomas T. Veblen

The impacts of widespread forest disturbances on wildlife communities must be understood in order to effectively preserve biodiversity into the future. We quantified relationships between occupancy of avian species and forest structure characteristics within spruce-fir forests of southern Colorado that had been logged and infested by bark beetles. We used a novel geographic information system (GIS) approach to explore American Three-toed Woodpecker (Picoides dorsalis; ATTW) relationships with bark beetle outbreaks across its range in the U.S. Rocky Mountains over the period 2010 to 2015. Results show that ATTWs are strongly associated with higher elevations (1.04, 95% CL [0.87,1.20]), decreasing distance to bark beetles (-1.29, 95% CL [-1.53,-1.04]), and increasing spruce-fir cover (0.25, 95% CL [0.18,0.31]) in the southern Rocky Mountain Ecoregion. In the U.S. Northern Rocky Mountain Ecoregion, our data suggested that ATTW abundance was most tied to higher elevations (0.22, 95% CL [0.05,0.39]), increased cover of mixed conifer (0.23, 95% CL [0.04,0.41]), spruce-fir (0.35, 95% CL [0.17,0.53]), and lodgepole pine (0.19, 95% CL [0.07,0.32]) forests, and decreased cover of ponderosa pine forest (-0.52, 95% CL [-1.04,-0.01]. In the northern region of our study, we did not find evidence that ATTW abundance was related to proximity to bark beetle species identified by U.S. Forest Service aerial detection survey data.
Our next objective was to determine if avian occupancy and species richness was significantly different in Engelmann spruce-subalpine fir forests that were logged > 20 years ago. We did not find any evidence of changes in species richness between sites as a result of selective thinning (90% of all BCIs for logging effects overlapped zero). However, occupancy of certain species changed in relation to a spruce beetle outbreak that began in 2015. We provide evidence that thinning does not negatively impact bird species occupancy in subalpine forests in the long term - an important contribution for assessing the impacts of management treatments on a key ecosystem service of spruce-fir forests.

The third research objective was to determine which forest structure attributes best predicted ATTW occupancy in spruce-fir forests of Colorado’s San Juan Mountains. We used an occupancy model to quantify relationships between woodpecker presence and forest structural attributes. ATTW occupancy probability jumped from 0.56 when there were zero infested spruce to 0.99 when there were 9 or more infested spruce per 20 m x 20 m plot. We did not find a relationship between ATTW occupancy and trees that were infested for more than five years. The number of snags per plot and increasing quadratic mean diameter of trees also did not have a supported effect on occupancy.

Taken together, our findings show that selective logging activities in spruce-fir forests that took place > 20 years prior to our study did not affect avian species richness. Presence of ATTWs at both broad and fine scales was largely related to the presence of beetle-infested trees. Our results suggest regional variation in ATTW associations with infestations of spruce beetles and mountain pine beetles, and provide evidence of habitat specialization in the southern Rockies and a tendency toward relative habitat generalization in the northern Rockies. As the primary cavity excavator in spruce-fir forests, conservation of ATTWs may stimulate an umbrella effect by protecting other cavity nester’s habitat in subalpine forests of Colorado. More importantly,
spruce-fir forests are extensively managed for resource output and to maximize resistance to ecological disturbances such as fire and bark beetle outbreaks. Because logging initiatives will continue, we argue that selective thinning activities in forests unaffected by spruce beetles should not harm avian species richness in the long term. However, thinning treatments in stands infested by spruce beetles should be done conservatively to protect food and nesting resources for cavity nesting species known to breed in our study region.
DEDICATION

I dedicate this dissertation to my mother, Carol Jean Hicks, my father, Robert Fisher Hicks, my brother, Robert Morgan Hicks, my husband, Patrick James Kelly, and my mini aussie, Leo.
ACKNOWLEDGMENTS

I am forever grateful to everyone that helped with my dissertation research and writing process. Tom Veblen was an outstanding advisor and always provided advice when I needed it and made me feel like an important member of the Biogeography Lab. The best part of working with Tom was getting to go to the field with him and learn about his career as a forest scientist. Tom taught me every thing I know about Rocky Mountain forest ecology including how to core a tree properly.

I am grateful for my field assistants Andy Cole, Luke Schmitt, Spencer Kerkhoff, and Bryan Hankinson. They brought endless positivity and energy to every day we shared together. Even the most challenging field days were completed with smiles and laughter. Andy and I became especially close and he returned to the field with me for three summers straight. Andy is the friendliest and happiest person I have ever done fieldwork with and I am forever thankful for our bond as “forest doctors.”

My labmates provided a huge amount of support over the years and have also become some of my closest friends. Sitting back-to-back with Brian Harvey in MCOL was the blessing of 2016. He was always there to talk science and provided academic advice free of charge. His wife, Denisse and son, Joaquin are both awesome as well. Thanks to Robbie Andrus, Kyle Rodman, and Rachel Chai for your support throughout the process. I met Monica Rother, Sarah Hart and Teresa Chapman all through the Veblen Lab and these wonderful women have become my closest CU friends. They are brilliant scientists that I am lucky to know them inside and outside of school. Teresa especially motivated me to see the Ph.D. through and has been a guiding light for my work ethic. She gave me strength to work with countless cups of coffee, crackers and cheese, and so many fits of laughter.

Talented scientists helped me with fieldwork and data analyses. Expert avian biologists Eric DeFonso, Brady Dunne, Grace Carpenter, Alex Greene, and Josh Olsen conducted point counts and helped me learn the spruce-fir birds. Quresh Latif made Chapter 3 and 4 possible with his expertise in occupancy modeling. Quresh spent the month of September working on my data and taught me everything I know about Bayesian analyses.

My co-advisor Vicki Saab was an instrumental part of this dissertation. Back in 2014, Vicki agreed to help me with this research and she has since become my ecology sensei. I value Vicki’s expert opinion on research methods and theoretical context. She is a great writer and has been incredibly supportive through the whole process. Vicki and Fresa were even kind enough to let me stay at their home for a week in Bozeman while I was crunching data.

I thank my friends and family for all of their support over the years. Mom, Dad, and Bobby – thank you for being good listeners and for lifting me up when I needed it most. Chris and Ellen – thanks for embracing my “birdnerd” tendencies. The friendliest friends – Joey, Samantha, Jon, Miranda, Rowan, Abbey, Stower, Scott A., Sarah, Dan, Cameron and Julie were always there to talk science. Thank you to my neighbors Maugs and Nate for being the heart of our Floral Drive family.
I owe a gigantic thank you to my husband Patrick who stuck by me when the writing got rough and stress levels were high. Meeting Patrick on the steps of Guggenheim was the best thing the Geography department ever gave me. Patrick is a brilliant scientist and was always there to work through problems and listen to practice talks. His unwavering support and encouragement got me to the finish line.

Finally, I want to acknowledge my dog Leo (aka Judy). He got me out when I was going stir crazy in front of the screen and he loves me no matter what I do.
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CHAPTER 1

INTRODUCTION

Justification

Biological diversity is a good in and of itself. Humans value biodiversity for its inherent worth and role in resource sustainability. Protecting biodiversity is fundamental to the persistence of ecosystem services in an unknown future (Mace et al. 2012). How natural and anthropogenic disturbances affect biodiversity and ecosystem function is a central question in forest ecology. Many different bird species are disturbance specialists, requiring broad-scale ecological perturbations such as fire and bark beetle irruptions for critical habitat. Although disturbances play a critical role in a vast number of marine, terrestrial, and aquatic systems, they do not receive adequate research (Turner 2010). The main goal of this dissertation research was to understand how different disturbances affect avian communities. Few studies have evaluated the influence of broad-scale regional changes caused by spruce beetle outbreaks on vertebrate species. To date, only one study without replication was conducted on a spruce beetle outbreak in white spruce and Sitka spruce. Likewise, research addressing the impacts of selective logging on the avian community in Colorado was also scarce. Since selective thinning is a management technique used to mitigate bark beetle infestations, so an understanding of the potential impacts of logging on the spruce-fir breeding bird community is needed.

Another component of this dissertation is to study the American three-toed woodpecker (*Picoides dorsalis*; ATTW), a unique spruce beetle specialist in the southern Rockies. This woodpecker species associates with spruce beetle epidemics in Colorado, but little was known about its connection to bark beetle outbreaks at the regional scale. Research investigating
relationships between ATTW occupancy and fine-scale forest attributes were also lacking. Logging to mitigate future spruce beetle outbreaks could jeopardize the availability of beetle resources and put pressure on populations of ATTWs in southern Rockies. Therefore, research was needed to identify the important forest structures associated with suitable ATTW habitat. This research is the first to describe mechanisms underlying the patterns of avian occupancy in two interconnected disturbance types – spruce beetle outbreaks, and selective logging.

**Background**

*Landscape Evolution via Disturbances*

Disturbances are fundamental components of ecological systems and play a central role in the patterns and processes of communities over time. The role of disturbance in species communities is one of ecology’s oldest paradigms. Pickett and White (1985) define disturbances as, “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment” (p. 7). Pickett and White’s definition is generalized because disturbances are unique to all ecological systems (aquatic, terrestrial, and marine) and must be described in a system-specific, temporal and spatial context (Turner 2010). The spatial and temporal dimensions of disturbance processes are major drivers of landscape formation. Biological communities evolve and are adapted to short-term, predisposed perturbations such that a community can bounce back from a single disturbance event without significant harm to the system (Paine et al. 1998). Disturbances create heterogeneous landscapes that are important for other trophic levels such as birds. When a spruce-fir forest experiences a spruce bark beetle outbreak, killing the majority of large diameter spruce, the suppressed subalpine fir and Engelmann spruce will experience a growth release and eventually become part of the regenerating canopy (Veblen et al 1991). A bark beetle
disturbance does not completely remove all species from the landscape, but creates a patchy, heterogeneous landscape of dead trees and newly regenerating trees. The dead trees harbor critical food resources for many bark insectivorous bird species and the gaps in the canopy allow understory regeneration, which is important for ground foraging bird species. This process of spatial regeneration following bark beetle infestation is a critical and natural component of forest development in subalpine forests of Colorado (Baker and Veblen 1990). In a sense, the bark beetle disturbance is a restorative process. Gaps in the canopy initiate an influx of young vigorous trees, continuing the cycle of regeneration while providing valuable habitat for other biota. Landscape ecologists research the timing and spatial variability of forest disturbances such as bark beetle outbreaks, fires, and logging. The goal is to understand processes and patterns of ecosystem formation and their consequences for other trophic levels.

Disturbances and Bird Habitat Formation

Across the western United States, climate change has increased the frequency, severity, and duration of broad-scale disturbances including wildfire (Westerling et al. 2006) and bark beetle outbreaks (Bentz et al. 2010, Logan et al. 2010). The recent mountain pine beetle (Dendroctonus ponderosae Hopkins) epidemic affected lodgepole pine (Pinus contorta) forests at historically unparalleled rates (Bentz et al. 2010), setting forests onto new regeneration trajectories (Collins et al. 2011, Diskin et al. 2011, Kayes and Tinker 2012). While the progression of the mountain pine beetle has largely slowed over the last few years, the lesser-known spruce beetle (Dendroctonus rufipennis Kirby) epidemic has been accelerating in southern Colorado since 2010. The presence of millions of dead trees has fueled scientific studies concerning increased wildfire risk and susceptibility to subsequent outbreaks (reviewed
Spruce trees may become more susceptible to bark beetle infestations due to climate warming and increased avalanche and windthrow events (DeRose et al. 2013). Although spruce beetle outbreaks are a natural part of subalpine forest development (Baker and Veblen 1990, Veblen et al. 1991), their impact on bird communities has not been formally described. In western North America, this beetle has killed nearly 80% of large trees over millions of hectares, making it a significant disturbance in this forest type (Raffa et al. 2008, Hicke et al. 2012), and influencing habitat quality and selection for birds from the local to regional scale (Brawn et al. 2001). In addition to the temperature driver, outbreaks are forecasted to accelerate as a result of heightened drought stress (Hart et al. 2013). Given that spruce beetle outbreaks could become more prevalent in the future, attention must be paid to the consequences of outbreaks on other forest communities. Moreover, management techniques such as selective logging that are used to promote resistance to bark beetle infestations (Hansen et al. 2010, Black et al. 2013) may also indirectly affect avian diversity.

Post-disturbance landscapes provide critical habitat for many bird species and field studies provide evidence that successional processes play a direct role in shaping avian habitats and communities (Brawn et al. 2001). It has long been recognized that increased foliage height diversity is associated with increased bird species diversity (MacArthur and MacArthur 1961, MacArthur 1964) and disturbances serve to increase plant diversity and patchiness on the landscape. Fires are ecologically significant disturbances and create mosaics of early successional habitat and dead trees for nesting and food. Fires enhance landscape complexity and provide primary habitat for many bird species. Standing dead trees are important keystone structures for bark insectivorous bird species that forage on deadwood for wood boring beetle
larvae (Tews et al. 2004). Bird species such as the Northern bobwhite, Red-cockaded
woodpecker, Black-backed woodpecker, Western bluebird and Mountain bluebird tend to occur
in burned habitats more often than unburned habitats and have been referred to as fire specialists
(Saab and Powell 2005). Bark insectivores, aerial insectivores, and ground insectivores also tend
to select burned habitats (Saab and Powell 2005). Post-fire landscapes in Montana contained
species (Clark’s nutcracker, Black-backed woodpecker, American three-toed woodpecker, Olive-
sided flycatcher, and Mountain bluebird) that appeared to be relatively restricted to early post-
fire conditions, with Black-backed woodpeckers expressing a nearly obligate dependence on
post-fire habitat (Hutto 1995). In the Okanogan-Wenatchee National Forest of Washington
State, prescribed fire increased probability of estimated occupancy by Black-backed
woodpeckers, Hairy woodpeckers, and White-breasted nuthatches in ponderosa pine forest
(Russell et al. 2009). Forest fires improve the forest mosaic, which allows for a range of
conditions that support avian diversity (Russell et al. 2009). Endogenous and exogenous
spatiotemporal patterns produced by disturbances, create the chance for species to coexist on the
landscape and nurture the persistence of biodiversity (Levin 2000).

Ecology of Spruce Beetle Outbreaks

Spruce beetles of the family Coleoptera are found naturally occurring at endemic (non-
outbreak) levels in most spruce forests. In the subalpine zone of Colorado, the Engelmann spruce
(Picea engelmannii Parry) is the primary host of the spruce beetle, and blue spruce (Picea
pungens Engelmann) is a less frequent host during outbreaks (Schmid and Frye 1977, Jenkins et
al. 2014). Endemic populations subsist in dead, downed trees or in live but weakened trees,
mostly of larger diameter (Jenkins et al. 2014). Epidemics arise when beetle populations erupt
and begin to attack seemingly healthy spruce trees. Increased susceptibility to outbreaks is correlated with single- or two-storied stands, and a higher percentage of canopy spruce that are large in diameter (Schmid and Hinds 1974). Spruce beetle outbreaks, along with fire and wind disturbances, are the most important natural disturbances in Colorado’s subalpine forests (Veblen et al. 1994). Spruce beetle epidemics drastically alter average tree height, density, diameter, and species composition (Schmid and Hinds 1974, Veblen et al. 1991). When bark beetles eliminate spruce trees, subalpine fir (Abies lasiocarpa) quickly becomes the dominant tree species by basal area (Veblen et al. 1991). Such radical changes in forest attributes are important to examine because over 392,000 hectares have been experiencing spruce beetle outbreak since 1998, and the rate of infestation has rapidly increased since 2010 (Colorado DNR 2005, Colorado State Forest Service 2012). 216,000 new acres were affected by spruce beetle in 2013 compared to 183,000 new acres in 2012 (Strebig and Lockwood 2014). The spruce beetle outbreak surpassed the mountain pine beetle in terms of acreage affected in 2012 and in 2013 (Colorado State Forest Service 2012, Strebig and Lockwood 2014). Additionally, spruce-fir forests occupy a large portion of the Rocky Mountain subalpine zone, and certain avian species are consistent throughout the region (Smith 1980). Changes in stand structure and understory composition during a spruce beetle epidemic drastically alters the resources available to the bird community. This research is the first to quantify the impact of spruce beetle outbreaks on avian communities in Engelmann spruce-subalpine fir forests.

**Silviculture Treatments**

Logging is another disturbance that alters forest structure and heterogeneity with potential consequences for forest avifauna, but results are highly mixed. Selective logging
creates gaps in the canopy, and gaps are thought to be the smallest spatial scale within the forest (Watt 1947, Veblen 1992). Such a small-scale disturbance creates space where new plants can colonize by monopolizing newly available light and water resources. Gaps in the canopy may only disrupt the forest community temporarily whereas a broad-scale disturbance could have a long lasting effect. Selective logging has a much different impact on forest structure and subsequent regeneration than a severe forest fire or a clear cut. Post-fire salvage logging negatively influences some bird species while positively affecting others (Saab et al. 2007). Selective logging in forests unaffected by fire either increases or decreases avian richness depending on the forest type (Brawn et al. 2001). Some bird species become more abundant in logged sites while others decline, which is why is it difficult to determine whether or not logging impacts overall avian diversity (Brawn et al. 2001). Salvage logging of burned trees can negatively impact the process of forest recovery (Noss et al. 2006) but expedites nesting habitat for certain bird species such as American kestrels and Lewis’s woodpeckers (Saab et al. 2009). Lewis’s woodpeckers were found to have higher nest densities in partially salvage logged sites compared to unlogged sites (Saab and Dudley 1998, Saab et al. 2007). In contrast, Black-backed woodpeckers prefer unlogged post-fire habitats with a relatively high density of hard and small standing snags (Saab and Dudley 1998). Thus, the scale and legacy of the disturbance can have different consequences depending on the species in question and that species’ resource and habitat requirements.

In Colorado, selective logging practices in spruce-fir forests may indirectly affect the forest’s composition of breeding birds. In recent years, spruce-fir forests have witnessed unprecedented conifer mortality driven by insect outbreaks and disease (Colorado State Forest Service 2012), and logging to mitigate bark beetle epidemics could become more common in
Colorado. In the past, specific landscape- and stand-level aspects of logged forests that alter bird community dynamics lacked quantitative analyses (Zhao et al. 2013). Logging studies have focused on the importance of various stand structure characteristics that are beneficial for avian diversity and the retention of old growth forest species (Thompson et al. 2013), but forest structure characteristics are better predictors of avian diversity than tree species richness (MacArthur and MacArthur 1961). Certain forest features such as leaf productivity and insect abundance have been associated with avian richness in other coniferous forest types (Keller et al. 2003, Tews et al. 2004, White et al. 2013) but not in spruce-fir. Forest thinning is a management technique that involves the removal of large diameter trees preceding outbreaks because large diameter spruce are more susceptible to beetle attack at the stand level (Schmid and Frye 1977). In the western U.S., researchers report mixed results on the effectiveness of the forest-thinning, beetle-prevention strategy (Black et al. 2013), and no single thinning recommendation is guaranteed to succeed since beetles can maintain their endemic population levels in logging residuals (Schmid and Frye 1976). Results vary depending on the landscape in question, but logging treatments have been associated with increased avian richness in the short term (Imbeau et al. 2000). Increased spatial heterogeneity within the landscape has been shown to promote greater avian diversity (Roth 1976, Brawn et al. 2001, Figure 1), and we wanted to know if logging to mitigate spruce beetle infestations in Colorado would generate a similar result.

