HABITAT SELECTION, NESTING SUCCESS AND GENETIC STRUCTURE OF THE AMERICAN THREE-TOED WOODPECKER (*PICOIDES DORSALIS*) IN THE BLACK HILLS OF SOUTH DAKOTA

BY

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ABSTRACT

HABITAT SELECTION, NESTING SUCCESS AND GENETIC STRUCTURE OF THE AMERICAN THREE-TOED WOODPECKER (*PICOIDES DORSALIS*) IN THE BLACK HILLS OF SOUTH DAKOTA

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Isolated, rare and sedentary species face unique ecological and conservation challenges that common, contiguous populations may not experience. The American Three-toed Woodpecker population in the Black Hills of South Dakota is of particular conservation concern because of its geographic isolation from other populations and sedentary behavior which may increase its risk of extirpation. Because of this species close association with dense high elevation conifer forests and its unobstrusive behavior, basic ecological and genetic data are lacking. In this comprehensive study, I combine ecological data such as foraging, nesting and home range habitat selection along with population abundance estimates and genetic population structure data to determine the overall status of the American Three-toed Woodpecker population in the Black Hills of South Dakota. Relative abundance estimates from population surveys indicated 0.20 birds per census point in white spruce forests in the Black Hills. This estimate is roughly similar to other populations in the Rocky Mountains. To determine foraging preferences, I compared use of foraging substrates to substrate availability and found that the Black Hills population preferred large (> 23 cm dbh) living and dead spruce and large ponderosa pine trees and selected against living small spruce. Although the American Three-toed Woodpecker is known to exploit areas of recent disturbances such as post-burn habitats because of increased foraging opportunities, the Black Hills population was not present in areas of recent burns. Aspen appears to be an important characteristic for nest site selection as 61% of nests were located in aspens and nest sites had significantly more large living and snag aspens compared to random sites. In contrast to previous research, our results do not support the importance of conifer snags for nesting substrates. Nesting success estimates in this study were lower than those for other primary cavity nesting birds. Overall apparent nesting success was 42.9% and nest success estimates that account for when nests were found were even lower (Mayfield nest success = 13.0% and simple-model maximum-likelihood nest success estimate = 17.4%). Consistent with other nesting success studies focusing on cavity nesting birds, most nest failures were attributed to predation. The home range size was comparable to that of Eurasian Three-toed Woodpecker (*Picoides tridactylus*), but smaller than for other western conifer forest woodpecker species. Edge habitats such as roads appear to be important within home ranges and at a landscape scale. Black Hills American Three-toed Woodpeckers show high genetic variation in microsatellite loci and high haplotype diversity and low nucleotide diversity in mtDNA sequences. Overall, these results are indicative of a population bottleneck and subsequent range expansion with extremely limited recent gene flow between the Black Hills population and other populations. Because of the geographic isolation, natural history characteristics and limited

amount of gene flow, the Black Hills population of American Three-toed Woodpeckers should be a priority in resource management planning.

Chapter 1: Introduction

General Life History

The American Three-toed Woodpecker (*Picoides dorsalis*) is an inconspicuous woodpecker which resides in high elevation conifer forests in Canada and the United States (Figure 1.1) and is considered a habitat specialist based on its close association with old-growth coniferous forests in boreal and montane regions (Hoyt and Hannon 2002). As such, it is used in several USDA Forest Service Region 2 National Forests, an area which encompasses Wyoming, Colorado, South Dakota, Nebraska and Kansas (Figure 1.2), as a management indicator species (MIS) to gage the effects of management actions on changes in population trends of the species and also to estimate the effects of management planning alternatives (Wiggins 2004).