*Species-energy Theory and Resource Waves*

Food availability and its relationship to habitat use by birds has been an important area of study since the beginnings of ecology as a discipline (Lack 1954, MacArthur 1958, Wiens 1992, Champlin et al. 2009). The positive relationship between species richness and energy available
for consumption was originally coined the “species-energy” theory (Wright 1983). The species-energy theory was tested using bird composition and abundance data during a mountain pine beetle epidemic in British Columbia (Drever et al. 2009) and a spruce beetle epidemic in Sitka spruce and white spruce in Alaska (Lance and Howell 2000), but had not been explored in Engelmann spruce-subalpine fir forests until now. In the short term, a bark beetle outbreak initializes a pulse of resources, which may be positively correlated with increased avian richness. In the longer-term, avian richness could be affected negatively by widespread tree mortality. Red-breasted nuthatches (*Sitta canadensis*) are known to increase in the short term during mountain pine beetle epidemics but exhibit a population crash in the long term when resources are depleted (Norris and Martin 2010). The level of species diversity and abundance could be largely dependent on the severity of the outbreak. In a higher severity outbreak there may be more available cavity nest sites due to additional snag availability, but thinning of the canopy caused by the loss of green foliage could greatly impact species such as the Hammond’s and olive-sided flycatchers which require mature, dense, conifers for suitable habitat (Colorado Partners in Flight 2000). Species such as pine grosbeaks, evening grosbeaks, and Clark’s nutcrackers could be negatively affected by the loss of spruce cones and mature conifer food resources (Tomback 1998, Adkisson 1999, Gillihan and Byers 2001). Certain bird species may play an important role in long-term ecosystem monitoring because they vary in their tolerances to disturbance and each species fills a unique space in the forest food web (Järvinen and Väisänen 1979). It has been suggested that spatial and temporal patterns of beetle attack may even be critical for maintaining biodiversity within forests (Martin et al. 2006).

The timing of resource availability exerts a strong control on foraging options of wide-ranging consumers. When a single population of consumers tracks pulses of resources across a
landscape, this is known as a “resource wave” (Armstrong et al. 2016). Foragers are thought to “surf” resource waves when they shift their range in order to consume a propagating resource (Armstrong et al. 2016). Examples of resource waves are grizzly bears (*Ursus arctos*) following salmon populations for food or wasps tracking flowering fig trees (Armstrong et al. 2016). Resource waves are species-specific and are a defining feature of species’ distributions because consumers can only exist where their primary prey is found. Our research examined bark beetle resource waves and their importance for ATTW consumers.

**Research Goals**

We utilized a whole-ecosystem perspective that integrated biodiversity management with natural forest disturbances, to address three main research questions:

1. Do bark beetle outbreaks lead to increased abundance of ATTWs across their range in the U.S. Rocky Mountains (Chapter 2)?

2. Does avian diversity change as a function of specific forest structure variables in forests that are logged to mitigate spruce beetle infestations (Chapter 3)?

3. What forest structure attributes are related to increased occupancy of ATTWs in spruce-fir forests of Colorado (Chapter 4)?

Using a combination of field research and data provided by the Bird Conservancy of the Rockies, we investigated the status of breeding birds within two different disturbances types across a range of spatial scales. Because controlled experiments on regional insect outbreaks are not possible, observational studies must be performed to understand the ecological consequences of landscape-altering beetle disturbances. Results of this research should aid in future management decisions directed at maximizing ecosystem services and biodiversity while
minimizing stand-level susceptibility to spruce beetle infestations.
CHAPTER 2

Spatiotemporal Relationships Between American Three-toed Woodpeckers (*Picoides dorsalis*) and Bark Beetle (*Dendroctonus* spp.) Outbreaks in the Rocky Mountains

INTRODUCTION

Food availability and its relationship to habitat use by birds has been an important area of study since the beginnings of ecological research (Lack 1954, MacArthur 1958, Wiens 1992, Champlin et al. 2009). Birds play fundamental roles in nearly every ecosystem. In forests, they promote reproductive fitness by dispersing seeds to ensure the genetic diversity of seedlings, and they consume insect predators. Many bird species rely on mature conifer forests for food and nesting resources. Similar to habitats resulting from high-severity fire, bark beetle-infested forests provide critical habitat for a variety of bird species due to an increase in food and nesting resources (Drever et al. 2009, Saab et al. 2014, Hutto et al. 2015). In the U.S. Rocky Mountains, the American three-toed woodpecker (*Picoides dorsalis*; ATTW) associates with Engelmann spruce (*Picea engelmannii*) and is highly adapted for digging out wood boring insect larvae (Bock and Bock 1974, Koplin 1969, Saab et al. 2014). Woodpeckers are the highest-ranked biological predator of the spruce beetle (*Dendroctonus rufipennis* Kirby; SB) and may significantly reduce the beetle brood when beetle populations remain at endemic levels (Koplin and Baldwin 1970, Schmid and Frye 1977). ATTWs are designated as a species of conservation concern in Region 2 of the U.S. Forest Service, but data on population trends are currently lacking (Wiggins 2004). Region 2 includes 17 national forests and 7 national grasslands in South Dakota, Nebraska, Wyoming, Colorado and Kansas (US Forest Service 2016). In Wyoming, the ATTW is listed as vulnerable throughout its range, with 21 – 100 sightings
reported (Wiggins 2004). In South Dakota, ATTWs are listed as imperiled due to rarity and vulnerability to extinction likely as a function of limited habitat in the state (Wiggins 2004). ATTWs are listed as a priority species in Utah, Idaho, Montana, Nevada, and Arizona (Wiggins 2004). They are known to occur in low densities, feeding on dead trees in recently burned, bark beetle-infested forests for up to 3 years, and it is likely that they are sensitive to loss of old-growth conifers (Wiggins 2004). In Region 2, SB outbreaks, along with fire and wind disturbances, are critical disturbances in subalpine forests and are central to forest succession and species composition (Baker and Veblen 1990, Veblen et al. 1991, Veblen et al. 1994). Here we highlight shifts in the primary habitat associations of ATTW in the U.S. Northern Rocky Mountain Ecoregion (NRE) and Southern Rocky Mountain Ecoregion (SRE). Our results may have important management applications in subalpine forests of the Rockies where SB outbreaks are likely to become more common and forest management activities will intensify in the coming years to mitigate insect outbreaks (Agricultural Act of 2014).

Previous studies of avian community responses to bark beetle outbreaks have found support for relationships with abundance but not with species richness. The positive relationship between species richness and energy available for consumption is known as the “species-energy” theory (Wright 1983) and has been explored for a mountain pine beetle (Dendroctonus ponderosae Hopkins; MPB) epidemic in British Columbia (Drever et al. 2009). In the short term, the boom of food resources available during a bark beetle epidemic was positively correlated with abundance of bark beetle insectivores (e.g. woodpecker spp.) no evidence existed for regulation of species richness by the MPB epidemic (Drever et al. 2009). During a light SB epidemic in Sitka spruce (Picea sitchensis) and white spruce (Picea glauca) on the Kenai Peninsula of Alaska Lance and Howell (2000) detected more ATTWs. In the U.S., the numerical
response of ATTWs to spruce beetle outbreaks was noted in the mid 1900s, but only at a very fine spatial scale, within one forest stand in Colorado (Koplin 1969). The response of ATTWs to MPB has not been documented in Colorado, but has been documented in forests of Utah and in the NRE (Saab et al. 2014). Because ATTWs are the primary consumers of spruce bark beetles (Hutchinson 1951, Koplin and Baldwin 1970, Schmid and Frye 1977), we wanted to know whether the presence of an outbreak would be a major factor in predicting regional ATTW abundance in the SRE. We hypothesized that landscape-level predictors of ATTW abundance would be different in the NRE and SRE because of differences in the relative dominance of the host tree, Engelmann spruce (*Picea engelmannii*), in the two regions (Peet 1988). Specifically, in SRE Rockies we expected ATTW abundance to be strongly related to the greater concentration of the host tree in the single cover type of Engelmann spruce-subalpine fir (*Abies lasiocarpa*) forest cover where a SB outbreak killed large numbers of trees over the past 6 years (Koplin 1969, Koplin and Baldwin 1970, USFS 2014). In the NRE, we expected abundance to be associated with a variety of forest cover types because Engelmann spruce is inter-mixed with other bark beetle hosts, and frequently occurs in the mixed-conifer cover type. We also projected ATTWs to be more strongly associated with MPB hosts vs. SB hosts in the NRE because MPB hosts (lodgepole pine, limber pine, and ponderosa pine) are more prevalent in the mixed-conifer cover type in that region. Spruce primarily occurs as a component of mixed-conifer forests in the NRE compared to the SRE where spruce occurs predominantly in the spruce-fir cover type. We also hypothesized that proximity to trees infested by bark beetles would be a strong predictor in both regions because of the ATTWs numerical responses to SB epidemics (Hutchinson 1951, Yeager 1955, Koplin 1969) and MPB epidemics (Drever and Martin 2010, Edworthy et al. 2011, Saab et al. 2014). Studies in Canada reported a positive
trend in ATTW numerical response to MPB infestation (Edworthy et al. 2011) and also a positive correlation between tree species richness and ATTW detection rates (Drever and Martin 2010). We did not exclude Douglas-fir beetles (*Dendroctonus pseudotsugae* Hopkins; DFB) from our analysis because we hypothesized that ATTWs may feed on this beetle species since it is also a member of the *Dendroctonous* genus and has the potential to infest trees in our study area.

Quantifying the association between ATTWs and outbreaks of SB, MPB, and DFB across space and time over large landscapes requires the use of tools such as GIS and remote sensing because field surveys cannot keep up with the pace of landscape change (Osborne et al. 2001). Analysis of spatial and temporal patterns is the foundation for studying ecological processes over large landscapes and in some cases, landscape-level complexities can tell us more about patterns of bird species richness than lower-level processes such as macro habitat patch dynamics (Saab 1999). GIS and satellite imagery are highly useful for species distribution mapping and predicting potential habitat at large spatial scales (Osborne et al. 2001). Forest inventory data and Landsat satellite imagery can be used to generate baseline habitat maps for indicator species (Betts et al. 2003). Local data and species life history traits can also be used in conjunction with remotely sensed data and GIS to enhance the ability to predict suitable habitat (Betts et al. 2003, Betts et al. 2006). We utilized a publicly available GIS dataset of bark beetle outbreaks (the Aerial Detection Survey of the U.S. Forest Service) in conjunction with a six-year dataset of ATTW detections across the U.S. Rockies from the southern Colorado border (37°N latitude) to the Canadian border (49°N latitude) to examine the relationship between three bark beetle species (SB, MPB, and DFB) and ATTW abundance. To our knowledge this is the first attempt
to quantify the relationship between ATTWs and these three bark beetle species at a regional scale.

METHODS

Bird Surveys

The Bird Conservancy of the Rockies (formerly the Rocky Mountain Bird Observatory) provided point count survey data for Colorado, Idaho, Montana, and Wyoming for the past six years (2010 to 2015, Figure 1). These data are collected as part of the Integrated Monitoring in Bird Conservation Regions (IMBCR) Program, which is coordinated by the Bird Conservancy of the Rockies. Each year field biologists conduct bird surveys and record associated forest cover types during the breeding bird season from May 15 - July 15. Field biologists are highly skilled in bird identification by sight and sound and are trained in basic botany to identify vegetation cover types and tree species (Hanni et al. 2013; Appendix D).

The IMBCR program utilizes a statistically rigorous sampling design to produce data that can be used to analyze population trends of diurnal landbird species (Hanni et al. 2013). Survey sites are selected using a spatially balanced algorithm that generally disregards habitat type (Blakesley and Hanni 2009, Hanni et al. 2013). Each sampling grid (transect) is composed of 16 points in a 4 x 4 grid with each point spaced 250 meters apart (Figure 2). The surveyor systematically locates each point using a pre-programmed GPS unit and conducts a 6-minute point count survey at each point location. Some points may not be sampled if they are inaccessible to the technician on a cliff face or in a body of water. During the 6 minutes, every species seen or heard is recorded (Hanni et al. 2013). Surveyors also record detailed descriptions of the habitat cover types, elevation, and other important features for each point count location.
About 15 field biologists are hired each season to survey Colorado alone and are required to complete 30 transects. Since 2010, the IMBCR program has expanded, allowing more transects to be sampled. Although sampling methods have remained consistent between 2010 and 2015, the total number of sampling points has increased since 2010. The final data product provided by the Bird Conservancy is a spreadsheet listing the UTM coordinates for each point, the elevation at that point, all bird species present, and the primary habitat (cover type) for each sampling point. We converted the raw data into ESRI shapefiles, with original attributes preserved.

**Aerial Detection Surveys**

To investigate the relationship between ATTWs and bark beetle infestation, we used aerial detection survey (ADS) data publicly available from the United States Forest Service (USFS 2010). Analysts manually map tree mortality during regional aerial flyovers and these data are converted to vector shapefiles. Acres of forest mortality are summarized from current year observations only and are not cumulative. The entire mortality footprint represents the area actually on the ground without re-counting of trees (USFS 2005). Yearly damage shapefiles contain polygons with forest cover information and these were downloaded for the entire US Rocky Mountain Region - Region 1, 2 and 4 (US Forest Service 2014). Region 1 and 4 encompass the NRE while Region 2 covers the SRE (Figure 1). In our study the NRE included Rocky Mountains coniferous forests of Montana, northern Wyoming, and Idaho (Bailey 1994). The SRE included Rocky Mountain coniferous forests of Colorado and southern Wyoming (Bailey 1994). For this project, we were interested in polygons mapped as infested by SB, MPB, and DFB because these are the primary food source for ATTWs. Although there is little
information regarding ATTW response to DFB, we wanted to include all *Dendrocotonous* species that could have accounted for bark beetle infestation during our time period. Western balsam bark beetle (*Dryocoetes confuses*) which affects subalpine-fir (*Abies lasiocarpa*) was only mapped by ADS in 2015 in the SRE so we excluded this specie from our analyses. Pinyon ips (*Ips confuses*) and pine engravers (*Ips* spp.) were also excluded because we could not find evidence that they are an important food source for ATTWs.

Polygon attributes contain information such as the primary and secondary mortality causal agents, area of infestation, and the number of dead trees within an area. Two other GIS datasets were used to perform a validation of the ADS data – the LANDFIRE (2012) existing vegetation layer and burn perimeter data from the Monitoring Trends in Burn Severity (MTBS) project. These two layers were used to cross-validate the SB, MPB, and DFB polygons from the ADS data with the presence of all conifer hosts to ensure that mortality polygons were not mapped outside forested landscapes or within recently burned areas that would have eliminated bark beetle hosts.

**GIS Covariates in Abundance Models**

We scaled the Bird Conservancy of the Rockies’ point count data to the transect level to obtain a total count of ATTWs per transect, 2010-2015. The home range of ATTWs is not well documented, highly variable, and collected primarily in Canada and Europe. These woodpeckers are non-migratory and typically occupy their home range year round in the northern extent of their distribution (Sandilands 2010). Winter ranges can be around 32 ha in British Columbia but breeding season ranges are much larger (Sandilands 2010). In Europe, Three-toed woodpeckers (*Picoides tridactylus*) have a larger home range during the breeding season and tend to occupy
about 1.12 km\(^2\), or 112 ha (Pechacek 2004). In order to convert points to transects, we buffered each point where at least one ATTW was detected by 1 km. For example, if 16 points counts were conducted by the surveyor in a single morning, and ATTWs were detected at two of those points, the resulting polygon was one transect composed of two points (Figure 3). Buffers were dissolved to create the final ATTW study area transects with ATTW counts summed for each transect. Mean elevation was calculated using the point-level data from Bird Conservancy of the Rockies. Using the same tools in GIS, control transects were created of points that were sampled but ATTWs were not detected. These methods resulted in six yearly shapefiles (2010-2015) for the SRE ecoregion and six shapefiles for the NRE (2010-2015). The final variables were counts per transect of ATTWs and mean elevation for each yearly polygon. Any transects that did not fall within the ADS coverage for that year were removed from the dataset. All shapefiles were projected to the North American Datum of 1983 coordinate system.

Percentage of each forest cover type was calculated for each transect by converting the original data for all surveyed points to a 100m x 100m raster of the primary habitat recorded by field biologists. The habitat raster was then re-classified to six new habitat categories - five that were potentially suitable for ATTWs and a sixth “other” category. Conifers in the genera *Picea, Pinus, Larix,* or *Pseudotsuga* of the family Pinaceae, are hosts for *Dendroctonus* species (Bentz 2008), so suitable ATTW habitat classifications included any cover type that may contain a *Pinaceae* host. Habitat classifications were “Spruce-fir,” “Lodgepole Pine,” “Mixed Conifer,” “Aspen,” and “Ponderosa Pine.” Habitat cell values that were not suitable habitat for ATTWs included “Montane Meadow,” “Riparian,” “Shrubland,” “Pinyon-Juniper,” “Alpine Tundra,” “Grassland,” among others, and these were reclassified to an “Other” category. We calculated the percentage of each forest type that was found within each transect by summing the number of
points containing one habitat type and dividing it by the total number of points that were surveyed at the transect. For example, if one study area contained 16 point counts and 5 of those points were classified as “Mixed Conifer,” we divided 5 by 16 and designated the site as 31.25% “Mixed Conifer” (Table 2). Next, we removed control transects where the majority of the primary habitat recorded was unsuitable for woodpeckers (e.g. 50% or more of the transect was classified as “Other”).

**Beetle Infestation Polygons and Forest Cover Validation**

We used the publicly available ADS data supplied by the US Forest Service to obtain polygons of bark beetle infestation. Six shapefiles were downloaded for the NRE (2010-2015) and six for SRE (2010-2015). For each yearly shapefile, we extracted all polygons where the primary or secondary bark beetle agent was listed as a SB, MPB, or DFB (Damage Causal Agent codes 11009, 11006, or 11007 respectively). We lumped all three beetle species into one bark beetle category because the accuracy of these data decreases significantly when subsampled to a finer grain. (Hart et al. 2015). To increase our confidence in the accuracy of the beetle infestation polygons, we performed a broad-scale validation of the beetle infestation polygons using the LANDFIRE (2012) existing vegetation type layer. We re-projected the LANDFIRE raster to the North American Datum of 1983 coordinate system with a grid size of a 990 m x 990 m (Hart et al. 2015). Cells were reclassified so that “Conifer” cells received a value of “1” and the rest were set to “NULL.” Yearly beetle infestation polygons were clipped to the Conifer raster to eliminate any polygons that were mapped outside of suitable *Pinaceae* hosts. Lastly, any beetle infestation polygons that had burned in the past two decades were removed because fire would also deplete potential conifer hosts. “Monitoring Trends in Burn Severity” fire
perimeter data for fires that burned between 1984 and 2015 (Eidenshink et al. 2007) were used in an overlay analysis to determine which bark beetle infestation polygons fell within recently burned forests. The final yearly shapefiles represented validated polygons of bark beetle infestation for the northern and southern ecoregions. We summed the total area of bark beetle infestation in each ecoregion to estimate the total acreage affected each year (Appendix C). Lastly, the ‘Generate Near Table’ tool was used to calculate proximity between the edge of an ATTW transect and the edge of the nearest beetle infestation polygon of the same year (Table 2). We calculated the near distance for bark beetle infestation areas that were recorded in the same year as the bird surveys. Although there is potentially a lag in detection of dead trees by aerial surveyors, we assumed that ATTWs would have already discovered the bark beetles the year prior, so the current year of infestation would be the closest approximation to the initial year of beetle attack (USFS 2010). A transect was located within a bark beetle infested polygon of the same year if distance to beetle = 0.

Statistical Models

We assessed 17 models of ATTW abundance across the Rocky Mountains to evaluate a priori hypotheses (Table 1) about relationships between abundance and environmental covariates across the Rocky Mountains. We used generalized linear mixed effects models with a poisson error to model abundance (discrete counts per transect). The distribution of the response variable was skewed, so we chose a generalized model, which does not assume normality. We applied the generalized linear modeling approach using the “lme4” package in R Version 0.99.903 (Bates et al. 2013, R Core Team 2015). Abundance was modeled as a function of year, distance to beetle infestation, elevation, and proportion of forest type covariates (Table 3). The
generalized linear models used a log link function for the poisson distribution to map the relationship between the mean response and linear combination of predictor variables (Zuur et al. 2009). Thus the basic structure of the model was:

\[
\log(\text{Count}_i) = \beta_0 + \beta_1 \text{Elevation} + \beta_2 \text{DistBeetle} + \beta_3 \text{CoverType}_i + \ldots + \beta_8 \text{CoverType}_j + \epsilon_i 
\]

We were interested in the significance of \(\beta\)-coefficients (fixed-effects) associated with elevation, distance to beetle infestation, the proportion of each forest cover type within a transect, and year (random-effect). Data were pooled by ecoregion (northern vs. southern Rockies) across all years so we included a random effect of year in each model to account for variations between years that could affect the response variable. Because we wanted absence transects to merely provide a reference for non-detection and not be a major component of model formation and evaluation, we randomly sampled absence points to equal the number of presence points for each year. Covariates were rescaled to mean = 0 and SD = 1. Before choosing predictor variables, we used Kendall’s tau coefficient for nonparametric data to determine the strength and direction of correlations between predictor variables. Fixed parameters were estimated using maximum likelihood and the random effect of year was estimated using the Laplace approximation of integrated likelihood (Bates et al. 2013).

Bayesian Information Criterion (BIC) was used to select the best model (Burnham and Anderson 2004). The BIC statistic is based on the posterior probability of a given model and depends on the number of covariates in the model (Delattre et al. 2014). We used \(\Delta\)BIC to rank each model from most plausible to least plausible and calculated the weights of each model given the weight of all models. Confidence limits (95%) were calculated for parameter estimates of the most plausible models in the NRE and SRE.
RESULTS

The extent of the bark beetle outbreak varied regionally. Every year from 2010-2015, the SRE far surpassed the NRE in terms of the total hectares affected by all bark beetles. The MPB outbreak was the most extensive across both ecoregions in 2010, but the SRE experienced a much greater outbreak extent (475,428.66 ha) than the NRE (76,084.48 ha). SBs attacked far more trees in the SRE compared to the NRE (Figure 5, Appendix C). In 2014, the peak of the SB outbreak in the SRE affected an order of magnitude more hectares than in the NRE (195,860.81 ha compared to 17,792.36 ha respectively). 418 transects were used to model ATTW abundance in the SRE and 326 transects were employed in NRE models. Abundance was much higher in the SRE (661 total detections) vs. the NRE (265 detections). Across both regions, the most ATTW detections (n=199) occurred in the SRE in 2014, which corresponded to the peak of the SB outbreak (Figure 5, Appendix C). Likewise, in the NRE, ATTWs were most abundant in 2010, which corresponded to the peak of the SB outbreak in that region for our time period.

ATTWs were associated with different habitats and elevation ranges depending on the ecoregion. In the SRE, ATTWs were detected at an average elevation of 3041 m (min = 1970 m, max = 3822 m, Number of transects = 210), compared to an average elevation of 1986 m (min = 466 m, max = 3196 m, Number of transects = 163) in the NRE (Appendix A). The mean elevation of 1983 m in the northern portion of the ATTW’s distribution was nearly equal to the minimum elevation (1970 m) of its range in the SRE (Figure 4). Absence transects occurred within the elevation range of presence transects indicating that that the random sample of absence points was non-biased. In general, the NRE had the greatest proportion of presence
transects that were classified as mixed-conifer and the SRE had more transects classified as spruce-fir. There was a greater proportion of lodgepole pine within transects in the NRE compared to the SRE (Appendix B). Kendall’s tau coefficient for nonparametric data indicated that none of the covariates were correlated above 0.5 (Figure 6).

Southern Rockies Mixed Effects Models

For the SRE we found strong supporting evidence that the best predictors of ATTW abundance were elevation, distance to bark beetles, and the proportion of spruce-fir in the transect (Table 3, model weight = 0.984). All other models were unsupported with weights=0 or weights ≤ 0.01. The proportion of mixed-conifer, lodgepole pine, ponderosa pine, and aspen had no apparent effect on abundance. Models with just elevation and distance to beetles, or just distance to beetles and the proportion of spruce-fir also had no discernable effect. Each model in the SRE included year as a random effect indicating an influence of year on changes in abundance over the study period. When abundance was estimated for elevation, distance to bark beetles, and proportion of spruce-fir, the number of woodpeckers increased at higher elevations (1.04, 95% CL [0.87,1.20]), decreasing distance to bark beetles (-1.29, 95% CL [-1.53,-1.04]), and increasing spruce-fir cover (0.25, 95% CL [0.18,0.31]) at each transect (Table 4, Figure 7).

Northern Rockies Mixed Effects Models

In the NRE, the story was much different and we did not find evidence that distance to beetle infestation had an effect on abundance. The estimated variance among years in the NRE equaled zero so the data were effectively pooled across years for estimating the model intercept. The most supported model was one that included elevation and the proportion of spruce-fir,
lodgepole pine, mixed-conifer, and ponderosa pine within the transect (weight = 0.991). The number of woodpeckers increased at higher elevations (0.22, 95% CL [0.05,0.39]) and in areas of more spruce-fir cover (0.35, 95% CL [0.17,0.53]). ATTW counts also increased in transects containing more lodgepole pine cover (0.19, 95% CL [0.07,0.32]), more mixed-conifer cover (0.23, 95% CL [0.04,0.41]), and less ponderosa pine cover (-0.52, 95% CL [-1.04,-0.01], Table 4, Figure 7).

DISCUSSION

The present research highlights relationships between ATTW abundance, elevation, habitat type, and distance to bark beetle infestation across this species’ range in the US Rocky Mountains. ATTW abundance increased with higher elevations in both ecoregions. In the NRE, high elevation forests are not predominantly spruce-fir and can encompass mixed-conifer cover and a variety of bark beetle hosts (Habeck 1987), whereas high elevation forests in the SRE are predominantly Engelmann spruce-subalpine fir where the SB prevails (Veblen et al. 1994, Peet 2000).

Our hypothesis that increased spruce-fir cover would have a positive relationship with increased ATTW abundance was supported in both regions. This likely points to the species’ strong association with spruce bark beetle outbreaks in the host tree species of Engelmann spruce. We also hypothesized that distance to bark beetle infestation would be a strong predictor of abundance in both regions, but could only find support for this in the SRE. This finding suggested that SBs were a more central food resource than MPBs in the SRE because inclusion of spruce-fir cover greatly increased our ability to estimate abundance. Lodgepole and Ponderosa pine are the primary hosts of MPBs in the SRE but we could not provide evidence
that MPB infestation in the SRE was related to ATTW abundance. The association with SBs may not be as strong in the NRE where the MPB was the most prominent agent of tree mortality over the past 6 years. A positive numerical response to MPB has been documented in the northern Rockies including Canada (Drever and Martin 2010, Edworthy et al. 2011, Saab et al. 2014), but little information exists concerning the response to MPBs in the SRE (Saab et al. 2014).

However, during our study period, outbreaks of both SB and MPB was minimal in the NRE compared to the SRE, so we cannot conclude that bark beetle presence was an unimportant predictor of ATTW abundance in the NRE. Had our dataset extended further back in time, we would have been able to test the numerical response during an expanding MPB outbreak. However, we reasonably limited our analyses to the previous six years because the Bird Conservancy of the Rockies changed its sampling protocol after 2009, so we were unable to use any data prior to 2010. The Bird Conservancy follows a random, spatially-balanced sampling procedure which promoted equal sampling of all forest cover types included in our study.

One limitation of conducting research at a regional scale using aerial detection survey data, is that we could not directly distinguish between SB and MPB infestation. ADS data are more accurate at the broad-scale of ~1km, which limited our ability to distinguish between bark beetle species and hosts (Hart et al. 2015). Our results, however, point to the importance of spruce-beetle infestations because spruce-fir habitat was an important predictor variable in both ecoregions. We did not trust the accuracy of the ADS data to distinguish between bark beetle species because MPB, SB, and DFB can overlap across their range and bark beetle host trees can co-occur within a forest stand. For example, in the northern Rockies, Engelmann spruce can co-occur with Douglas-fir and lodgepole pine. Such a broad scale analysis can only accommodate more generalized variable calculations in order to avoid errors in conclusions about fine scale
habitat/bark beetle associations. The past six years of data captured the progression of the SB outbreak and years of extensive MPB outbreak in the SRE. In the NRE, enough area may not have been affected by SBs and MPBs to influence ATTW abundance during our study period.

Our results indicate a meaningful connection between ATTWs and bark beetle outbreaks across their range in the U.S. Rocky Mountains, which has not been shown previously. Our model results suggest that ATTWs are functioning as SB specialists in the SRE due to their strong connection with spruce-fir, distance to beetles, and elevation. Spruce-fir forest is recognized as a dominant forest type at high elevations in the SRE with *Pinus flexilis* and *P. aristata* sometimes occurring on xeric sites (Allen at al 1991). Mixed conifer forest occurs at lower elevations than spruce-fir forests and are composed of a range of conifers such as *Pseudotsuga menziesii, Pinus contorta, Abies concolor, and Populus tremuloides* (Allen et al. 1991). In the NRE, our results imply that ATTWs are operating more as generalists of MPB, SB, and potentially other *Dendroctonus* spp. Our distinction in regional differences in specialization result from the connection to mixed conifer and tree species diversity in the north (Drever and Martin 2010), where a variety of *Dendroctonus* hosts can be found. Subalpine forests in the NRE can include tree species other than spruce and fir such as *Pinus contorta* which dominates the subalpine forest of Yellowstone National Park (Peet 1988). *Pseudotsuga menziesii* is more common in the NRE compared to the SRE, mixing with *Pinus flexilis* at lower timberline (1,800 – 2,300 m, Habeck 1987). In the Wind River, Salt River, and Wyoming mountain ranges of western Wyoming, *Pinus albicaulis* achieves notable dominance at upper timberline and can occur with *Picea engelmannii* and *Abies lasiocarpa* (Habeck 1987). Latitudinal shifts in elevation gradients of forest types warrant the possibility of ATTW generalist tendencies in the NRE, however the coarse scale of our study prevents definitive
conclusions about the exact bark beetle species that ATTWs associate with in the NRE. Our use of data collected by the Bird Conservancy of the Rockies is novel by examining regional spatial relationships between birds, elevation, disturbances, and forest cover. The methods used here could be extended to other bark insectivorous birds such as the Black-backed woodpecker, which is known to depend on recently burned forests. This project emphasizes a new and valuable tool for estimating food and nesting resources at broad spatial scales for disturbance-associated bird species.

ACKNOWLEDGEMENTS

Data for this research was provided by the Bird Conservancy of the Rockies. We thank Chris White at the Bird Conservancy for extensive help with acquiring these data. The Colorado Mountain Club also provided financial support for this work. Thank you to Quresh Latif for providing statistical advice for the data analyses. Teresa Chapman aided in the GIS analyses and taught me some valuable ArcGIS tricks. Sarah Hart provided important statistical advice and Patrick Kelly helped compile data for ArcGIS. Thank you to my collaborators for reviewing each draft with attention to detail.
**Table 1.** Candidate models and supporting hypotheses comparing elevation, proximity to bark beetle infestation (including SB, MPB, and DFB), and forest cover type influences on abundance of ATTWs in the northern and southern Rocky Mountains, 2010-2015.

<table>
<thead>
<tr>
<th>Models</th>
<th>Alternative Hypothesis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null (Intercept-only with random effect of year)</td>
<td>Distribution is random likely due to unmeasured year effects.</td>
</tr>
<tr>
<td>Global model (elevation, all cover types, and distance to bark beetle infestation)</td>
<td>Equal amounts of forest cover types, higher elevation, and shorter distances to bark beetle infestation provide the best conditions for woodpecker abundance and diverse foraging opportunities.</td>
</tr>
<tr>
<td>Elevation, spruce-fir, lodgepole pine, mixed-conifer, and ponderosa pine</td>
<td>Higher elevation and a variety of bark beetle hosts will have a stronger influence on abundance.</td>
</tr>
<tr>
<td>Elevation, distance to bark beetle infestation, spruce-fir, mixed-conifer, and aspen</td>
<td>Higher elevation, shorter distances to bark beetle infestation, increased cover of spruce-fir and mixed conifer, and availability of nesting sites will have a stronger influence on abundance.</td>
</tr>
<tr>
<td>Elevation, spruce-fir, distance to bark beetle infestation</td>
<td>Higher elevation, greater amounts of spruce-fir forest cover, and shorter distances to bark beetle infestation will have the strongest influence on abundance in the southern vs. northern Rockies.</td>
</tr>
<tr>
<td>Elevation, mixed conifer, and distance to bark beetle infestation</td>
<td>Higher elevation, greater amounts of mixed-conifer forest cover, and shorter distances to bark beetle infestation will have the strongest influence on abundance in the northern vs. southern Rockies.</td>
</tr>
<tr>
<td>Distance to beetle infestation, spruce-fir</td>
<td>Shorter distance to bark beetle infestation and greater amounts of spruce-fir cover will have a stronger influence on abundance regardless of ecoregion.</td>
</tr>
<tr>
<td>Elevation, distance to bark beetle infestation</td>
<td>Shorter distances to bark beetle infestation and higher elevations will have a stronger influence on abundance regardless of forest cover type.</td>
</tr>
</tbody>
</table>
Table 2. Independent variables used to model American three-toed woodpecker abundance across the northern and southern Rocky Mountains from 2010-2015.

<table>
<thead>
<tr>
<th>Variable Name</th>
<th>Variable Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance (m)</td>
<td>Distance from each transect to the nearest bark beetle infestation polygon of the same year. Bark beetles included are SB, MPB, and DFB.</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>Mean elevation of each transect. Measured by Bird Conservancy field biologists.</td>
</tr>
<tr>
<td>Per_sf</td>
<td>Proportion of spruce-fir forest within each transect</td>
</tr>
<tr>
<td>Per_mc</td>
<td>Proportion of mixed-conifer forest within each transect</td>
</tr>
<tr>
<td>Per_lp</td>
<td>Proportion of lodgepole pine forest within each transect</td>
</tr>
<tr>
<td>Per_as</td>
<td>Proportion of aspen forest within each transect</td>
</tr>
<tr>
<td>Per_pp</td>
<td>Proportion of ponderosa pine forest within each transect</td>
</tr>
<tr>
<td>Per_o</td>
<td>Proportion of cover type other than those listed above within each transect</td>
</tr>
</tbody>
</table>
Table 3. Results for generalized linear mixed effects models fit by maximum likelihood explaining variation in counts of American three-toed woodpeckers in transects sampled across the Rocky Mountains from 2010 – 2015. Northern Rockies data were effectively pooled across years because the variance among years was estimated to be zero. Models are ranked according to Bayesian Information Criterion (BIC) differences from most plausible (ΔBIC = 0) to least plausible; k = number of parameters. The best supported model is listed on top. We include the null model of year effect only, without covariates.* 

<table>
<thead>
<tr>
<th>Model Description</th>
<th>ΔBIC</th>
<th>k</th>
<th>ω</th>
</tr>
</thead>
<tbody>
<tr>
<td>Northern Rockies Model</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>elevation + per_sf + per_lp + per_mc + per_pp</td>
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<td>5</td>
<td>0.991</td>
</tr>
<tr>
<td>elevation + dist_beetle + per_sf + per_lp + per_mc + per_as + per_pp</td>
<td>10.98</td>
<td>7</td>
<td>0.004</td>
</tr>
<tr>
<td>elevation + dist_beetle + per_sf</td>
<td>11.40</td>
<td>3</td>
<td>0.003</td>
</tr>
<tr>
<td>elevation + dist_beetle</td>
<td>13.31</td>
<td>2</td>
<td>0.001</td>
</tr>
<tr>
<td>dist_beetle + per_sf</td>
<td>15.96</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>elevation + dist_beetle + per_mc</td>
<td>18.82</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>elevation + dist_beetle + per_mc + per_mc + per_as</td>
<td>18.88</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Year effect only</td>
<td>19.82</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Southern Rockies Model</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>elevation + dist_beetle + per_sf</td>
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<td>3</td>
<td>0.984</td>
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<td>6</td>
<td>0.006</td>
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<td>0</td>
</tr>
<tr>
<td>elevation + dist_beetle + per_mc</td>
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<td>0</td>
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<tr>
<td>elevation + dist_beetle</td>
<td>47.97</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>dist_beetle + per_sf</td>
<td>150.0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>elevation + per_sf + per_lp + per_mc + per_pp</td>
<td>177.33</td>
<td>5</td>
<td>0</td>
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<tr>
<td>Year effect only</td>
<td>595.67</td>
<td>0</td>
<td>0</td>
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</tbody>
</table>

k = number of fixed effects parameters
ω = model weight, or the relative likelihood of the model as the best model given the set of models

* Cover class covariate codes - per_sf, per_mc, per_as, per_pp, per_lp = proportion of transect that was spruce-fir, mixed conifer, aspen, ponderosa pine, and lodgepole pine respectively. Elevation covariate is the mean elevation of the transect. Dist_beetle is the proximity (m) of the transect to the nearest beetle infestation polygon of the same year.
Table 4. Fixed-effects parameter estimates and lower 95% confidence limit (LCL) and upper 95% confidence limit (UCL) for parameters in the top models of ATTW abundance in the southern and northern Rockies (2010 – 2015).

<table>
<thead>
<tr>
<th>Ecoregion</th>
<th>Parameter*</th>
<th>Estimate</th>
<th>LCL</th>
<th>UCL</th>
</tr>
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<tr>
<td>Northern Rockies</td>
<td>Intercept</td>
<td>-0.25</td>
<td>-0.48</td>
<td>-0.03</td>
</tr>
<tr>
<td></td>
<td>Elevation</td>
<td>0.22</td>
<td>0.05</td>
<td>0.39</td>
</tr>
<tr>
<td></td>
<td>per_sf</td>
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<td>0.17</td>
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</tr>
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<td></td>
<td>per_lp</td>
<td>0.19</td>
<td>0.07</td>
<td>0.32</td>
</tr>
<tr>
<td></td>
<td>per_mc</td>
<td>0.23</td>
<td>0.04</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td>per_pp</td>
<td>-0.52</td>
<td>-1.04</td>
<td>-0.01</td>
</tr>
</tbody>
</table>

No Random Effect of Year, Variance=0, SD=0

| Southern Rockies  | Intercept  | -0.79    | -1.07| -0.51|
|                   | Elevation  | 1.04     | 0.87 | 1.20 |
|                   | Distance   | -1.29    | -1.53| -1.04|
|                   | per_sf     | 0.25     | 0.18 | 0.31 |

Random Effect of Year, Variance=0.066, SD=0.256

*See Table 2. for list of covariate codes
FIGURES

Figure 1. Map of study area where spatially balanced point counts were conducted in the northern Rocky Mountain Ecoregion (top polygon) and southern Rocky Mountain Ecoregion (bottom polygon). Each triangle represents a sampling grid of point counts.