Additionally, as a primary nest excavator it is likely to be a keystone species similar to that of the closely related Eurasian Three-toed Woodpecker *Picoides tridactylus* (Pechacek 2004) due to the service it provides by creating nesting and roosting cavities that can be used by secondary cavity nesters such as other avian species or mammals (Aitken et al. 2002). Secondary cavity nester populations are considered to be limited by the number of available cavities within the community as successful reproduction is largely dependent upon the reuse of cavities (Aitken et al. 2002). Forest management exacerbates the limited supply of cavities in many areas due to the removal of dead or dying trees that are often sought after by primary nest excavators. With fewer potential nesting and roosting trees in the community for primary excavators such as the American Three-toed Woodpecker, the effects will be felt further down the "nest web" to the secondary cavity nesters (Martin and Eddie 1999).

The American Three-toed Woodpecker's importance at the community and ecosystem level is discordant with the lack of basic life history information for the species (Leonard 2001). Due to its rarity throughout its range, its elusive nature and consequently the difficulty in locating the species, there is limited basic ecological information on the American Three-toed Woodpecker. Most of what is known of the American Three-toed Woodpecker is anecdotal or based on the research of the closely related Eurasian Three-toed Woodpecker (Leonard 2001). The few studies that have been conducted have concluded that the American Three-toed Woodpecker is a sedentary species, but is also known to be irruptive in areas outside its geographic range if food resources increase due to natural disturbances such as fire, insect outbreaks or disease (West and Speirs 1959, Yunick 1985) that can weaken conifer trees and thereby increase the abundance of beetles which are preferred prey. It forages mainly by pecking,

flaking or scaling tree trunks for Cerabycidae (wood-boring beetles) (Short 1974), but will also consume bark beetles (Scolytidae) (Wiggins 2004). In addition, it is known to occupy recent burns in many portions of its range for up to three years, but occupancy decreases from 3- 8 years post-burn (Hoyt and Hannon 2002). Although other studies have cited burned coniferous forests as important habitats for the American Three-toed Woodpeckers (Murphy and Lehnhausen 1998, Hutto and Young 1999) , in the Black Hills American Three-toed Woodpeckers do not occupy burns (Giroir et al. 2007). The majority of burns occur in ponderosa pine (*Pinus ponderosa*) forests in the southern regions where conditions are warmer and dryer (Shepperd and Battaglia 2002). The subalpine belt of white spruce (*Picea glauca*) occurs in the cooler and moister northern hills (Shepperd and Battaglia 2002). Because the American Three-toed Woodpecker is closely associated with white spruce forests (Imbeau et al. 1999), the predominance of fires in ponderosa pine forests may explain the lack of occupancy of recent burns in the Black Hills.

The American Three-toed Woodpecker is a medium-sized bird with a body mass of 46-66g. Its underparts are white, but include black barring on the sides, black upperparts and varying amounts of white on the back which is a defining feature for subspecies identification. The crown on males is a patch of yellow with streaks of white (Leonard 2001). It is often found in sympatry with other woodpecker species including Hairy (*Picoides villosus*), Downy (*Picoides pubescens*) and the closely related Black-backed (*Picoides arcticus*) woodpeckers. Both American Three-toed and Black-backed woodpeckers posses three toes (lacking the hallux), with two forward and one backward instead of the common four-toe (zygodactylous) condition as in other woodpeckers (Goggans et al. 1989). The lack of a hallux along with skull

modifications are thought to be part of an adaptive complex that provide greater force when striking a tree surface during excavation, foraging or drumming. The adaption comes at the cost of greater energy expenditure during climbing when compared to other woodpecker species that possess four toes (Spring 1965).

Systematics and Distribution

Prior to 2003, the currently named Eurasian Three-toed Woodpecker was classified as conspecific with the American Three-toed Woodpecker. The Three-toed Woodpecker was considered the only woodpecker that was found both in the Nearctic and Palearctic. However, genetic research along with observations of morphological and vocalization differences led the American Ornithologists union to impose a species-level split between the two species resulting in the recognition of the Palearctic species as the Eurasian Three-toed Woodpecker (*Picoides tridactylus*) and the Nearctic species as the American Three-toed Woodpecker (*Picoides dorsalis*; Leonard 2001). Three subspecies of the American Three-toed Woodpecker are differentiated based on morphological differences: *Picoides dorsalis bacatus*, *P.d. fasciatus* and *P.d. dorsalis*. *P.d. bacatus*, the smallest of the subspecies, resides in northern Canada south to northern Minnesota and Michigan and east to New England in the United States and possesses the defining morphological feature of a mostly black back with narrow white stripes. *P.d. fasciatus* resides in Alaska, east to Alberta Canada and south down to British Columbia, Montana, Oregon and Washington. It has a mostly black back with narrow barring and is intermediate in size among the other subspecies. *P.d. dorsalis* is a resident in the Rocky Mountains from western Montana to northwestern New Mexico and western Arizona. It is