Figure 2. Example of one transect (MT-BCR10-HE6) where 14 point counts were conducted in 2012.
**Figure 3.** Examples of buffers with a 1 km radius around survey points where ATTWs were detected within a given year. 3a.) Yellow polygons are forested areas infested by bark beetles during 2010. In the area depicted, only two points were surveyed where ATTWs were detected so only two points were buffered. 3b.) Orange polygons are forested areas infested by bark beetles during 2014. This area contained a total of 11 points where ATTWs were detected so 11 total points were buffered.
Figure 4. Violin plots showing the distribution of ATTW presence (black) and absence (grey) transects by elevation and ecoregion. Each violin plot combines a box plot and smoothed histogram to show the shape of the distribution of the observed data, which allows for better visual comparison between years (Hintze and Nelson 1998). The median of each plot is the widest bulge in the center. The interquartile ranges are shown by the bulges above and below the median bulge.
**Figure 5.** Bar graphs showing the total areas newly infested by both SB and MPB in blue, SB in red, and MPB in green in the northern Rocky Mountain Ecoregion (top panel) and southern Rocky Mountain Ecoregion (bottom panel) from 2010 – 2015.
Figure 6. Correlation matrix of predictor variables by ecoregion using Kendall’s tau-b coefficient appropriate for non-parametric data samples with tied ranks. Variables are uncorrelated if their correlation coefficient is zero. Variables included are elevation (“elev”), distance to nearest beetle infestation polygon (“dist2beetle”), and habitat percentages by transect (eg. “SF” = percentage of spruce-fir). Dark orange colors indicated a more negative correlation whereas dark blue colors indicate a more positive correlation.

<table>
<thead>
<tr>
<th></th>
<th>elevation</th>
<th>dist2beetle</th>
<th>SF</th>
<th>LP</th>
<th>MC</th>
<th>AS</th>
<th>PP</th>
<th>O</th>
</tr>
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<td>0.23</td>
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<td>0.09</td>
<td>-0.22</td>
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<td>-0.02</td>
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<tr>
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<td>-0.1</td>
<td>-0.13</td>
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<tr>
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<td>-0.08</td>
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<tr>
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<tr>
<td>PP</td>
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<tr>
<td>O</td>
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<td>0.04</td>
<td>0.08</td>
<td>-0.48</td>
<td>0.1</td>
<td>0.01</td>
<td>1</td>
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<table>
<thead>
<tr>
<th></th>
<th>elevation</th>
<th>dist2beetle</th>
<th>SF</th>
<th>LP</th>
<th>MC</th>
<th>AS</th>
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<th>O</th>
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</thead>
<tbody>
<tr>
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</tr>
<tr>
<td>SF</td>
<td>0.39</td>
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<td>-0.01</td>
<td>-0.32</td>
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</tr>
<tr>
<td>LP</td>
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<td>-0.14</td>
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<td>-0.13</td>
<td>-0.1</td>
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</tr>
<tr>
<td>MC</td>
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<td>-0.32</td>
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<td>0.09</td>
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<tr>
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<td>-0.01</td>
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<td>1</td>
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</tr>
<tr>
<td>PP</td>
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<tr>
<td>O</td>
<td>0.04</td>
<td>0.08</td>
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<td>-0.25</td>
<td>-0.09</td>
<td>-0.11</td>
<td>1</td>
</tr>
</tbody>
</table>
Figure 7. Plots showing the direction of relationships between the most important predictor variables ($P < 0.05$) and ATTW counts per transect in northern Rocky Mountains for the best ($\Delta \text{BIC} = 0$) model. All other variables are held constant to show each relationship. Blue regression lines are fitted to the observed data at their original scale.
Figure 8. Plots showing the direction of relationships between the most important predictor variables (P < 0.05) and ATTW counts per transect in southern Rocky Mountains for the best (ΔBIC = 0) model. All other variables are held constant to show each relationship. Blue regression lines are fitted to the observed data at their original scale.
CHAPTER 3

Influence of Selective Thinning on Subalpine Bird Communities in the San Juan Mountains of Colorado

INTRODUCTION

Concurrent with climate change, the western United States has witnessed an increase in the frequency, severity, and duration of broad-scale disturbances including wildfire (Westerling et al. 2006) and bark beetle (*Dendroctonus* spp.) outbreaks (Bentz et al. 2010, Logan et al. 2010). In response to high levels of tree mortality due to bark beetle outbreaks affecting vast areas in the western United States there has been increasing consideration of management actions aimed at reducing forest susceptibility to outbreaks and/or mitigating the effects of the outbreaks that do occur (Fettig et al. 2007). Pre-emptive management typically involves silvicultural treatments designed either to increase resistance to outbreaks or favor post-outbreak resilience (DeRose and Long 2014). However, there are few field studies that assess either the effectiveness of vegetation treatments on forest resistance or resilience, and even fewer on the effects of treatments on ecosystem services such as biodiversity. As a result proposed management responses to bark beetle outbreaks are often controversial (Black et al. 2013). In the current study, we examine the effects of logging treatments in Engelmann spruce (*Picea engelmannii*)-subalpine fir (*Abies lasiocarpa*) in Colorado on avian occupancy.

In the Rocky Mountains, forests are managed to decrease vulnerability to bark beetle outbreaks by removing large-diameter trees, which are more susceptible to bark beetle colonization (Schmid and Hinds 1974, Hansen et al. 2010, Hart et al. 2014). Selective thinning alters forest composition and structure which results in significant habitat changes for forest-
dwelling bird communities. The effects of logging on forest communities should be monitored to evaluate ecosystem recovery from early to intermediate to late stages of succession. Timber harvest is likely the most extensive anthropogenic disturbance type within forested landscapes (Brawn et al. 2001). Timber harvest decreases the terrestrial biosphere carbon storage and indirectly leads to increased risk of natural disasters including fire and insect outbreaks (IPCC 2014). Given the increase in acreage affected by the spruce beetle (*Dendroctonus rufipennis* Kirby) since 2010 (Strebig and Lockwood 2014), managing healthy Engelmann spruce (*Picea engelmannii*)-subalpine fir (*Abies lasiocarpa*) forests is a priority for Colorado’s Forest Service (Colorado State Forest Service 2013). Despite extensive management, including shelterwood preparatory cuts, sanitation cuts, salvage cuts, group selection cuts, and improvement cuts that have taken place in spruce-fir forests of Colorado for over half a century (Alexander 1987), no formal research has assessed the long-term impacts of logging on other forest-dwelling species in Engelmann spruce-Subalpine fir forests. Understanding how ecological disturbances affect ecosystem function can provide valuable insight into the status and stability of inter-connected species communities. Our research provides the first quantitative assessment of the impacts of logging on avian community composition in one of the most important forest types in Colorado and the Rocky Mountains in general. This study is relevant for subalpine forests across the Rocky Mountains and the western U.S. because the bird communities are exceptionally consistent throughout the region (Smith 1980).

Forest thinning is a management technique that involves the removal of large diameter trees preceding outbreaks because large diameter spruce are more susceptible to beetle attack at the stand level (Schmid and Frye 1977). In the western U.S., researchers report mixed results on the effectiveness of the forest-thinning, beetle-prevention strategy (Fettig et al. 2007, Black et al.
2013), and no single thinning recommendation is guaranteed to succeed because beetles can maintain their endemic population levels in logging residuals (Schmid and Frye 1976). A recent study found no effect of selective harvesting treatments on resistance to spruce beetle outbreaks (Temperli et al. 2014). While a wealth of knowledge exists concerning the relationship between logging and cavity nesting bird species across a range of forest types (e.g. Saab et al. 2007, Saab et al. 2011, Thompson et al. 2013), this relationship has not been examined in Engelmann spruce forests. Engelmann spruce is Colorado’s most valuable forest type not only for timber but also for important wildlife habitat, livestock forage, and recreation (Alexander 1987). To ensure that this forest type functions as it is intended for society and native biota, an understanding of how management impacts forest communities is needed.

Birds are valuable for evaluating ecological integrity because large quantities of species can be simultaneously monitored using just a single detection method (Hutto 1998, Hutto et al. 2014). Additionally, birds play fundamental roles in the functioning of forest ecosystems. They promote tree regeneration and reproductive fitness by dispersing seeds to ensure the genetic diversity of seedlings, and they consume insect predators (Fayt et al. 2005). In turn, many bird species rely on mature conifer forests for food and nesting resources. Thus, the selective removal of large diameter spruce, could reduce the presence of seed-dependent avian species.

The effects of silviculture treatments, post-fire salvage logging, and clear-cutting have been examined in tropical lowland forests (Lambert 1992, Johns 1996), ponderosa pine/Douglas-fir forests (Saab et al. 2007, 2009, 2011), and in coniferous-deciduous forests (Keller et al. 2003) respectively. Results vary depending on the landscape in question. Logging treatments have been associated with increased avian richness in the short term (Imbeau et al. 1999). In deciduous forests of the Midwest, there was no significant difference in bird diversity between
logged and unlogged forests even when time since logging was considered (Robinson and Robinson 1999). Thompson et al. (2013) emphasized the importance of various stand structure characteristics that are beneficial for avian diversity and the retention of old growth forest species. Increased spatial heterogeneity within the landscape has been shown to promote greater avian diversity (Roth 1976, Brawn et al. 2001, Figure 1), yet this relationship remains inadequately described in spruce-fir forests of the U.S. To address this gap in literature, we examined the following research questions:

1. Do forests that are managed (selectively logged) to reduce host-susceptibility to spruce beetle infestation support higher or lower bird species richness than control (unlogged) forests?

2. Are certain avian species more strongly associated with managed spruce-fir forests?

3. What forest structure variables are associated with occupancy of avian species in spruce-fir forests?

4. How is occupancy of certain bird species affected by the addition of a spruce beetle outbreak in logged and unlogged sites?

We hypothesized that avian richness would not differ significantly between treated and control sites because we conducted surveys > 20 years post treatment. We expected avian occupancy in relation to thinning treatments to vary by species and life history traits. Cavity nesters such as the hairy woodpecker are known to favor unlogged, burned forests so may have a negative relationship with treated stands (Saab et al. 2002). Other birds like the northern flicker may benefit from more open-space for foraging created by fallen dead trees (Saab et al. 2007). Birds associated with mature conifers such as Ruby-crowned Kinglets and Townsend’s Warblers, rely on old trees for food and habitat and could show a negative change in occupancy after forest treatments due to diminished overstory structure (Lance and Howell 2000). More
generally, we expected a positive correlation between habitat heterogeneity and species richness as a function of niche space availability. To answer these research questions, we conducted point counts of breeding birds in paired, logged and un-logged, spruce-fir forests in the San Juan Mountains of Colorado over four years. During 2013 and 2014 there was minimal to no spruce beetle infestation in all three sample sites. During the second two years, a spruce beetle outbreak infested the majority of trees in all 18 plots of the Tuckerville site, allowing us to assess the impact of multiple disturbances on the avian community.

METHODS

Study Area

Sampling occurred in subalpine spruce-fir forests of Colorado in the San Juan National Forest. The subalpine zone occurs above the montane zone (~2,850 m) and below treeline (~3,500 m; Peet 1981). Southwestern Colorado’s climate is characterized by a bi-seasonal precipitation regime with snow from December to March and rain from July through September (Toney and Anderson 2006). The nearest climate station to the study area recorded data at an elevation of 2,691 m with maximum summer temperatures (June – August) ~23°C and minimum winter temperatures ~14°C (data for Rico, CO, retrieved from: http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?corico). Three sites were sampled in the San Juan National Forest during the breeding bird seasons of 2013, 2014, 2015, and 2016 (Figure 1). Two of these (Stoner Mesa Trail and Winter/Calico Trail) are located near Highway 145 in Rico, CO. The other site (Tuckerville) is located on Forest Road 501 near Lake Vallecito, CO. We sampled a paired, logged forest stand and a nearby unlogged forest stand at each of these three sites.
Site Selection

We located regions of spruce-fir forest that had been selectively harvested using the Rocky Mountain Management Activities dataset (RMACT) to locate polygons of logged forests in the San Juan Mountains (Figure 1, US Forest Service, 2013). Colorado Region 2, Aerial Detection Survey (ADS) maps created by the U.S. Forest Service were used to locate sites of recent spruce beetle outbreak (USFS 2010). Defoliation and mortality data are estimated during aircraft flyovers, converted to shape file format, and available for download at: http://www.fs.usda.gov/detail/r2/forest-grasslandhealth/?cid=fsbdev3041629. Digitized mortality polygons estimate the number of dead trees per acre and the agent of mortality, including bark beetle and defoliator insect species. ADS maps are available from 1996 to present (Chapman et al. 2012). The ADS data was used to control for the amount of spruce beetle activity in the logged plots, such that areas > 1 km from sites affected by spruce beetle in 2012 were excluded. The RMACT dataset was provided by the USFS San Juan Office. To identify thinning treatments that occurred in spruce-fir forest in the San Juan National Forest, a spatial overlay was performed in ArcGIS 10.1 with data selected from the post-1989 management activities dataset (i.e. salvage/sanitation cuts, shelterwood cuts, and commercial cuts) and the spruce-fir vegetation cover type layer from the Region 2 vegetation dataset (USDA 1998, Available at: http://www.fs.usda.gov/detail/r2/forest-grasslandhealth/?cid=fsbdev3041629). Based on this overlay, nine potential logging treatments were visited during Spring 2013 and three were determined suitable (Table 1). Plots were determined suitable if there was a large enough area to fit at least nine point counts within each paired plot (Figure 1), the dominant cover type was spruce, time since initial logging was 22–24 years, and there was less than 25% spruce beetle severity. Next to each logged plot, a site of comparable area that was not affected
by logging was chosen for a control plot following the paired plot method (following Veblen et al. 1989; Table 1; Figure 2; Figure 3). Control stands were located between 1 and 3 km away from the logged site to ensure the avian source pool was the same for both sites.

**Point Counts**

To explore the relationship between avian richness, logging, and spruce beetle outbreaks, point counts of breeding birds were conducted at the landscape scale. Point count stations were stratified within each homogeneous (either logged or unlogged) forest stand. Point count stations were spaced at least 250 m apart and at least 75 m from the forest edge to ensure each count was independent (Hanni et al. 2013). Each treatment and control plot was ~ 2 km² (Figure 1) and located 1 - 3 km apart from one another.

Point counts were conducted during the breeding bird season of 2013 and 2014 between June 10 and July 15 on days with minimal or no wind and no rain. Counts took place between about 0500 and 0900. Point count methods are based on the Rocky Mountain Bird Observatory’s “Field Protocol for Spatially Balanced Sampling of Landbird Populations” (Hanni et al. 2013). Each transect was sampled once during 2013 and three times during 2014, and each consecutive count was repeated by a different observer to minimize observer bias. During each 6-minute count, every bird species seen or heard was recorded. Using a Nikon Prostaff 5 Rangefinder, the radial distance from the observer to each individual bird detected was recorded and later classified into distance classes. A total of 54 point count stations (27 within treated stands and 27 within control stands) were sampled once during the summer breeding bird season of 2013 and thrice during 2014, 2015, and 2016.
**Logging and Habitat Variables**

We sampled a range of logged stands and control stands within the three study sites (Table 1). Treated stands were first cut between 22 and 24 years ago (Shelterwood or Preparatory cuts between 1989-1991; Table 1; Figure 3). Sanitation cuts followed primary cuts between 1992 and 1998. The most recent thinning treatment occurred at the Winter Trail Site in 1998, 15 years before we began conducting surveys, but the majority of management activities took place two decades ago (Table 1). We collected a variety of habitat and stand structure data (Lindenmayer 1999). We randomly centered a 20 m x 20 m plot around each point count tree, and measured plot- and tree-level data. Plot-level data included the elevation, UTM coordinates, slope, aspect, topographic position, and proportion of plot occupied by shrubs, graminoids, forbes, and litter. Shrubs were defined as woody stems < 5 m. Any needles, downed trees, branches, or dead material from trees was defined as litter. For each standing dead or live tree within the 400 m² plot, we documented the species, diameter at breast height (DBH), whether the tree was live or dead, decay class status (Table 2), and mortality agent. Decay class gives an estimate of mortality date or time since beetle onset. We also recorded the number of stumps (tree cut by chainsaw) in each plot. Covariates used in analyses were compiled at the plot-level (Table 3).

Logged plots had greater ratio of stumps to standing trees (Mean = 0.15, SD = 0.16) compared to unlogged plots (Mean = 0, SD = 0.01; Table 4). All logged and unlogged plots at the Tuckerville site became infested with spruce beetles in 2015 and remained infested in 2016 (Figure 4). Logged plots had fewer trees infested by spruce beetles (Mean = 0.39, SD = 1.18) than unlogged plots (Mean = 2.48, SD = 4.49). Winter Trail and Stoner Mesa sites remained at endemic levels of spruce beetles throughout the course of our study. Unlogged plots had a
higher number of snags in general (Mean = 5.07, SD = 2.41) than logged plots (Mean = 2.72, SD = 2.59). Quadratic Mean Diameter of trees was higher in unlogged plots (Mean = 1066.08, SD = 473.32) than logged plots (Mean = 654.99, SD = 199.88). Greater percent shrub cover was found in unlogged plots (Mean = 17.04, SD = 9.64) compared to logged plots (Mean = 14.83, SD = 8.68). No significant correlation existed between the ratio of stumps to standing dead trees and logged plots (Pearson’s r < 0.5; Table 4).

Data Analysis

We used a community-level, multi-species occupancy model to analyze the effect of logging and other habitat features on species occupancy and richness at our sites. Occupancy models use repeated survey data to estimate species detectability (p) conditional upon occupancy (species occurrence), to allow unbiased estimation of occupancy probabilities (ψ) given adequate data (MacKenzie et al. 2002, MacKenzie et al. 2006). We assumed that the occupancy state for a species at a given site could not change between visits within a year because our sampling occurred over a relatively short period of time (~ 1 month). Because of the potential for physical movement between visits, the occupancy state of a site described whether the site intersected at least one home range for a given species (Efford and Dawson 2012, Latif et al. 2016a, contra Hayes and Monofils 2015). Community-level parameters inform species-specific parameter estimates, which improves precision of species-specific parameters (Dorazio et al. 2006, Russell et al. 2009). Raptors, ravens, and grouse were excluded from analyses because they are not reliably detected by our survey methods and detections of these species do not necessarily indicate association with the survey point. We also excluded species that were outside of their
breeding range (Rodewald 2015). We removed any unidentified species and flyover detections. Only species that were within 100 m of the point count location were included in analyses.

We compiled and analyzed a three-dimensional data matrix $y$, where element $y_{ijt}$ was the sum of binary indicators for species detection (Sanderlin et al. 2014). Given a binary indicator $x_{ijkt} = 1$, we detected species $i$ ($i = 1,\ldots,N$) at point count station $j$ ($j = 1,\ldots,J$) during visit $k$ ($k = 1,\ldots,K; K = 1$ in 2013, $K = 3$ in 2014–2016) in year $t$ ($t = 1,\ldots,T; T = 4$). Because we did not have covariates that differed for detection between visits, we analyzed the sum of all binary detections for species $i$ over all visits at each point count station $j$ in year $t$, where $y_{ijt} = \sum_{s=1}^{3} x_{ijts}$ and $y_{ijt} \in \{0,1,\ldots,K\}$. Essentially, detection/nondetection data were collapsed across within-year visits so that each species had a detection frequency of 0, 1, 2, or 3 (Kéry and Royle 2016). We modeled the occupancy state for species $i$ at site $j$ in year $t$ given probability of occupancy $\psi_{ijt}$ as a Bernoulli latent variable $z_{ijt}$:

$$[z_{ijt}|\psi_{ijt}] \sim Bern(\psi_{ijt})$$  
(Equation 1)

We analyzed avian occupancy relationships with logging, early infestation, quadratic mean diameter of all tree species, number of snags, and shrub cover (Table 3). We modeled occupancy probability $\psi_{ijt}$ for species $i$ at point count station $j$ in year $t$ as a logit-linear function of logging ($\beta_{\text{log}}$) while controlling for effects of other forest structure covariates ($\beta_{\text{inf}}, \beta_{\text{QMD}}, \beta_{\text{sng}},$ and $\beta_{\text{shr}}$):

$$\begin{align*}
\text{logit}(\psi_{ijt}) &= \begin{cases} 
\beta_{0i} + \beta_1 \times z_{ij0} + \beta_{\text{log},i} \times Log_j + \beta_{\text{inf},i} \times Inf_{ij1} + \beta_{\text{QMD},i} \times QMD_j + \beta_{\text{sng},i} \times Sng_j + \beta_{\text{shr},i} \times Shr_j & t = 1 \\
\beta_{0i} + \beta_1 \times z_{ij(t-1)} + \beta_{\text{log},i} \times Log_j + \beta_{\text{inf},i} \times Inf_{ij1} + \beta_{\text{QMD},i} \times QMD_j + \beta_{\text{sng},i} \times Sng_j + \beta_{\text{shr},i} \times Shr_j & t > 1 
\end{cases}
\end{align*}$$  
(Equation 2)
Additionally to examine relationships with logging irrespective of other covariate effects, we modeled occupancy probability $\psi_{ijt}$ as a logit-linear function of the logging covariate alone:

$$\logit(\psi_{ijt}) = \left\{ \begin{array}{ll} \beta_{0,i} + \beta_1 \times z_{ij0} + \beta_{log,i} \times Log_j & t = 1 \\ \beta_{0,i} + \beta_1 \times z_{ij(t-1)} + \beta_{log,i} \times Log_j & t > 1 \end{array} \right.$$  

(Equation 3)

In both models, $\beta_1$ quantified the partial dependency of $\psi_{ijt}$ on the previous year’s occupancy state ($z_{ij(t-1)}$, $z_{ij0}$), which accounts for resampling of individual point count stations across years. Thus, the quantity $\beta_0 + \beta_1$ is the logit probability of persistence for species $i$. We modeled the occupancy state in year 0 ($z_{ij0}$) as a Bernoulli latent variable with probability $\psi_{i0}$ (see Russell et al. 2006). Covariate effects were $\beta_{log,i}$ for the logging effect, $\beta_{inf,i}$ for the early infestation effect, $\beta_{QMD,i}$ for the quadratic mean diameter effect, $\beta_{sng,i}$ for the snag effect, and $\beta_{shr,i}$ for the shrub effect. All parameters varied by species-specific random effects governed by community-level parameters with normally distributed priors. We examined the overlap of 90% Bayesian credible intervals (BCI) for covariate effects with zero to assess their statistical support. All covariates were scaled to mean = 0, SD = 1 to facilitate computation and comparison of covariate effect estimates. We were cautious about interpreting covariate relationships for species detected during ≤ 10 point × year occasions.

We derived species richness estimates by summing posterior estimates for each point count station $j$ in year $t$ across species: $N_{jt} = \sum_{i=1}^{I} z_{ijt}$. We did not model unobserved species, so community-level inferences were restricted to species observed at least once during our study (see also Russell et al. 2009, Latif et al. 2016b). We plotted $N_{jt}$ estimates across covariate gradients to explore how species richness changed with changing covariate values.
For both models (Equations 2, 3), we modeled the probability of observing species i at point count station j during year t, $y_{ijt}$, given the probability of detection $p_i$ and occupancy latent state $z_{ijt}$ as a binomial distribution with K trials ($K = \text{number of visits}$):

$$[y_{ijt} | p_i, z_{ijt}] \sim Bin(K, p_i \times z_{ijt})$$

(Equation 4)

Posterior estimates were sampled using JAGS v. 3.3.0 (Plummer 2003) operated with the R2jags package (Su and Yajima 2014) in the R statistical computing environment (R Core Team 2016). We used independent non-informative priors for all parameters (for priors, see Appendix A) and model code adapted from Latif et al. (2016b). We ran 4 parallel MCMC chains of length 45,000–55,000 iterations, with the first 5,000 iterations discarded as burn-in and no thinning. We verified that $n_{\text{effective}} \geq 100$ and $R \leq 1.1$ for all parameters (Gelman and Hill 2007). All R scripts, including BUGS code, are posted at https://github.com/qureshlatif/Julia-Kelly-Ch3.

We examined model goodness-of-fit for the fully parameterized model (i.e., with all covariates) using a posterior predictive test based on deviance. We simulated data from the model's posterior predictive distribution, and calculated a p-value quantifying the probability of deviance for observed data $\geq$ simulated deviance, where $p < 0.05$ or $p > 0.95$ would indicate lack of fit.

RESULTS

Surveyors detected 43 species within sampling locations (Table 5). Pine Siskins, Dark-eyed Juncos, Yellow-rumped Warblers, Mountain Chickadees, and Ruby Crowned Kinglets were the most common species detected with $\geq 180$ point x year detections each. Western Tanagers, Hermit’s Thrushes, American Robins, American Three-toed Woodpeckers, Brown Creepers, Chipping Sparrows, and Gray Jays were also abundant in our study area (105–150 point x year
detections each). Rare species included the Wilson’s Warbler, Band-tailed Pigeon, Green-tailed Towhee, Townsends’ Solitaire, Mountain Bluebird, White-breasted Nuthatch, Pygmy Nuthatch, Olive-sided Flycatcher, MacGillivray’s Warbler, Hammond’s Flycatcher, Williamson’s Sapsucker, Violet-green Swallow, Black-headed Grosbeak, Red-naped Sapsucker, and White-crowned Sparrow (fewer than 10 point x year detections). Detection probabilities were highest for Yellow-rumped Warblers, Ruby-crowned Kinglets, Pine Siskins, Dark-eyed Juncos, American Three-toed Woodpeckers, Western Tanagers, Hermit’s Thrushes, and Mountain Chickadees (p > 0.50; Table 5). Posterior median detection probabilities for species ranged 0.05–0.82 (Table 5). Our goodness-of-fit test for the model that included all covariates provided no evidence for a lack of model fit (p = 0.51).

We found no statistically supported relationships between logging and avian occupancy. Regardless of whether logging was the only covariate or other covariates were included, 90% BCIs for all logging effects overlapped zero and the magnitude of posterior median estimates were small (Figure 5). Not surprisingly, occupancy showed no notable changes with increased selective logging. In contrast, we found statistically supported relationships with the number of beetle-infested trees, the number of snags, quadratic mean diameter of all standing trees, and shrub cover (Figure 6). American three-toed Woodpeckers, Clark’s Nutcrackers, Northern Flickers, Broad-tailed Hummingbirds, and Hairy Woodpeckers exhibited positive occupancy relationships with early bark beetle infested trees, whereas Warbling Vireos, Western Wood Pewees, and Western Tanagers exhibited negative relationships (Figure 6). We also found positive relationships between Lincoln’s Sparrow occupancy and snags and Western Wood Pewee occupancy and quadratic mean diameter of trees. White-crowned Sparrows and House Wrens showed positive occupancy relationships with shrub cover (Figure 6), although White-
crowned sparrow parameters were estimated with limited detection data. No evidence existed that species richness was strongly affected by logging or beetle infestation (Figure 7).

Occupancy relationships with beetle-infested trees were most supported and strongest. American three-toed Woodpeckers showed the strongest positive relationship with infestation and were detected at 90% of plot × year occasions with 7 or more infested spruce trees (Figure 8). When the number of infested spruce was > 7, the probability of occupancy for Broad-tailed hummingbirds, Clarks Nutcrackers, Hairy Woodpeckers increased to > 75%, and increased to ~73% for Northern Flickers. Warbling vireos occupied 2–3 times as many of surveyed plots with 0 – 5 infested trees compared to plots with 7 – 23 infested trees (Figure 8). Occupancy for Western Tanagers decreased with increasing infested trees (Figure 8). Western Wood Pewee occupancy dropped by > 50% from low to high levels of infestation (Figure 8). In general, relationships with other forest structure covariates were less supported and weaker than were those with infestation (Figure 9).

DISCUSSION

We found no evidence for effects of logging c. 20–25 years later on species occupancy or richness, regardless of whether we accounted for effects of other forest structure features. This is likely because we sampled more than two decades after the first management activities occurred, allowing the forest sufficient time to recover. Additionally, logging intensity was relatively low at each site. We found occupancy relationships with other covariates, suggesting that sampling was sufficient to observe logging relationships had they been present.

Although, our primary goal was to analyze the long-term impacts of logging on avian occupancy and species richness, the onset of a spruce beetle outbreak in 1/3 of our sites allowed
us to explore avian community relationships with an active bark beetle infestation. The American three-toed woodpecker has responded numerically to spruce beetle infestations in the past and is thought to be the most important biological predator of spruce beetles (Koplin 1969, Koplin and Baldwin 1970, Schmid and Frye 1977). Although Hairy Woodpeckers are more generalized in terms of foraging behavior, as bark insectivores they may exploit bark beetle resources in freshly killed spruce trees (Koplin 1969).

Relationships with other forest structure features were generally consistent with species life histories with some exceptions. White-crowned Sparrows breed in shrubby habitats including forest edges (Chilton et al. 1995) and showed a positive change in occupancy to increased shrub cover in our study area. House wrens forage on a variety of insects in shrubs and low tree branches (Johnson 1998) and also had positive change to increased shrub cover. Lincoln’s Sparrows forage and nest on the ground in shrubby areas (Ammon 1995) but showed a positive response to snags. One explanation could be that plots with more snags tended to be shrubbier and therefore more suitable to Lincoln’s Sparrows. Western Wood Pewees are open cup nesters and forage on flying insects such as flies, wasps, and moths (Bemis and Rising 1999). They breed in open forests and forest edges and flycatch from perches (Bemis and Rising 1999), so their increased occupancy in relation to larger trees could be due to better perch and forage selection.

The main goal of this research was to contribute a greater understanding of how management applications within subalpine forests impact the avian community. We chose the paired-plot sampling method (cf. Veblen et al. 1989) to minimize the amount of topographic and climatic variability between sites. The paired-plot design ensured that the local breeding bird community had an equal opportunity to visit both sites and was not restricted by flying distance.
However, the paired-plot requirement limited the amount of sites that were suitable for our study because many of the potential sites that were scouted did not have a nearby reference spruce-fir stand. We wanted to control for variation in elevation, aspect, forest type, and slope, which also restricted the number of suitable sites. Increasing the number of replicated paired plots would have increased our statistical power and may have reduced potential spurious species relationships with snags and QMD.

Quantitative studies of avian occupancy in relation to logging in spruce-fir forests of Colorado were previously obsolete. Broad scale disturbances such as logging and spruce beetle outbreaks cause considerable change to subalpine forests. In addition to evaluating logging effects, we had the opportunity to study the impacts of an early onset spruce beetle outbreak during 2015 and 2016. Although we found no effects of logging on occupancy or avian species richness, we observed both positive and negative relationships with spruce beetle infested plots. Our research suggests that selective thinning techniques do not significantly disrupt the avian community two decades post-logging and represents the first assessment of logging effects avian occupancy and bird species richness in Engelmann spruce-Subalpine fir forests.

ACKNOWLEDGEMENTS

A Doctoral Dissertation Research Improvement Award (No. 1457894) funded this research. Financial support was also provided by the Neil Kindig Fellowship from the Colorado Mountain Club. The University of Colorado funded this research through the Undergraduate Research Opportunities Program, the Beverly Sears Student Research Grant, Dissertation Completion Fellowship, Jennifer Dinaburg Memorial Research Fellowship, and James A. & Jeanne D. DeSana Graduate Research Scholarship. Field assistants Andy Cole, Luke Schmitt,
Spencer Kerkhoff, and Bryan Hankinson were hard-working and dedicated to the data collection process. Field biologists Eric DeFonso, Alex Green, Josh Olsen, Brady Dunne, and Grace Carpenter were fantastic teachers and made the entire project possible. Thank you to the Veblen Lab group for their support and feedback on this project.
### Table 1. Site descriptions and history of management activities at each site composed of two site types – “Treated” or “Control”. Descriptions are adapted from Temperli et al. (2014).

<table>
<thead>
<tr>
<th>Site Name</th>
<th>Site Type</th>
<th>Management Activity Description*</th>
<th>Elevation</th>
<th>Aspect</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter Trail</td>
<td>Treated</td>
<td>Shelterwood Preparatory Cut 1989-1990; Sanitation (salvage) 1998</td>
<td>3150</td>
<td>NW</td>
</tr>
<tr>
<td>Winter Trail</td>
<td>Control</td>
<td>none</td>
<td>3200</td>
<td>N</td>
</tr>
<tr>
<td>Stoner Mesa</td>
<td>Treated</td>
<td>Shelterwood Preparatory Cut 1989; Sanitation (intermediate treatment, not regeneration) 1995</td>
<td>3150</td>
<td>N</td>
</tr>
<tr>
<td>Stoner Mesa</td>
<td>Control</td>
<td>none</td>
<td>3100</td>
<td>N</td>
</tr>
<tr>
<td>Tuckerville</td>
<td>Treated</td>
<td>Improvement Cut 1991, Sanitation (salvage) 1992</td>
<td>3350</td>
<td>NW</td>
</tr>
<tr>
<td>Tuckerville</td>
<td>Control</td>
<td>none</td>
<td>3450</td>
<td>NW</td>
</tr>
</tbody>
</table>

*Management treatments are as listed in the RMACT database (US Forest Service 2013b).

### Table 2. Status classes for each tree measured within the plot. Visual assessments of each tree were used to classify trees into status categories.

<table>
<thead>
<tr>
<th>Time Since Beetle Infestation</th>
<th>Status</th>
<th>Classification Criteria Based on Visual Assessment</th>
</tr>
</thead>
<tbody>
<tr>
<td>none</td>
<td>Live</td>
<td>No evidence of spruce beetles</td>
</tr>
<tr>
<td>0 - 1 year</td>
<td>Green</td>
<td>Beetle entrance holes, pitch tubes, live bark beetles or larvae on tree, green needles indicating first year of attack</td>
</tr>
<tr>
<td>1 - 2 years</td>
<td>Yellow</td>
<td>Yellow needles, frass, pitch tubes</td>
</tr>
<tr>
<td>3 - 5 years</td>
<td>Needle Drop</td>
<td>&lt; 50% of needles remain on tree</td>
</tr>
<tr>
<td>6 - 10 years</td>
<td>Twig</td>
<td>&lt; 50% of needles remain on tree, &gt;90% bark retention, &gt;50% of &lt;1 cm twigs on tree</td>
</tr>
<tr>
<td>11 - 15 years</td>
<td>Branch</td>
<td>&lt; 10% of needles remain on tree, bark retention variable, &lt;50% of &lt;1 cm twigs on tree</td>
</tr>
<tr>
<td>&gt; 15 years</td>
<td>Snag</td>
<td>No branches, &gt;1.37 m</td>
</tr>
<tr>
<td>none</td>
<td>Stump</td>
<td>&lt; 1.37 m, cut by chainsaw</td>
</tr>
</tbody>
</table>
Table 3. Covariates used to model species richness in logged and unlogged spruce-fir forests in the San Juan Mountains, Colorado. Covariates were compiled for each plot for each year (2013-2016).

<table>
<thead>
<tr>
<th>Variable Name</th>
<th>Variable Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Logging</td>
<td>Ratio of stumps to standing trees (live or dead) within plot</td>
</tr>
<tr>
<td>QMD</td>
<td>Quadratic Mean Diameter (squared diameter at breast height) of all spruce in plot regardless of status</td>
</tr>
<tr>
<td>Early Infestation</td>
<td>Total number of trees with a status classified as Green* and Yellow* within plot</td>
</tr>
<tr>
<td>Snag</td>
<td>Total number of standing dead trees classified as Needle Drop,* Twig,* Branch,* or Snag,* and ≥ 23 cm diameter at breast height.</td>
</tr>
<tr>
<td>Shrub</td>
<td>Percent shrub-cover within plot</td>
</tr>
</tbody>
</table>

*See Table 2 for list of status classification names and criteria

Table 4. Summary statistics and correlation coefficient (Pearson’s r) for covariates used to model species richness in logged and unlogged spruce-fir forests of the San Juan Mountains, Colorado. Correlations (Pearson’s r) are between covariates and the continuous index of logging intensity (Ratio of stumps to standing trees (live or dead) within plot).

<table>
<thead>
<tr>
<th>Covariate*</th>
<th>Logged Mean (SD)</th>
<th>Unlogged Mean (SD)</th>
<th>Pearson’s r</th>
</tr>
</thead>
<tbody>
<tr>
<td>Logging</td>
<td>0.15 (0.16)</td>
<td>0 (0.01)</td>
<td>1</td>
</tr>
<tr>
<td>EarInf</td>
<td>0.39 (1.18)</td>
<td>2.48 (4.94)</td>
<td>-0.073</td>
</tr>
<tr>
<td>Snag</td>
<td>2.72 (2.59)</td>
<td>5.07 (2.41)</td>
<td>-0.423</td>
</tr>
<tr>
<td>QMD</td>
<td>654.99 (199.88)</td>
<td>1066.08 (473.32)</td>
<td>-0.223</td>
</tr>
<tr>
<td>Shrub</td>
<td>14.83 (8.68)</td>
<td>17.04 (9.64)</td>
<td>-0.141</td>
</tr>
</tbody>
</table>

*See Table 3 for covariate descriptions
Table 5. List of species, species codes, total number of point x year detections (2013-2016), and species-specific detection probabilities (medians and 95% BCIs) from occupancy models fitted to data collected at logging and control sites in the San Juan National Forest, Colorado.