identified by its white back with few or no white bars and is considered the largest of the three subspecies. The geographically isolated population in the Black Hills of South Dakota is also classified as *P.d. dorsalis* based on its morphology; however, no genetic studies prior to the current study have been conducted on this population to confirm this classification.

Justification

This study focuses on the American Three-toed Woodpecker in the Black Hills, South Dakota. The sedentary nature of the American Three-toed Woodpecker along with the geographic isolation of the population in the Black Hills are important reasons to conduct a basic ecology and genetic study of a species that appears to be largely dependent on old growth and mature spruce forest, which is a limited habitat within the Black Hills. The Black Hills are known as one of the most heavily logged National Forests in the United States with almost every hectare cut at least once within the last 125 years (Ball and Schaefer 2000, Wienk et al. 2004). Logging changes the composition and structure of vegetation, thereby affecting the distribution and abundance of bird communities (Mills et al. 2000). Because of the limited availability of its preferred habitat and the high levels of habitat disturbance in the Black Hills, it is clear that the population status of the Black Hills population of American Three-toed Woodpecker is potentially a cause for concern. In Region 2 of the USDA Forest Service, the Black Hills population is listed as management indicator species (MIS), and at the regional scale it is listed as a sensitive species due to its rarity. A sensitive species is defined as a population whose current or predicted downward trends in abundance or habitat requirements will reduce its distribution (Wiggins 2004). The rarity, isolation, habitat specialist requirements, importance in

the community and ecosystem and lack of information available on the Black Hills population of American Three-toed Woodpecker demonstrate the need for a broad study of this unique population. Due to the lack of management plans for white spruce habitat in the Black Hills, which is the preferred habitat for the American Three-toed Woodpecker (Giroir et al. 2007), it is imperative that information on population abundance, distribution, foraging and nesting characteristics along with home range size and associated habitat attributes be studied in order to guide future white spruce management plans. In addition, past genetics research conducted on the American Three-toed Woodpecker concluded that there was little variability and no phylogeographic structure among subspecies (Zink 2002); however, this study was limited to small population sizes in contiguous habitats. Isolated populations such as those in the Black Hills were not sampled. Based on the life history characteristics of American Three-toed Woodpecker as a sedentary species and the geographic isolation of this population, a genetics study is important to further elucidate the current status of the population in the Black Hills. Results from ecology and genetics studies of the American Three-toed Woodpecker may have broad implications in the future for landscape management and conservation plans, not only in the Black Hills, but across their geographic range.

Study Area

The Black Hills, South Dakota is a mountain range that is often referred to as an "island on the plains" (USDA Forest Service, 2005). The highest peak rises over 2215 m above sea-level, and the mountain range spans 200 km from north to south and 100 km east to west (Froiland 1978). Two-thirds of the Black Hills lie in southwest South Dakota (Figure 1.3) and

one-third in northeast Wyoming, a portion of which is also known as the Bearlodge Mountains, which are geologically similar and often included in the Black Hills proper when referenced.

Figure 1.3. American Three-toed Woodpecker study area Black Hills National Forest, South Dakota.

The Black Hills are considered an eastern outlier of the Rocky Mountains, and the nearest mountain ranges are the BigHorns to the west and the Laramies to the southwest, each of which are 240-320 km from the Black Hills (Froiland 1978). During the Cenozoic era the Black Hills began their development as part of the Laramide mountain building event which later formed the Rocky Mountains. Over millions of years, a core of granite uplifted the surrounding sedimentary rock and over time, erosion has left an older crystalline granite core in the east of central Black Hills with younger steeply sloping sedimentary deposits at different stages of metamorphosis surrounding the core (Froiland 1978).