<table>
<thead>
<tr>
<th>Species Taxonomic Name</th>
<th>Code</th>
<th>Number of point x year detections</th>
<th>Detection Probability ($p$) and Upper and Lower Confidence Limits</th>
</tr>
</thead>
<tbody>
<tr>
<td>American Robin (Turdus migratorius)</td>
<td>AMRO</td>
<td>138</td>
<td>0.46 (0.42,0.51)</td>
</tr>
<tr>
<td>American Three-toed Woodpecker (Picoides dorsalis)</td>
<td>ATTW</td>
<td>114</td>
<td>0.53 (0.48,0.59)</td>
</tr>
<tr>
<td>Black-headed Grosbeak (Pheucticus melanocephalus)</td>
<td>BHGR</td>
<td>5</td>
<td>0.07 (0.02,0.19)</td>
</tr>
<tr>
<td>Brown Creeper (Certhia americana)</td>
<td>BRCR</td>
<td>107</td>
<td>0.38 (0.31,0.44)</td>
</tr>
<tr>
<td>Broad-tailed Hummingbird (Selasphorus platycerus)</td>
<td>BTLH</td>
<td>47</td>
<td>0.18 (0.12,0.26)</td>
</tr>
<tr>
<td>Band-tailed Pigeon (Patagioenas fasciata)</td>
<td>BTPI</td>
<td>1</td>
<td>0.05 (0.01,0.16)</td>
</tr>
<tr>
<td>Cassin's Finch (Haemorhous cassinii)</td>
<td>CAFI</td>
<td>16</td>
<td>0.18 (0.1,0.3)</td>
</tr>
<tr>
<td>Chipping Sparrow (Spizella passerina)</td>
<td>CHSP</td>
<td>105</td>
<td>0.4 (0.35,0.44)</td>
</tr>
<tr>
<td>Clark's Nutcracker (Nucifraga columbiana)</td>
<td>CLNU</td>
<td>37</td>
<td>0.14 (0.09,0.19)</td>
</tr>
<tr>
<td>Cordilleran Flycatcher (Empidonax occidentalis)</td>
<td>COFL</td>
<td>56</td>
<td>0.36 (0.28,0.45)</td>
</tr>
<tr>
<td>Dark-eyed Junco (Junco hyemalis)</td>
<td>DEJU</td>
<td>197</td>
<td>0.73 (0.7,0.76)</td>
</tr>
<tr>
<td>Evening Grosbeak (Coccothraustes vespertinus)</td>
<td>EVGR</td>
<td>67</td>
<td>0.33 (0.26,0.41)</td>
</tr>
<tr>
<td>Golden-crowned Kinglet (Regulus satrapa)</td>
<td>GCKI</td>
<td>51</td>
<td>0.27 (0.19,0.36)</td>
</tr>
<tr>
<td>Gray Jay (Perisoreus canadensis)</td>
<td>GRAJ</td>
<td>105</td>
<td>0.33 (0.27,0.4)</td>
</tr>
<tr>
<td>Green-tailed Towhee (Pipilo chlorurus)</td>
<td>GTTO</td>
<td>2</td>
<td>0.08 (0.03,0.24)</td>
</tr>
<tr>
<td>Hammond's Flycatcher (Empidonax hammondii)</td>
<td>HAFL</td>
<td>4</td>
<td>0.07 (0.02,0.18)</td>
</tr>
<tr>
<td>Hairy Woodpecker (Picoides villosus)</td>
<td>HAWO</td>
<td>59</td>
<td>0.2 (0.15,0.25)</td>
</tr>
<tr>
<td>Hermit's Thrush (Catharus guttatus)</td>
<td>HETH</td>
<td>140</td>
<td>0.51 (0.47,0.55)</td>
</tr>
<tr>
<td>House Wren (Troglodytes aedon)</td>
<td>HOWR</td>
<td>19</td>
<td>0.23 (0.14,0.35)</td>
</tr>
<tr>
<td>Lincoln's Sparrow (Melospiza lincolnii)</td>
<td>LISP</td>
<td>69</td>
<td>0.43 (0.35,0.51)</td>
</tr>
<tr>
<td>MacGillivray's Warbler (Geothlypis tolmiei)</td>
<td>MGWA</td>
<td>4</td>
<td>0.08 (0.02,0.21)</td>
</tr>
<tr>
<td>Mountain Bluebird (Sialia currucoides)</td>
<td>MOBL</td>
<td>3</td>
<td>0.07 (0.02,0.2)</td>
</tr>
<tr>
<td>Mountain Chickadee (Poecile gambeli)</td>
<td>MOCH</td>
<td>181</td>
<td>0.63 (0.59,0.68)</td>
</tr>
<tr>
<td>Northern Flicker (Colaptes auratus)</td>
<td>NOFL</td>
<td>22</td>
<td>0.1 (0.05,0.19)</td>
</tr>
<tr>
<td>Olive-sided Flycatcher (Contopus cooperi)</td>
<td>OSFL</td>
<td>4</td>
<td>0.1 (0.03,0.25)</td>
</tr>
<tr>
<td>Pine Grosbeak (Pinicola enucleator)</td>
<td>PIGR</td>
<td>59</td>
<td>0.17 (0.13,0.24)</td>
</tr>
<tr>
<td>Pine Siskin (Spinus pinus)</td>
<td>PISI</td>
<td>200</td>
<td>0.76 (0.72,0.79)</td>
</tr>
<tr>
<td>Pygmy Nuthatch (Sitta pygmaea)</td>
<td>PYNU</td>
<td>4</td>
<td>0.09 (0.03,0.27)</td>
</tr>
<tr>
<td>Red-breasted Nuthatch (Sitta canadensis)</td>
<td>RBNU</td>
<td>90</td>
<td>0.32 (0.25,0.39)</td>
</tr>
<tr>
<td>Ruby-crowned Kinglet (Regulus calendula)</td>
<td>RCKI</td>
<td>180</td>
<td>0.82 (0.79,0.85)</td>
</tr>
<tr>
<td>Red Crossbill (Loxia curvirostra)</td>
<td>RECR</td>
<td>75</td>
<td>0.23 (0.18,0.29)</td>
</tr>
<tr>
<td>Red-naped Sapsucker (Sphyrapicus nuchalis)</td>
<td>RN SA</td>
<td>7</td>
<td>0.07 (0.02,0.19)</td>
</tr>
<tr>
<td>Steller's Jay (Cyanocitta stelleri)</td>
<td>STJA</td>
<td>29</td>
<td>0.16 (0.09,0.25)</td>
</tr>
<tr>
<td>Townsend's Solitaire (Myadestes townsendi)</td>
<td>TOSO</td>
<td>3</td>
<td>0.06 (0.02,0.18)</td>
</tr>
<tr>
<td>Species</td>
<td>Code</td>
<td>Abundance</td>
<td>Percentage</td>
</tr>
<tr>
<td>-------------------------------------</td>
<td>-------</td>
<td>-----------</td>
<td>------------</td>
</tr>
<tr>
<td>Violet-green Swallow (<em>Tachycineta thalassina</em>)</td>
<td>VGSW</td>
<td>5</td>
<td>0.07 (0.02,0.2)</td>
</tr>
<tr>
<td>Warbling Vireo (<em>Vireo gilvus</em>)</td>
<td>WAVI</td>
<td>28</td>
<td>0.2 (0.13,0.3)</td>
</tr>
<tr>
<td>White-breasted Nuthatch (<em>Sitta carolinensis</em>)</td>
<td>WBNU</td>
<td>4</td>
<td>0.07 (0.02,0.2)</td>
</tr>
<tr>
<td>White-crowned sparrow (<em>Zonotrichia leucophrys</em>)</td>
<td>WCSP</td>
<td>9</td>
<td>0.17 (0.08,0.33)</td>
</tr>
<tr>
<td>Western Tanager (<em>Piranga ludoviciana</em>)</td>
<td>WETA</td>
<td>150</td>
<td>0.52 (0.47,0.56)</td>
</tr>
<tr>
<td>Western Wood-pewee (<em>Contopus sordidulus</em>)</td>
<td>WEWP</td>
<td>35</td>
<td>0.38 (0.29,0.48)</td>
</tr>
<tr>
<td>Williamson's Sapsucker (<em>Sphyrapicus thyroideus</em>)</td>
<td>WISA</td>
<td>5</td>
<td>0.07 (0.02,0.18)</td>
</tr>
<tr>
<td>Wilson's Warbler (<em>Cardellina pusilla</em>)</td>
<td>WIWA</td>
<td>1</td>
<td>0.05 (0.01,0.16)</td>
</tr>
<tr>
<td>Yellow-rumped Warbler (<em>Setophaga coronata</em>)</td>
<td>YRWA</td>
<td>182</td>
<td>0.85 (0.82,0.88)</td>
</tr>
</tbody>
</table>
FIGURES

**Figure 1.** Study area map of point locations within logged and unlogged spruce-fir stands in the San Juan National Forest, Colorado.
Figure 2. Photo of control (unlogged) plot within spruce-fir stand. Winter Trail Site, San Juan Mountains, Colorado. Photo taken by Julia Kelly.
Figure 3. Photo of treatment (logged) plot within spruce-fir stand. Winter Trail Site, San Juan Mountains, Colorado. Photo taken by Julia Kelly.
Figure 4. Photo of spruce beetle (*Dendroctonus rufipennis* Kirby) infesting an Engelmann spruce (*Picea engelmannii*) at Tuckerville Control Site in 2015, San Juan Mountains, Colorado. Photo taken by Julia Kelly.
Figure 5. Posterior parameter estimates (medians and 90% BCIs) illustrating occupancy relationships with the ratio of stumps to standing trees (live or dead) within plot ($\beta_{\text{Logging}}$; Panel A) and total number of trees classified as Green and Yellow within plot ($\beta_{\text{Infestation}}$; Panel B) for all bird species observed at least once within our study area. BCIs of statistically supported relationships do not cross zero (Panel B). See Table 4 for taxonomic species names and codes and Table 2 for tree status classifications.
Figure 6. Posterior parameter estimates (medians and 90% BCIs) illustrating species-specific occupancy relationships with the ratio of stumps to standing trees (live or dead) within plot ($\beta_{\text{Logging}}$; Panel A), total number of trees classified as Green and Yellow within plot ($\beta_{\text{Infestation}}$; Panel B), total number of standing dead trees $\geq 23$ cm diameter at breast height classified as Needle Drop, Twig, Branch, or Snag ($\beta_{\text{Snag}}$; Panel C) quadratic mean diameter (squared diameter at breast height) of all spruce in plot regardless of status ($\beta_{\text{QMD}}$; Panel D), total number of trees with a status classified as Green and Yellow within plot, and percent shrub-cover within plot ($\beta_{\text{Shrub}}$; Panel E). Positive relationships that are statistically supported are colored orange and statistically supported negative relationships are colored blue. See Table 4 for taxonomic species names and codes and Table 2 for tree status classifications.
Figure 7. Posterior estimates of species richness (median and 90% BCIs) for point x year survey occasions plotted against proportion of cut stumps (Panel A) and number of early infested (Green and Yellow phase) trees (Panel B). Community relationships with logging and beetle infestation were investigated using this information.
Figure 8. Point occupancy for single-species relationships with the number of early-infested spruce trees (Green or Yellow phase). Solid lines are finite-sample estimates (median and upper and lower 90% confidence limits) for three bins of infested trees: 0 trees, 1 – 5 trees, and 7 – 23 trees. E.g., top left plot: when there were zero infested trees, we found at least one ATTW ~60% of the time and when there were 7 – 23 infested trees, we found at least one ATTW ~90% of the time. Dashed lines are predicted occupancy probabilities. See Table 4 for taxonomic species names and codes.
Figure 9. Point occupancy for single-species relationships with total number of standing dead trees ≥ 23 cm diameter at breast height classified as Needle Drop, Twig, Branch, or Snag, quadratic mean diameter (squared diameter at breast height) of all spruce in plot regardless of status, and percent shrub-cover within plot. Solid lines are finite-sample estimates (median and upper and lower 90% confidence limits) for three bins of infested trees; 0 trees, 1 – 5 trees, and 7 – 23 trees. Dashed lines are predicted occupancy probabilities. See Table 4 for taxonomic species names and codes.
CHAPTER 4

Habitat relationships of American three-toed woodpeckers (*Picoides dorsalis*) during a spruce beetle (*Dendroctonus rufipennis* Kirby) outbreak in southern Colorado

INTRODUCTION

Periodic resource pulses characterize a variety of terrestrial ecosystems and directly influence primary consumer populations. Pulsed resources are defined as the ephemeral availability of greater than usual resources, which are then exhausted through time (for background see Ostfeld and Keesing 2000). Mast seeding by trees, pulses of nitrogen to aquatic systems, and irruptions of edible insects are all examples of pulsed resources that affect populations at higher trophic levels (Ostfeld and Keesing 2000). Super-annual resource pulses of spruce beetles (*Dendroctonus rufipennis* Kirby) elicit local increases in American three-toed woodpecker (*Picoides dorsalis*; ATTW) populations, which are key bark-beetle consumers (Koplin 1969, Koplin and Baldwin 1970, Koplin 1972, Schmid and Frye 1977). However, ATTWs also occur in forests that are unaffected by spruce beetle outbreaks so we investigated the relationship between ATTW presence across a range of spruce-fir forest stands and beetle infestation in Colorado.

Although disturbances play a critical role in a vast number of marine, terrestrial, and aquatic systems, they do not receive adequate research (Turner 2010). Understanding how disturbances affect ecosystem function can provide valuable insight into the vigor and stability of inter-connected species communities. Across the western United States, climate change has increased the frequency, severity, and duration of broad-scale disturbances including wildfire (Westerling et al. 2006) and bark beetle outbreaks (Bentz et al. 2010, Logan et al. 2010). Spruce
beetles are native to spruce trees (Picea spp.) and periodic irruptions are a major component of forest succession in Colorado (Baker and Veblen 1990, Veblen et al. 1991). The most recent spruce beetle infestation in Colorado expanded across 894,000 acres of spruce-fir forest in 2014 and 2015 alone and has affected 1.5 million acres in Colorado since 1996 (US Forest Service 2015). The presence of millions of dead trees has fueled scientific studies concerning increased wildfire risk and susceptibility to subsequent outbreaks (reviewed by Hicke et al. 2012, Jenkins et al. 2012, Kulakowski and Veblen 2015). Spruce trees may become more susceptible to bark beetle infestations due to climate warming and increased avalanche and windthrow events (DeRose et al. 2013). In addition to the temperature driver, outbreaks are forecasted to accelerate as a result of heightened drought stress (Hart et al. 2013), motivating the need to understand the impacts of spruce beetle disturbances on beetle-dependent avian species.

In North America, ATTWs are distributed nearly everywhere that spruce trees are found and can subsist when spruce is the only conifer present (Bock and Bock 1974). ATTWs are the highest-ranked biological predator of the spruce beetle, specifically adapted for digging out wood boring insect larvae (Koplin 1969, Koplin and Baldwin 1970, Koplin 1972, Schmid and Frye 1977, Saab et al. 2014). Studies of stomach contents revealed that ATTWs feed more heavily on spruce beetles than any other woodpecker species and exert the strongest control on prey density in spruce-fir forests of Colorado (Koplin 1972). Breeding ATTW density can increase to six nests per mile² within spruce beetle-infested forest stands (Koplin 1972). ATTWs are thought to be barometers of old-growth conifer persistence in North America (Wiggins 2004). The goal of our study was to inform ATTW management decisions by pinpointing key habitat structure variables associated with increased occupancy of ATTWs.
METHODS

Study Area

Sampling occurred in subalpine spruce-fir forests of Colorado in the San Juan National Forest. The subalpine zone occurs above the montane zone (~2,850 m) and below treeline (~3,500 m; Peet 1988). Southwestern Colorado’s climate is characterized by a bi-seasonal precipitation regime with snow from December to March and rain from July through September (Toney and Anderson 2006). The nearest climate station to the study area recorded data at an elevation of 2,691 m with maximum summer temperatures (June – August) ~23°C and minimum winter temperatures ~14°C (data for Rico, CO, retrieved from: http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?corico). Three sites were sampled in the San Juan National Forest during the breeding bird seasons of 2014, 2015, and 2016. Two of these (Stoner Mesa Trail and Winter/Calico Trail) are located near Highway 145 in Rico, CO. The other site (Tuckerville) was located on Forest Road 501 near Lake Vallecito, CO. One site was sampled in the Gunnison National Forest near Slumgullion Pass.

Site Selection

Colorado Region 2, Aerial Detection Survey (ADS) maps created by the U.S. Forest Service were used to locate sites of recent spruce beetle outbreak (USFS 2010). Defoliation and mortality data are estimated during aircraft flyovers, converted to shape file format, and available for download at: http://www.fs.usda.gov/detail/r2/forest-grasslandhealth/?cid=fsbdev3041629. Digitized mortality polygons estimate the number of dead trees per acre and the agent of mortality, including bark beetle and defoliator insect species. ADS maps are available from 1996 to present (Chapman et al. 2012). The ADS data was used to control for the amount of
spruce beetle activity within forest stands. Plots were determined suitable if there was a large enough area to fit at least 18 point counts within continuous spruce-fir. Two sites (Winter Trail and Stoner Mesa) containing 18 point count locations had little to no spruce beetle activity in 2014, 2015, and 2016 (Figure 1). The third site, Tuckerville, was free of bark beetles in 2014 but became infested in 2015 and remained infested in 2016 (Figure 2). In 2014, a fourth site (Slumgullion), was added to the study. At Slumgullion the onset of bark beetle infestation was 2013 or 2014, trees remained infested in 2015, and the outbreak tapered off in 2016.

**Point Counts**

To explore the relationship between ATTWs, spruce beetle outbreaks, and forest structure attributes, point counts of ATTWs were conducted in 4 different forest stands experiencing a range of bark beetle severity. Eighteen point count stations were stratified within each homogeneous spruce-fir forest stand, spaced at least 250 m apart and at least 75 m from the forest edge (Hanni et al. 2013). Each site was ~ 3 km² and located at least 10 km from another site.

Point counts were conducted at three sites during the breeding bird season of 2013, 2014, 2015, and 2016 between June 10 and July 15 on days with minimal or no wind and no rain. Points were sampled once during 2013 and thrice during the following three years. Counts took place between about 0500 and 1000. Point count methods are based on the Rocky Mountain Bird Observatory’s “Field Protocol for Spatially Balanced Sampling of Landbird Populations” (Hanni et al. 2013). Each transect was sampled once during 2013 and three times during 2014, and each consecutive count was repeated by a different observer to minimize observer bias. During each 6-minute count, we recorded every bird species seen or heard within 100 m of the
point count tree. Using a Nikon Prostaff 5 Rangefinder, the radial distance from the observer to each individual detected was recorded. For the purpose of this study, only records of ATTW detections were used in statistical analyses. ATTW detection data and forest structure attributes within 72 plots were used to assess occupancy relationships.

_Habitat Variables_

We randomly centered a 20 m x 20 m plot around each point count tree, and measured plot- and tree-level data. Plot-level data included the elevation, UTM coordinates, slope, aspect, topographic position, count of trees and proportion of plot occupied by shrubs, grasses, forbs, and litter. Shrubs were defined as woody stems < 5 m. Any needles, downed trees, branches, or dead material from trees was defined as litter. For each standing dead or live tree within the 400 m² plot, we documented the species, diameter at breast height (DBH), whether the tree was live or dead, decay class status (Table 1), and mortality agent. Decay class gives an estimate of mortality date or time since beetle onset. Using this field data we quantified the quadratic mean diameter of each tree regardless of status, the number of trees recently infested by spruce beetles, and the number of trees previously infested by spruce beetles within each plot (Table 2).