The granite core area is considered one of the most productive areas for ponderosa pine which is the most dominant overstory species in the Black Hills, covering almost 95% of the

forested area (Sheppard and Battaglia 2002, Brown and Cook 2006). The Limestone Plateau and Minnelusa Foothills encircle the granite core, and the width of the Limestone Plateau varies from 3 km in the southeast to 25 km in the west and elevations range from 1850-2200 m. Due to the higher elevations, the climate is cooler and the annual precipitation is often higher; therefore these conditions are conducive to the production of subalpine belts of white spruce along with the more common ponderosa pine. The Black Hills are one of only a few areas south of the Canadian border where pure populations of white spruce grow (Hoffman 1987).

The Limestone Plateau and Minnelusa Foothills are encircled by the Red Valley which consists of sandstone, sandy clay and shale soils. This topographical feature is unfavorable for many types of vegetation, most likely due to dry conditions and high salt content in the soils. Therefore, usually only grasses, junipers and a few ponderosa pine trees are found here. Surrounding the Red Valley is the Hogback Ridge which is the outermost rim of the Black Hills. It consists of sandstones and readily supports ponderosa pines and grasses (Radeke and Westin 1963, Shepperd and Battaglia 2002). Although the geology greatly affected the current distribution of vegetation in the Black Hills, the recent Pleistocene geologic period also had a profound effect on the composition and distribution of vegetation.

The Pleistocene was a geologic period of numerous glacial advances and retreats that ranged from 1.8 million to 10,000 years ago. During the Wisconsin glacial maxima, which was the most recent at 12,000 years B.P. (Lomolino et al. 2006), areas north, east and west of the Black Hills were glaciated, and although the Black Hills remained an unglaciated pocket, its vegetation composition and distribution was strongly affected by the cool, moist climate during

the glacial maxima (Froiland 1978). It is likely that the boreal-type coniferous forests expanded from the higher elevations in the Black Hills to the lower elevations and that areas around the Black Hills became contiguous montane/boreal coniferous forests. When the glaciers receded, the climate became warmer and dryer and the boreal-type coniferous forests became isolated to higher elevations in the Black Hills (Froiland 1978). Some species that lacked dispersal abilities or developed specific adaptations to their environments became stranded on high elevation isolated mountains such as the Black Hills (Lomolino et al, 2006).

Today, the climate in the Black Hills is variable due to its location in the middle of the continent along with its elevational variations. Although it is considered to have a continental climate, which typically consists of cold winters and hot summers, the higher elevation of the Black Hills tends to lessen the variations such that the climatic differences are not as dramatic as those experienced in the surrounding plains (Froiland 1978). The differences in elevational gradient between the northern and southern Black Hills affect the climate such that in general, the northern Black Hills are cooler and moister, whereas the southern Black Hills are warmer and drier. The varied climate, topography, geology and isolation from other mountain ranges have created a variety of habitats in the Black Hills that are considered a refuge for biodiversity within the Northern Great Plains (Shepperd and Battaglia 2002).

The study area for this project focuses on the American Three-toed Woodpecker's preference for white spruce habitat (Bock and Bock 1974), which is mainly found on the Limestone Plateau in the northern Black Hills. The majority of the study was conducted in the northern Black Hills (Figure 1.4) due to its high abundance of white spruce (and consequently American Three-toed

Woodpeckers), however, there is a small distribution of white spruce that reside in the southern Black Hills near Custer, South Dakota which was part of the study area for the first year of research. The first year focused on surveys to document the abundance and distribution of the American Three-toed Woodpecker in the Black Hills. In addition, a few east, central and southern locations in both non-white spruce and white spruce habitat were part of the study area for the population survey and vegetation analyses.

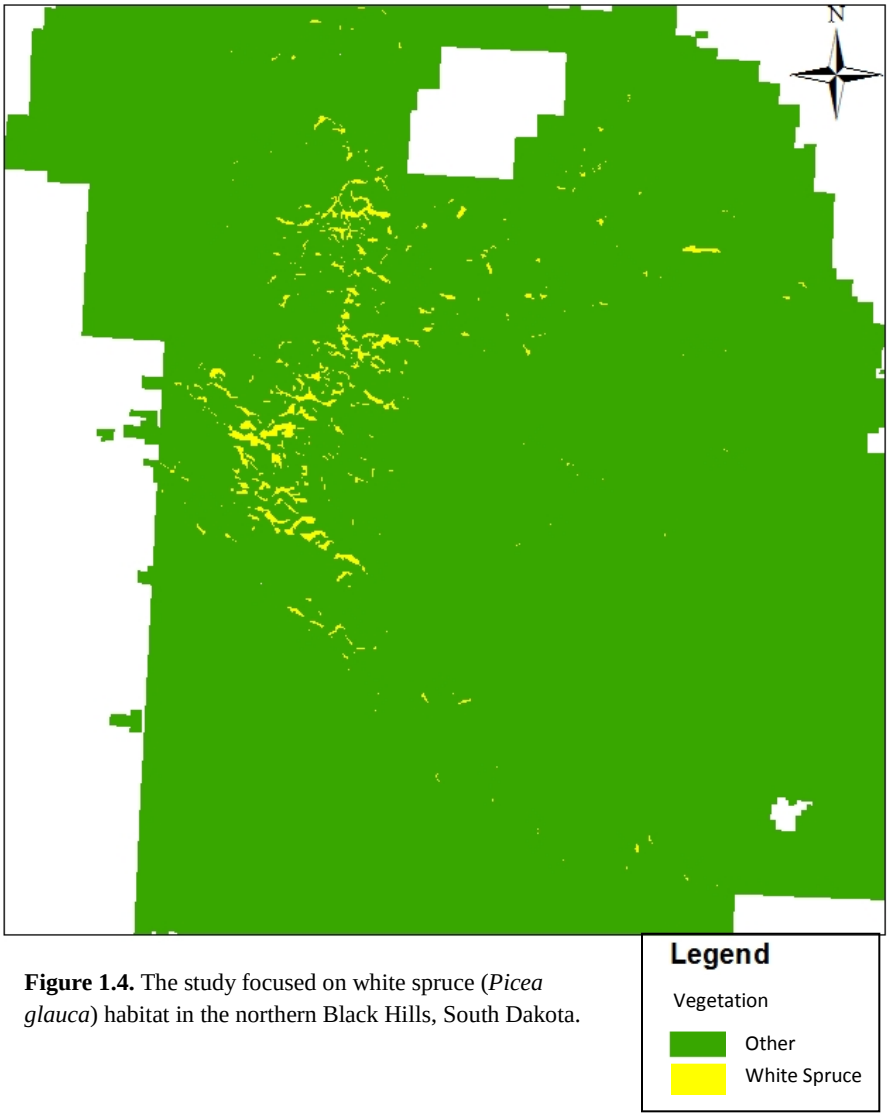

Figure 1.4. The study focused on white spruce (*Picea glauca*) habitat in the northern Black Hills, South Dakota.

The genetic analyses mainly involved a comparison between the Black Hills American Three-toed Woodpecker population and the Lolo National Forest population in northwest Montana. A few genetic samples from Alaska, Washington and Alberta, Canada were obtained for additional comparative analyses.