_Data Analysis_

We used an occupancy model to analyze the effect of bark beetle infestation and forest structural attributes on ATTW occupancy at our sites. Given adequate data, occupancy models estimate species detectability (p) conditional upon occupancy (species occurrence), to allow unbiased estimation of occupancy probabilities (ψ) utilizing repeated survey data (MacKenzie et
al. 2002, MacKenzie et al. 2006). Because our sampling occurred over a relatively short period of time (~ 1 month), we assumed that the occupancy state for a species at a given site could not change between visits within a year. Individual movement was likely between visits, so the occupancy state of a site described whether the site intersected at least one ATTW home range (Efford and Dawson 2012, Latif et al. 2016a, contra Hayes and Monofils 2015). Only ATTW detections within 75 m of the point count station were analyzed.

We compiled and analyzed a two-dimensional data matrix y, where element $y_{jt}$ was the sum of binary indicators for ATTW detections (Sanderlin et al. 2014). Given a binary indicator $x_{jkt} = 1$, we detected one ATTW at point count station j ($j = 1, \ldots, J$) during visit k ($k = 1, \ldots, K$; $K = 1$ in 2013 and $K = 3$ in 2014, 2015, and 2016) in year t ($t = 1, \ldots, T$; $T = 4$). Because we did not have covariates that differed for detection between visits, we analyzed the sum of all binary detections for ATTWs over all visits at each point count station j in year t, where $y_{jt} = \sum_{s=1}^{3} x_{jts}$ and $y_{jt} \in \{0,1,\ldots,K\}$. Essentially, detection data were summed across visits within each year to produce a detection frequency of 0, 1, 2, or 3 (Kéry and Royle 2016). We modeled detection frequencies given the probability of detection $p$ and occupancy latent state $z_{jt}$ as a binomial distribution with K trials ($K =$ number of visits):

$$[y_{jt}|p, z_{jt}] \sim Bin(K, p \times z_{jt})$$

(Equation 1)

We modeled the occupancy state for site j in year t given probability of occupancy $\psi_{jt}$ as a Bernoulli latent variable $z_{jt}$:

$$[z_{jt}|\psi_{jt}] \sim Bern(\psi_{jt})$$

(Equation 2)
We analyzed occupancy relationships with 4 covariates of interest (Table 2). We modeled occupancy probability $\psi_{jt}$ for point count station $j$ in year $t$ as a logit-linear function of early infestation ($\beta_{Ein}$), mid infestation ($\beta_{MInf}$), snags ($\beta_{sng}$), and quadratic mean diameter ($\beta_{QMD}$):

$$
\logit(\psi_{jt}) = \left\{
\begin{array}{ll}
\beta_0 + \beta_1 \times z_{j0} + \beta_{Ein} \times Einf_{jt} + \beta_{MInf} \times Minf_{jt} + \beta_{QMD} \times QMD_{jt} + \beta_{sng} \times Sng_{jt} & t = 1 \\
\beta_0 + \beta_1 \times z_{j(t-1)} + \beta_{Ein} \times Einf_{jt} + \beta_{MInf} \times Minf_{jt} + \beta_{QMD} \times QMD_{jt} + \beta_{sng} \times Sng_{jt} & t > 1 \\
\end{array}
\right.
$$

(Equation 3)

where $\beta_1$ quantified the partial dependency of $\psi_{jt}$ on the previous year’s occupancy state ($z_{j(t-1)}$, $z_{j0}$) and thereby accounts for resampling of individual point count stations across years (Latif et al. 2016b). Thus, the quantity $\beta_0 + \beta_1$ is the logit probability of ATTW persistence. We examined the overlap of 95% Bayesian credible intervals (BCI) for covariate effects with zero to assess their statistical support. All covariates were scaled to mean = 0, SD = 1 to facilitate computation and comparison of covariate effect estimates.

Posterior estimates were sampled using JAGS v. 3.3.0 (Plummer 2003) operated with the R2jags package (Su and Yajima 2014) in the R statistical computing environment (R Core Team 2016). We used independent non-informative priors for all parameters, i.e., a Normal (0,100)T(-30,30) prior for all parameters in Equation 3 and Uniform(0,1) for detection probability (all R scripts, including BUGS code, are posted at https://github.com/qureshlatif/Julia-Kelly-Ch4). We verified that $n_{\text{effective}} \geq 100$ and $\hat{R} \leq 1.1$ for all parameters (Gelman and Hill 2007).

Model goodness-of-fit was examined for the fully parameterized model (i.e., with all covariates) using a posterior predictive test based on deviance. We simulated data from the model's posterior predictive distribution, and calculated a p-value quantifying the probability of deviance for observed data $\geq$ simulated deviance, where $p < 0.05$ or $p > 0.95$ would indicate lack of fit.
RESULTS

Between 2013 and 2016, we detected 259 ATTWs. The greatest number of detections (N = 107) occurred in 2016. We detected the fewest ATTWs (N = 10) in 2013, when all sampled plots were free of spruce beetles. ATTWs were common in our study sites and detection probability was generally high (mean = 0.51, SD = 0.03). We witnessed extensive debarking (i.e. spruce beetle predation by ATTWs) in Slumgullion plots that were infested in 2014, 2015, and 2016 (Figure 3).

Three plots at the Slumgullion site were removed prior to conducting analyses because they went into a timber sale and were clearcut during the fall of 2014. Model results did not change substantially when these plots were included or removed, but because they varied significantly from other plots, we omitted them from analyses. The number of early-infested trees was slightly correlated with the number of mid-infested trees (r = 0.41; Table 3). Quadratic mean diameter of trees and the number of snags within the plot showed a minor negative correlation (r = -0.29; Table 3). Our goodness-of-fit test for the model that included all covariates provided no evidence for a lack of model fit (p = 0.68). Median and 95% BCIs for detectability = 0.51 (0.45, 0.56).

We found statistically supported relationships with ATTW occupancy and the number of early-infested spruce trees within plots. The number of early-infested trees was the only covariate where the posterior median estimates and 95% BCIs did not overlap zero (Figure 5). When the number of early-infested trees was 0, the probability of finding at least one ATTW was 57%. The presence of 1 – 8 beetle-infested spruce trees increased the probability of finding ATTWs to 71%. More importantly, the probability of finding one ATTW was 99.9% when there were > 8 infested trees within a plot (Figure 6).
In contrast, we found no statistically supported relationships between the number of mid-infested trees, the number of snags, or larger trees (QMD) and ATTW occupancy. The magnitude of posterior median estimates was small and 95% BCIs overlapped zero for each of these covariates (Figure 5). ATTW occupancy probability was 0.64 when there were 0-1 mid-infested spruce and occupancy probability only increased to 0.81 when there were 7 – 39 mid-infested spruce. When the quadratic mean diameter of trees increased within plots, occupancy probability (0.75) of ATTWs did not change. Occupancy estimates for ATTWs in our plots remained near 0.73 regardless of the number of snags within plots.

DISCUSSION

Spruce beetle outbreaks provide a critical food resource for ATTWs in spruce-fir forests of southern Colorado. Our results showed that current spruce beetle infestation was the most important predictor of ATTW occupancy in our study area. ATTWs are classified as a sensitive species in the southern Rocky Mountains (Region 2 of the USDA Forest Service) and our results could aid in protecting this species’ important habitat (Wiggins 2004). Our fine-scale analysis of tree-level habitat associations between ATTW occupancy and forest structural attributes, revealed some key findings useful to forest management efforts in subalpine forests of Colorado.

Our research represented a snapshot of ATTW use of spruce-fir forest habitat in the San Juan National Forest. Results of Chapter 2 suggested that the ATTW distribution in the southern Rockies was also closely tied to elevation, indicating a stronger connection to spruce habitat, which occurs at higher elevations in the southern Rockies. The majority of research investigating the numerical response of ATTWs to spruce beetles has come from the southern Rockies of Colorado (Hutchinson 1951, Baldwin 1968, Koplin 1969, Koplin and Baldwin 1970,
Koplin 1972, and reviewed by Fayt et al. 2005) The strong association with spruce beetles could explain why ATTWs are absent from the Sierra Nevada, which lacks spruce (Bock and Bock 1974). A detailed study of ATTW habitat relationships across its range in the Rocky Mountains is still needed. Chapter 2 results revealed that ATTW habitat associations were not as clear in the northern Rockies compared to the southern Rockies. The extent to which ATTWs feed on mountain pine beetles (*Dendroctonous ponderosae* Hopkins) in the southern Rockies remains unclear. ATTWs have not been reported inhabiting mountain pine beetle-infested forests in Colorado or southern Wyoming, but it is possible that they use these forests because they have been shown to respond numerically to mountain pine beetle epidemics in Canada (Drever et al. 2009, Edworthy et al. 2011). A recent review by Saab et al. (2014) highlighted positive relationships between ATTWs and mountain pine beetle outbreaks but only for northern Rockies locations. A detailed survey of habitat associations in pine forests in the southern Rockies and forests containing spruce in the northern Rockies is needed to better quantify regional shifts in ATTW-bark beetle associations.

We did not quantify nest site selection or nesting success for this study, so our results are only indicative of foraging rather than reproduction. Breeding success could increase in spruce beetle-infested stands but quantification of this relationship would require a more comprehensive study of ATTW demographics (Fayt et al. 2005). Information is needed on the types of trees ATTWs prefer for nesting. ATTWs are primary cavity nesters, excavating a new cavity each year (Martin and Eadie 1999, Martin et al. 2004, Rodewald 2015). Primary cavity nesters are keystone species within forests because small mammals and secondary cavity nesters rely on primary excavators for creation of tree cavities (Martin and Eadie 1999, Burdett and Niemi 2002). Primary cavity builders are essential components of nest webs - the interdependence
among cavity nesters for the creation and use of cavity resources (Martin and Eadie 1999, Martin et al. 2004). A variety of secondary cavity nesting birds can occur in our study area, including wrens, swallows, bluebirds, some owls, flycatchers, and others (Scott et al. 1980). Maintaining sufficient populations of primary cavity nesters will enhance biodiversity, a priority of forest managers. ATTWs were the most abundant primary cavity excavators detected in our study area (see Chapter 3), so protecting their habitat requirements, will ensure the continued production of cavities for other nest web species. Although ATTWs are known to nest in snags (Hutto 1995) and a variety of standing dead trees containing soft inner wood (Lorenz et al. 2015), we did not find a statistically supported relationship between occupancy and snags in our study area. Nor did we find a relationship between occupancy and large tree diameter. Future work must address nest site selection over a broader study area to determine which trees ATTWs prefer for nesting and which types of trees are associated with better nesting success.

The relationship between ATTW occupancy and current spruce beetle infestation was further illustrated by the supported relationship to early-infested spruce trees and the unsupported relationship with mid-infested trees. In our study area, we detected at least one ATTW 99.9% of the time when there were ≥ 9 early-infested trees within a plot. The number of mid-infested trees did not have an effect on ATTW occupancy within our study area. A slight correlation existed between mid-infestation and early-infestation because many of the beetle-infested trees transitioned to the mid-infestation category by the end of our study period (2016). Occupancy was still relatively high in mid-infestation sites likely because these sites also had some trees with active bark beetles.

Although forest management efforts are currently aimed at reducing the risk of beetle infestations, our results indicate that beetle-disturbed forests provide a critical food resource for
ATTWs. ATTWs likely track spruce beetles as outbreaks expand across the landscape. Similar to the Black-backed woodpecker’s (*Picoides arcticus*) intimate relationship with post-fire habitat and wood-boring beetles (Hutto 1995), ATTWs are strongly connected to bark beetle-infested forests (Murphy and Lehnhausen 1998). Just as Black-backed woodpeckers are limited in their distribution to recently burned forests, ATTWs may be restricted to recent spruce beetle infestations (Bock and Bock 1974, Hutto 1995) in the southern Rockies. Logging to mitigate future spruce beetle attacks could jeopardize the availability of beetle resources and put pressure on populations of ATTWs in southern Rockies. Timber management strategies in post spruce beetle-infested stands should be modified to reduce impacts to primary cavity nesting species and spruce beetle predators in general. As a focal cavity excavator in spruce-fir forests, conservation of ATTWs may stimulate an umbrella effect by extending habitat security to other cavity nesting species in subalpine forests of Colorado (Simberloff 1998, Martin and Eadie 1999, Fleishman et al. 2000, Fleishman et al. 2001).

ACKNOWLEDGEMENTS

A Doctoral Dissertation Research Improvement Award (No. 1457894) funded this research. Financial support was also provided by the Neil Kindig Fellowship from the Colorado Mountain Club. The University of Colorado funded this research through the Undergraduate Research Opportunities Program, the Beverly Sears Student Research Grant, Dissertation Completion Fellowship, Jennifer Dinaburg Memorial Research Fellowship, and James A. & Jeanne D. DeSana Graduate Research Scholarship.
Table 1. Status classes for each tree measured within the plot. Visual assessments of each tree were used to classify trees into status categories (adapted from Temperli et al. 2014)

<table>
<thead>
<tr>
<th>Time Since Beetle Infestation</th>
<th>Status</th>
<th>Classification Criteria Based on Visual Assessment</th>
</tr>
</thead>
<tbody>
<tr>
<td>none</td>
<td>Live</td>
<td>No evidence of spruce beetles</td>
</tr>
<tr>
<td>0 - 1 year</td>
<td>Green</td>
<td>Beetle entrance holes, pitch tubes, live bark beetles or larvae on tree, green needles indicating first year of attack</td>
</tr>
<tr>
<td>1 - 2 years</td>
<td>Yellow</td>
<td>Yellow needles, frass, pitch tubes</td>
</tr>
<tr>
<td>&lt; 5 years</td>
<td>Needle Drop</td>
<td>&lt; 50% of needles remain on tree</td>
</tr>
<tr>
<td>6 - 10 years</td>
<td>Twig</td>
<td>&lt; 50% of needles remain on tree, &gt;90% bark retention, &gt;50% of &lt;1 cm twigs on tree</td>
</tr>
<tr>
<td>11 - 15 years</td>
<td>Branch</td>
<td>&lt; 10% of needles remain on tree, bark retention variable, &lt;50% of &lt;1 cm twigs on tree</td>
</tr>
<tr>
<td>&gt; 15 years</td>
<td>Snag</td>
<td>No branches, &gt;1.37 m</td>
</tr>
<tr>
<td>none</td>
<td>Stump</td>
<td>&lt; 1.37 m, cut by chainsaw</td>
</tr>
</tbody>
</table>

Table 2. Covariates used to model American three-toed woodpecker occupancy in spruce-fir forests of the San Juan Mountains, Colorado. Covariates were compiled for each plot for each year (2014, 2015, and 2016).

<table>
<thead>
<tr>
<th>Variable Name</th>
<th>Variable Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>QMD</td>
<td>Quadratic Mean Diameter (squared diameter at breast height) of all spruce in plot regardless of status</td>
</tr>
<tr>
<td>Early Infestation</td>
<td>Total number of trees with a status classified as Green* and Yellow* within plot. This variable represents active spruce beetle infestation.</td>
</tr>
<tr>
<td>Mid Infestation</td>
<td>Total number of trees with a status classified as Needle Drop* and Twig* within plot. This variable represents trees killed by spruce beetles for &gt; 2-3 years, where galleries are visible but spruce beetles are no longer present on tree.</td>
</tr>
<tr>
<td>Snag</td>
<td>Total number of standing dead trees classified as Branch,* Snag* and ≥ 23 cm diameter at breast height. Includes trees killed by any mortality agent &gt; 10 years ago.</td>
</tr>
</tbody>
</table>

*See Table 1 for list of status classification names and criteria
Table 3. Covariate correlation (Pearson’s $r$) matrix for variables used to model occupancy of American three-toed woodpeckers in spruce-fir forests of the San Juan Mountains, Colorado. See Table 2 for variable descriptions.

<table>
<thead>
<tr>
<th></th>
<th>Early Infestation</th>
<th>Mid Infestation</th>
<th>Snag</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early Infestation</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mid Infestation</td>
<td>0.41</td>
<td>1.00</td>
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</tr>
<tr>
<td>Snag</td>
<td>0.06</td>
<td>0.21</td>
<td>1.00</td>
</tr>
<tr>
<td>QMD</td>
<td>-0.23</td>
<td>-0.26</td>
<td>-0.29</td>
</tr>
</tbody>
</table>
FIGURES

Figure 1. Spruce-fir forest stand at the Winter Trail site, which remained unaffected by bark beetles from 2014 – 2016. Photo taken by Julia Kelly.
Figure 2. Tuckerville site, which became infested by bark beetles in 2015 and remained infested in 2016. Tree needles are still green because the infestation began when the photo was taken. The point count tree was marked by pink tape for relocation purposes each year. Photo taken by Julia Kelly.
Figure 3. Example of spruce beetle excavation by American three-toed woodpeckers at the Slumgullion site in 2015. Foraging is concentrated on bark beetle larvae residing in the bole of the spruce tree. Photo taken by Julia Kelly.
Figure 4. Example of point count locations within a spruce-fir forest stand. Point counts were spaced > 250 m apart and > 75 m from transition to another habitat type such as a meadow or aspen grove.
Figure 5. Parameter estimates (median) and 95% BCIs for occupancy of American three-toed woodpecker. The quantities $\beta_0$ and $\beta_0 + \beta_1$ are the logit-linear probabilities of occupancy at average covariate values for previously unoccupied and occupied points, respectively. Covariate effects quantify the estimated logit-linear effect of covariates scaled to mean = 0 and SD = 1. Covariates are described in Table 2.
Figure 6. American three-toed woodpecker occupancy in relation to the number of early-infested spruce trees (Green or Yellow status). The solid and dashed lines are median and 95% BCIs respectively for predicted occupancy probabilities. Points and error bars are finite sample estimates (median and 95% confidence limits) for three bins of early-infested trees; 0, 1–8, and 9–50 within sampled plots.
CHAPTER 5
DISCUSSION

Patterns of Avian Richness

We investigated relationships between avian occupancy and two different disturbance types – logging and spruce beetle outbreaks. Previous studies have documented changes in avian richness as a result of logging in other forest types (Lambert 1992, Imbeau et al. 1999), yet we did not find evidence that selective logging changed occupancy of breeding birds in our study area > 20 years post logging. To understand the long-term impact of selective harvesting in spruce-fir forests of southern Colorado, we targeted sampling in forests that were initially logged 22-24 years ago to allow for recovery to a later successional stage. In boreal black spruce forests, time since logging was associated with presence of certain bird species (Imbeau et al. 1999). Open-land species such as Lincoln’s Sparrows tended to characterize early- to mid-successional post-logging black spruce stands whereas species such as Boreal Chickadees, Winter Wrens, and Golden-crowned Kinglets tended to occupy later-successional forest stages (Imbeau et al. 1999). A community-level occupancy model revealed no effect of selective logging on avian richness in our study area, although we found relationships between certain bird species and the number of infested spruce trees, quadratic mean diameter of trees, shrub cover, and the number of snags within sampled plots. Our analyses did not reveal changes in occupancy for similar late-successional species detected in our sites such as the Mountain Chickadee and Golden-crowned Kinglet (Rodewald 2015). Nor did we find an effect of logging on occupancy of early-successional species such as Lincoln’s and White-crowned Sparrows detected during surveys.
We sampled in stands with minimal logging over a small area (~ 1–3 km) and did not sample clearcuts, so most of the logged plots retained a relatively high proportion of standing trees. Thus, we are cautious in extending our results to forests that have been extensively harvested over a larger area. However, we suggest that thinning treatments that yield a logging ratio (number of cut to standing trees) of < 0.30 should not have a long-term effect on avian richness after 20 years in un-infested spruce-fir forests of southern Colorado. To our knowledge this is the first occupancy analysis of bird species in Engelmann spruce-Subalpine fir forests to report species-specific habitat relationships. Our results should be used as a baseline report on the presence of 43 breeding bird species in Colorado’s subalpine forests. If future logging activities in spruce-fir forests aim to maintain a logging ratio similar to what we observed at our sites, we expect the avian community to maintain species richness in the long term.