Objectives

The objectives of this study were to:

1. Survey white spruce habitat to determine abundance of American Three-toed Woodpeckers in the Black Hills

2. Record information on foraging behavior to determine if American Three-toed Woodpeckers in the Black Hills demonstrate a preference for particular foraging substrates

3. Monitor reproductive success and determine vegetative characteristics important to nest site selection and reproductive success

4. Conduct a home range study to determine home range size and habitat associations

5. Conduct a genetic analysis to determine the genetic structure and the extent of genetic variation between the Black Hills population and other populations

There are several study questions that are addressed by this research project. First, a population study was conducted in order to determine the abundance of the American Three-toed Woodpecker in the Black Hills. Results from North American Breeding Bird Surveys from 1980-2003 indicate low densities throughout its western geographic range although this result may be

partially due to the low number of survey routes through difficult terrain where the American Three-toed woodpecker is often located (Wiggins 2004). More recently, a study conducted from 2001-2008 by the Rocky Mountain Bird Observatory (RMBO) using non-play back point counts along transects determined that the estimated density (birds/km²) of the American Three-toed Woodpecker in the Black Hills ranged from 0.7 in 2001 to 3.9 in 2003. They were almost always found in white spruce habitat and unlike in other parts of their geographic range they were not found in burn sites (Giroir et al. 2007). Play back of conspecific calls on point counts can increase detectability and reveal higher abundances than non-play back point counts particularly for secretive species like the American Three-toed Woodpecker (Johnson 1995). Thus, we compared our results using play back with RMBO results from the same transects without play back to refine estimates of American Three-toed Woodpecker abundance in the Black Hills. The estimation of population abundance is important in order to provide baseline data and thereafter monitor population trends for use in setting conservation objectives and guiding management activities.

My second objective was to observe foraging behavior and to determine what foraging substrates were preferred by comparing substrate use to availability. The American Three-toed Woodpecker primarily forages on bark and wood boring beetle larvae found in disturbed habitats in coniferous forests. A study conducted in 34.7 km^2 mixed conifer forest of the Deschutes National Forest in Oregon documented 63% of foraging bouts on Lodgepole pine trees and 25% on Engelman spruce. Foraging occurred on dead trees for 88% of the observations and 77% of the dead trees were recently dead. In general it appeared that mature and old growth trees were

selected for foraging and smaller-sized trees, multi-storied stands and logged areas were avoided (Goggan et al. 1989).

A more recent study conducted in a Quebec, Canada boreal forest composed of black spruce, jack pine, balsam fir, white birch, aspen and tamarack determined that the American Three-toed Woodpecker foraged mainly (78-93%) on snags with a large dbh and recently dead trees were used more often than later stage snags (Imbeau and Desrochers 2002). The results indicate the importance of natural disturbances creating new snags and thereby increasing wood boring beetles populations so that American Three-toed Woodpecker populations may be sustained (Imbeau and Desrochers 2002).

In concordance with the American Three-toed Woodpecker's response to habitat disturbances, it is known to opportunistically shift its range in response to fires in coniferous forests that damage trees resulting in increases in bark and wood boring beetle abundances (Murphy and Lehnhausen 1998, Leonard 2001). A study conducted in a northeastern boreal forest in Alberta, Canada determined that American Three-toed Woodpeckers were observed only in old growth stands and in 2-year post-burn areas. Their occupancy in the burn site decreased significantly from 3-8 years post burn. They were more likely to occupy burns with a high density of lightly burned trees, low density of moderate burned trees and jack pine trees (Hoyt and Hannon 2002). This behavior is probably due to the large increase of bark and wood boring beetles infesting the damaged trees immediately after the burn and as the moisture content of the burned trees decreases over time, the beetle density decreases (Hoyt and Hannon 2002),

and consequently the American Three-toed Woodpecker density decreases as it leaves the burned site for more prey-dense areas in the old growth areas surrounding the burn.

Although the American Three-toed Woodpecker is known to exploit post-fire sites, the Black Hills population appears to be unique due to its lack of presence in recent post-burn areas such as the 33,800 hectare Jasper Burn area in the southern Black Hills that consisted mainly of ponderosa pine forest (Shepperd and Battaglia 2002, Giroir 2007). Fire regimes in the Black Hills have changed significantly since Euro-American settlement in the late 1800s. Historically, the Black Hills ponderosa pine forests consisted of a diverse forest structure of open areas with dispersed closed canopy stands (Shepperd and Battaglia 2002), whereas today it is more homogenous, consisting of dense areas of younger and smaller trees due to surface fire suppression regimes (Brown and Cook 2006).

The American Three-toed Woodpecker in the Black Hills may not exploit post-burn areas due to the majority of fires occurring within the ponderosa pine forests in the southern Black Hills. Considered a fire adapted species, the bark of ponderosa pine is thicker than white spruce and because the American Three-toed Woodpeckers are not strong excavators, it seems probable that the difficulty flaking off the thicker bark may discourage irruption into post-burn ponderosa pine habitats. The American Three-toed Woodpeckers dependence on white spruce forests may largely be due to the ease of flaking the thin bark as they forage for beetles. Indeed, it has been documented that the American Three-toed Woodpecker is closely associated with spruce forests to such an extent that its geographic range follows that of southern limit of the geographic range of spruce trees and can survive in areas in which the only conifers are spruces (Bock and Bock

1974). Its close association with spruce is further demonstrated by its absence in the conifer forests in Sierra Nevada, which lack spruce habitats. All woodpecker species that breed in the Rocky Mountains also occur in the Sierra Nevada, except for the American Three-toed Woodpecker (Bock and Bock 1974).

The third study question focused on nest site selection and estimated nest success of the American Three-toed Woodpecker in the Black Hills. More specifically, I examined the vegetation characteristics important for nest site selection and the factors affecting their ability to successfully fledge offspring. Nesting success can be influenced by many different variables. Attributes of the nesting tree such as height of nest (Li and Martin 1991), location and stage of decay of nesting tree (Bull et al. 1986), temporal factors such as nest age (Grant et al. 2005), and spatial factors such as proximity to food source (Goggans et al. 1989) and potential predators (Li and Martin 1991, Saab and Vierling 2001) have all been cited as influences on nesting success. Reviews of nesting success of cavity-nesting birds reveal typical nesting success rates of 60%-80% (Gentry and Vierling 2007). A comparison study of open-nesting species, excavator cavity-nesting species and nonexcavator cavity species in the Mogollon Rim in Coconino National Forest in Arizona determined that five different species of woodpecker species varied in their nesting success from 73.8% for the Hairy Woodpecker (n =8) to 100.0% for the Northern Flicker (n= 34) and Red-naped Sapsucker (n=18) (Martin & Li 1992).

On a local level, there have been a few studies conducted on nesting success of excavator cavity nesters in the Black Hills. A recent study focusing on the closely related Black-backed Woodpecker determined the maximum likelihood nesting success over a two-year period varied

from 41-78%, and that the age of the nest was the best predictor of nest survival (Bonnot et al. 2008). The Lewis's Woodpecker resides in the Black Hills and similar to the American Three-toed Woodpecker has a low population size and restricted distribution. However, it is considered a burn specialist and is often found in the southern Black Hills in post-burn areas (Gentry and Vierling 2007). Gentry and Vierling (2007) determined that the Lewis's Woodpecker had an overall nesting success of 90% (n=55) in the Black Hills. The low rate of predators documented within the old post-fire study area may be one cause for the high nesting success rate and productivity of the population and therefore the population may be functioning as an ecological source (Gentry and Vierling 2007).

Unlike the Lewis's and Black-backed woodpeckers in the Black Hills which are considered burn specialists and mainly utilize habitats in the southern Black Hills which are warmer and drier, the American Three-toed Woodpecker is considered a habitat specialist of old-growth and mature spruce forests which are largely located in the cooler, moister northern Black Hills. The rarity of stand replacing, high intensity fires in the northern hills may increase nest predation here as small mammal populations increase in areas of greater vegetation cover (Jones et al. 2002). On a local level, the northern flying squirrel *Glaucomys sabrinus* and red squirrel *Tamiasciurus hudsonicus* reside in the Black Hills and prefer mature trees, large diameter snags and woody debris, all of which are common features of forests in the northern Black Hills. The prevalence of these two species in the preferred breeding habitat of the American Three-toed Woodpecker may have a negative impact on its nesting success and productivity in the Black Hills.