While we could not report an effect of logging on avian richness, we found supported occupancy relationships between active spruce beetle infestation and eight bird species in our study area. Primary cavity nesters, including ATTWs, Hairy Woodpeckers, and Northern Flickers had a positive relationship with bark beetle-infested trees. Such species are likely to find suitable nesting locations within beetle-infested stands containing trees that are more easily excavated. While ATTWs and Hairy Woodpeckers drill bark and forage for bark beetles, Northern Flickers primarily forage on the ground. Clark’s Nutcrackers and Broad-tailed Hummingbirds had a positive association with beetle-infested trees as well. Broad-tailed Hummingbirds are known to feed on sap and visit Red-naped Sapsucker sapwells (Camfield et al. 2013). We observed multiple sapwells in beetle-infested plots. Sap is the tree’s primary defense against bark beetle infestation and sap accumulates in recently attacked sites around beetle entrance holes (Schmid and Frye 1977). Clark’s Nutcrackers are known to
opportunistically feed on beetles, but their primary food source is pine seeds (Tomback 1998). Clearcutting in beetle-infested spruce-fir stands could negatively affect occupancy of ATTWs, Hairy Woodpeckers, and Northern Flickers, and should be considered before treatments are performed.

We observed negative occupancy relationships between beetle-infested spruce trees and Warbling Vireos, Western Wood Pewees and Western Tanagers in our study area. Warbling Vireos forage in treetops mainly eating caterpillars, pupae, and moths, and nest in mature deciduous woodlands at high elevations, which would include aspen but not spruce-fir in our study area (Gardali and Ballard 2000). Western Wood Pewees breed along forest edges and in open woodlands, flycatch a range of flies and bugs, and are open cup nesters (Bemis and Rising 1999). It is possible that beetle-infested stands did not offer preferred foraging and nesting resources for Western Wood Pewees. Western Tanagers forage for insects and fruit in the tops of trees and shrubs and are not particularly associated with one forest type over another (Hudon 1999). Their diverse diet and need for forest canopy as nesting sites could explain their negative relationship to beetle-infestation where the canopy foliage is dying. Notably, our analysis of avian occupancy relationships with spruce beetle infestation is only for a three-year period, so continued monitoring of these sites is needed over a longer time scale, to determine whether our observed relationships change through time.

We also found supported positive relationships between occupancy of Lincoln’s Sparrows and increasing snags and occupancy of Western Wood Pewees and larger trees. White-crowned Sparrow and House Wren occupancy was also positively related to increasing shrub cover. Lincoln’s sparrows associate with meadows, bogs, and riparian thickets in montane zones. They nest in willow shrubs and forage on spiders, larvae, beetles, etc. (Ammon 1995).
We did not find a correlation between snags and shrub cover in our study sites, so the positive relationship between occupancy of Lincoln’s Sparrows and increased snags is potentially spurious. Since Western Wood Pewees are perching flycatchers, it is possible that occupancy increased in plots with larger trees because suitable perch sites increased, although we did not test this relationship directly. The positive relationship between White-crowned sparrow occupancy and increasing shrub cover was meaningful given that they nest and forage in shrubs. House Wrens nest in crevices including old woodpecker holes and nest boxes and use a variety of trees and shrubs for foraging (Johnson 1998) which, may explain their association with shrubs in our study area. Positive relationships between occupancy and increasing shrub cover suggest the need for structural heterogeneity within forests to promote a wider variety of bird species.

**Research Limitations and Future Directions**

The number of avian field biologists available for sampling limited the scope of this research. In any given summer field biologists could only commit to about one week of sampling at a time. Another limitation was site accessibility at high elevations, which was dictated by snowmelt in early to mid June, and permitted a short time frame (~1 month) for sampling. The short window for sampling combined with limited avian field technicians meant that fewer plots could be included in our study because each plot was visited thrice per year. A broad-scale, detailed census of the avian community in spruce-fir forests is needed to determine if the relationships we report here are true for spruce-fir forests in other parts of Colorado. Since spruce-fir is the most extensive forest type in the southern Rockies, it is critical to assess the impacts of spruce-fir disturbances on forest dwelling species at the regional scale. Likewise, continued surveys within our study area are needed to assess the long-term impacts of bark
beetle outbreaks on the avian community. Occupancy of certain species such as bark insectivores could change in relation to time since beetle infestation as the food supply diminishes. We did not have the resources to study breeding success of bird species in our study area. Data on nest site selection and reproductive success in beetle-infested and selectively logged forests are needed to inform breeding bird management decisions in Colorado.

American three-toed Woodpecker Habitat Associations

Recent bark beetle infestations in the U.S. Rocky Mountains provided the opportunity to explore ATTW relationships with bark beetles temporally and spatially. During our study period, ATTW abundance was best explained by elevation and presence of spruce-fir forest in both the northern and southern Rockies. ATTW relationships with spruce suggested that ATTWs were more strongly tied to spruce beetles compared to mountain pine beetles or Douglas-fir beetles. Nonetheless, analyses of occupancy relationships with habitat in spruce in the U.S. northern Rockies are needed to verify this prediction. Our analysis in the southern Rocky Mountain region revealed a meaningful connection between ATTW abundance and decreased distances to bark beetle-infested forests, while the distance to bark beetle variable was not related to ATTW abundance in the northern Rockies. This could be due to a lack of beetle activity in general in the northern Rockies. The Bird Conservancy of the Rockies provided data for 2010 – 2015, which limited our ability to test ATTW associations with bark beetles in early years when the mountain pine beetle infestation was expanding across the region. Nevertheless, our approach is novel in its use of spatially explicit point count data and aerial detection survey data at a regional scale.
To complement the coarse-scale analysis of ATTWs across the Rockies, we conducted an analysis of ATTW occupancy relationships with tree-level attributes. The spruce beetle outbreak in the San Juan Mountains of Colorado provided a unique chance to study this relationship from 2013-2016. We could only find a statistically supported relationship between ATTW occupancy and the number of currently infested spruce trees. ATTWs were detected at least once in all plots containing eight or more infested spruce, suggesting a strong relationship with outbreak stages compared to stands experiencing minimal to no infestation. Therefore, we expect the availability of beetle-infested spruce to limit the population size of ATTWs in Colorado. A few of our plots at the Slumgullion site went into a timber sale and were clearcut as part of a post-beetle salvage. While we did not find a relationship between ATTW occupancy and snags, it is highly plausible that ATTWs use snags for nest sites and post-beetle logging could degrade breeding habitat. We did not search for nests or monitor nesting success and research into ATTW reproductive requirements are necessary.

Persistence of ATTWs is essential for Colorado’s spruce-fir forests due to their role as primary cavity excavators in this forest type. Density of ATTWs could have an influence on richness and abundance of other cavity nesting species that require primary excavators to provide them with breeding sites (Martin and Eadie 1999). Primary excavators detected in our study area also included Red-naped Sapsuckers, Hairy Woodpeckers, Northern Flickers, and Williamson’s Sapsuckers but these species were not as common. Mountain Chickadees and Red-breasted nuthatches are weak cavity excavators (Martin and Eadie 1999). Both were common in our study area and they also use holes excavated by primary cavity nesters when they do not excavate their own holes. Secondary cavity nesters rely entirely on primary excavators for nesting sites (Martin and Eadie 1999). Secondary cavity nesters detected in our study area
included Mountain Bluebirds, Violet-green Swallows, Brown Creepers, House Wrens, Pygmy Nuthatches and White-breasted Nuthatches (Kingery and Ghalambor 2001, Martin and Eadie 1999, Grubb and Pravosudov 2008). Protection of ATTW habitat including beetle-infested trees will inherently promote future nesting sites of both weak and secondary cavity nesters that breed in Colorado’s forests. Old beetle-infested trees may also provide suitable nesting structures for other cavity builders that prefer to excavate softer wood. We argue that ATTWs are a keystone species in Colorado and their persistence on the landscape is a critical component of maintaining richness of cavity nesters in spruce-fir habitats. More research is needed to better understand ATTW connections to different conifer and bark beetle species across their range.

Research Limitations and Future Directions

It is still unknown whether or not ATTWs feed on mountain pine beetles in the southern Rockies. Studies documenting ATTWs in the southern Rockies have been in relation to spruce beetles in spruce-fir forests of Colorado (Hutchinson 1951, Yeager 1955, Koplin 1969, Koplin and Baldwin 1970). We were unable to incorporate surveys of lodgepole pine into this dissertation research due to the timing of bird surveys at high elevations. ATTWs have been documented feeding on mountain pine beetles in the northern Rockies of the U.S. (Mosher 2011) and in Canada (Martin et al. 2006, Drever et al. 2009, Edworthy et al. 2011). Surveys of beetle-infested lodgepole pine forests in the southern Rockies are needed to determine if mountain pine beetles are an important food resource in the southern portion of the ATTW’s range. A comparison of the relative importance of each bark beetle species in the ATTW’s diet would be a valuable research effort in the future. Likewise, more research is needed to document ATTW relationships to spruce and spruce-beetles in Wyoming, Idaho and Montana. Because spruce is
not as widely distributed in the U.S. northern Rockies it is possible that mountain pine beetles are more abundant and therefore more widely used by ATTWs in this part of their range. Moreover, an analysis of ATTW nest site selection and nesting success would also be beneficial. Research should investigate ATTW preference for nesting in beetle-infested stands, the types of trees that are selected for cavities, and nest sites that lead to increased nesting success. Selective logging and clearcutting in beetle-infested spruce-fir forests should be studied to determine if such activities degrade important nesting habitat for ATTWs and other cavity nesters in general.
REFERENCES


APPENDICES

**Appendix A.** Summary statistics for elevation and distance to bark beetle infestation variables for presence and absence transects by ecoregion (2010-2015).

<table>
<thead>
<tr>
<th>Year</th>
<th>Total ATTW detections</th>
<th>Number of presence and absence transects</th>
<th>Elevation (m) for Presence Transects</th>
<th>Elevation (m) for Absence Transects</th>
<th>Distance (m) to Beetle Infestation for Presence Transects</th>
<th>Distance (m) to Beetle Infestation for Absence Transects</th>
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<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mean</td>
<td>Min</td>
<td>Max</td>
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<td>69</td>
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Appendix B: Summary statistics for forest habitat in presence (P) and absence (A) transects from 2010-2015

<table>
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<tr>
<th>Year</th>
<th>Total ATTW detections</th>
<th>Number of presence and absence transects</th>
<th>Average proportion (%) of habitat classified as &quot;Mixed Conifer&quot;</th>
<th>Average proportion (%) of habitat classified as &quot;Spruce-Fir&quot;</th>
<th>Average proportion (%) of habitat classified as &quot;Ponderosa Pine&quot;</th>
<th>Average proportion (%) of habitat classified as &quot;Lodgepole Pine&quot;</th>
<th>Average proportion (%) of habitat classified as &quot;Aspen&quot;</th>
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Appendix C. Summary of ATTW abundance and total area affected by the primary bark beetle mortality agents (SB and MPB) in the study area from 2010 - 2015 in the Northern and Southern Rockies Ecoregions.

<table>
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<tr>
<th>Year</th>
<th>Number of presence and absence transects</th>
<th>Total ATTW detections</th>
<th>Total area of SB and MPB infestation (ha)</th>
<th>Total area of SB infestation (ha)</th>
<th>Total area of MPB infestation (ha)</th>
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<tbody>
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<td>2010</td>
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<table>
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<th>Year</th>
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<th>Total area of SB and MPB infestation (ha)</th>
<th>Total area of SB infestation (ha)</th>
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<td>199</td>
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<td>195,860.81</td>
<td>5,209.05</td>
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<td>2015</td>
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<td>86</td>
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**Appendix D.** Habitat Classification Codes and Descriptions used by Bird Conservancy of the Rockies Field Biologists to classify forest cover types at each point count location (Hanni et al. 2013)

<table>
<thead>
<tr>
<th>Code</th>
<th>Habitat Classification</th>
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<tr>
<td>AR</td>
<td>&quot;Agricultural/Rural&quot; vegetation has been planted by humans for food production or ornamental purposes in sparsely developed areas. Examples include a farmed field with wheat, corn, millet, etc., a fallow field, or a rural home site with planted non-native species. Please make note of crop spp., if fallow, etc.</td>
</tr>
<tr>
<td>AS</td>
<td>&quot;Aspen&quot; overstory dominated by aspen although scattered ponderosa pine or Douglas-fir may be present. The overstory cover should be 10% and consist of 50% Aspen. Aspen stands often have an abundant and diverse shrub layer. Typical shrub species in aspen habitats include snowberry, willow, sagebrush, mountain mahogany and oak. On occasion there may be no shrub layer. Typically the ground under aspen stands is covered by grasses and forbs.</td>
</tr>
<tr>
<td>AT</td>
<td>&quot;Alpine Tundra&quot; high-elevation, open landscapes that occur above treeline. These areas should have no overstory and often lack a significant shrub component. Ground cover consists of short grasses (generally 10cm in height), wild flowers, mosses, lichens and succulents.</td>
</tr>
<tr>
<td>BU</td>
<td>&quot;Burned Area&quot; forest habitat with &gt;5% overstory cover where &gt;50% of canopy is dead and shows evidence of severe fire scars or where &gt;50% of trees have burned and fallen.</td>
</tr>
<tr>
<td>CR</td>
<td>&quot;Cliff/Rock&quot; area is dominated by rock and/or generally lacking vegetative cover (e.g., talus slopes, boulder fields, and rocky outcroppings). Areas described as Cliff/Rock should have 20% shrub and vegetated ground cover.</td>
</tr>
<tr>
<td>DS</td>
<td>&quot;Desert/Semi desert Shrubland&quot; dry landscape containing shrubs, but lacking a co-dominant grass component. Shrubs often include sagebrush, greasewood, fremont mahonia and saltbush (see Sage Shrubland). Ground cover layer is typically dominated by bare ground and rock with limited forbs and grasses present. Grass and forbs make up 20% of ground cover.</td>
</tr>
<tr>
<td>GR</td>
<td>&quot;Grassland&quot; landscape lacking an overstory and significant shrub component. Ground cover is dominated by grasses and perhaps some forbs. Shrub component must be 20%. The sum of live and dead standing grass 20%</td>
</tr>
<tr>
<td>II</td>
<td>&quot;Insect Infested&quot; 10% of the overstory dead or sickly - typically referring to pine bark beetle affecting lodgepole and ponderosa pine. Canopy cover must be 10%.</td>
</tr>
<tr>
<td>LP</td>
<td>&quot;Lodgepole Pine&quot; 10% canopy cover that is dominated by lodgepole pine. Canopy may have other conifer species or some aspen but lodgepole pine must be dominant. Shrub layer can be conspicuous or nearly absent.</td>
</tr>
<tr>
<td>MC</td>
<td>&quot;Mixed Conifer&quot; forested habitat consisting of several species of conifers, such as ponderosa pine, lodgepole pine, Douglas-fir or spruce/fir spp. If the area is dominated by Douglas-fir, use Mixed Conifer as the primary habitat type. 10%. Overstory may range from very dense to relatively open. Undergrowth is complex and typically contains deciduous shrubs and/or conifer saplings. Stands with dense overstory may have little or no shrub and ground cover layers.</td>
</tr>
<tr>
<td>MM</td>
<td>&quot;Montane Meadow&quot; Areas with little to no overstory that are surrounded by forests. Elevations should be 7,000'. Soils should be moist to wet with forbs or grass as the dominant ground cover.</td>
</tr>
<tr>
<td>OW</td>
<td>&quot;Open Water&quot; habitat consisting of 50% open water, bank, and shoreline. Any other habitat type may be present, but must be &lt;50%.</td>
</tr>
<tr>
<td>PJ</td>
<td>&quot;Pinyon-Juniper&quot; vegetative communities largely influenced by pinyon pine, juniper or a combination of the two species. The overstory and shrub cover must sum to 10%. Semi-arid conditions often produce a relatively short overstory. Juniper tends to dominate at lower elevations while pinyon dominates at higher elevations. Typically, shrub layer includes sagebrush, rabbit brush, oak or mahogany. Ground cover is usually dominated by grasses with fewer forbs.</td>
</tr>
<tr>
<td>PP</td>
<td>&quot;Ponderosa Pine&quot; areas with 10% overstory cover that is made up primarily of Ponderosa Pine. This habitat often includes other tree types such as fir, pine and aspen. Shrub layer relatively open and often includes common juniper, oak, cliffrose and currents. Ground cover typically dominated by grass species.</td>
</tr>
<tr>
<td>RI</td>
<td>&quot;Riparian&quot; stands or strips of trees or shrubs near a permanent or seasonal water source. Typical tree and shrub species include cottonwood, box elder, maple, aspen, alder and willows. Typically isolated areas surrounded by coniferous forest, grassland, shrubland or sagebrush habitat. If riparian habitat is present within the 50m radius, this should be the primary habitat type.</td>
</tr>
<tr>
<td>SA</td>
<td>&quot;Sage Shrubland&quot; habitat where grasses and shrubs are co-dominant and the shrub cover is 20%. Typical ground cover is dominated by grasses with limited forbs and bare ground.</td>
</tr>
<tr>
<td>SF</td>
<td>&quot;Spruce-fir&quot; coniferous forest that is dominated by spruce and fir species (typically occurring at elevations 7000'). Note that Douglas-fir is not a true fir species (see Mixed Conifer). Overstory cover should be greater than or equal to 10% with spruce and fir species dominating the overstory cover. Variable understory typically includes shrubs and forbs with few grasses.</td>
</tr>
<tr>
<td>SH</td>
<td>&quot;Shrubland&quot; landscape co-dominated by grass and shrub species. Shrub cover must be 20%. Sagebrush must be &lt;30% of shrub layer (see Sage Shrubland). Typical shrub species include ceonothus, manzanita, sage, rabbitbrush, currant, skunkbrush, serviceberry and plum. Ground cover dominated by grasses.</td>
</tr>
<tr>
<td>UR</td>
<td>&quot;Urban/Residential&quot; areas highly impacted by human development in which 20% of the ground is covered by impermeable surfaces. Typically describing relatively dense development including houses, lawns, sidewalks and streets.</td>
</tr>
<tr>
<td>WE</td>
<td>&quot;Wetland&quot; habitat influenced by permanent or seasonal flooding resulting in tall reeds, grasses, and/or cattails with little to no overstory. This habitat is defined by the presence of some emergent vegetation that is adapted to wet soils or inundation. Typical species include cattails, sedges, rushes and sphagnum mosses. Overstories are limited to drier areas around the wetland and overstory cover must be 20%.</td>
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