The fourth objective of this study was to determine the home range size of the American Three-toed Woodpecker in the Black Hills during the breeding season and to identify habitat attributes that are related to the home range. Prior to this study, there was only one other breeding season home range study conducted on the American Three-toed Woodpecker. A study in Deschutes National Forest using the minimum convex polygon (MCP) home range estimation method indicated that the breeding season home range for American Three-toed Woodpeckers (n=3) was mean (± SE) 411 ±181 ha. The majority of locations included in analyses were after the young fledged the nest or nesting attempts failed (Goggans et al. 1989). The sizes of the home ranges were not related to the number of young or the amount of mature and immature forest stands. However, birds selected home ranges with a high abundance of single-storied mature/overmature sawtimber and low abundance of single-storied saplings, seedlings and poles(Goggans et al. 1989).

In Berchtesgaden National Park, Germany, a home range study was conducted on the Eurasian Three-toed Woodpecker (n=24) during the breeding season in order to determine home range size, use of habitat structures within home ranges and factors that affect home range size. Using the adaptive kernel home range estimation method, it was determined that home range size during the nesting period averaged mean (± SE) 59.6 ± 49.3 ha. The size of home range among individuals varied greatly, but there were no significant differences between the sexes. Additionally, the size of the home range increased significantly in non-forested areas and in areas with higher diversity of tree species, suggesting that birds adjust their home range size to the amount of forest present and that higher tree diversity may indicate a more stable environment less conducive to arthropods requiring large amounts of dead wood (Pechacek and

d'Oleire-Oltmanns 2004). If the food supply becomes too limited in the stable environments, the home range may expand. In contrast, the shallow root system of spruce trees makes them more likely to be affected by windthrow (Shepperd and Battaglia 2002), and therefore in areas of homogeneous spruce stands where the likelihood of insect infestation is greater, a small home range size may provide an adequate food supply for the American Three-toed Woodpecker (Pechacek and d'Oleire-Oltmanns 2004). This pattern may apply especially to the Black Hills population as spruce habitats in the Black Hills, typically occur in a narrow linear arrangement following the bottoms of canyons. The homogeneous composition and linear arrangement of the spruce forests may be able to meet the habitat requirements for the American Tree-toed such that a small home range will be sufficient for its productivity.

In addition to basic ecology research, the last objective of this project was to obtain genetic information in order to determine the genetic structure and phylogeographic patterns of the American Three-toed Woodpecker in the Black Hills. Specifically, this project focused on the following questions:

1. Do populations reflect a geographic structure?
2. Does gene flow occur between populations?
3. If there is gene flow, what is the amount of genetic variation within the Black Hills population and between the Black Hills and other populations?
4. What effect did the Pleistocene have on the Black Hills population genetic structure?

Due to the sedentary nature, habitat specialist requirements and isolation of the Black Hills population of the American Three-toed Woodpecker, the current taxonomic status of the population is not defined. The difficulty in locating the American Three-toed Woodpecker is a likely reason why there are a limited number of studies that have investigated the genetic structure and phylogeographic patterns of the species. One study that focused on the phylogeographic patterns of the Three-toed woodpeckers prior to the current study determined that the 4% mtDNA sequence divergence between the currently named Eurasian Three-toed Woodpecker and American Three-toed Woodpecker was great enough to warrant a species-level taxonomic split. Additionally, the study determined that there was a lack of genetic variation across the North American continent. However, the study was limited to a small sample size (n=8) and sampled only in contiguous forests (Zink et al. 2002). American Three-toed Woodpeckers typically are associated with naturally fragmented habitats, and it is unknown if populations in isolated habitats, such as the Black Hills, have become genetically differentiated from the contiguous populations (Wiggins 2004).

Additional phylogeographic studies have also indicated shallow phylogeographic structure in other woodpecker species (Ball and Avise 1992, Zink et al. 2002). Woodpeckers typically are sedentary in nature, and the lack of phylogeographic structure may be suggestive of a rapid range expansion after the end of the Pleistocene 10,000 years ago. Events during the Pleistocene likely played an important role in the current distribution and consequently the genetic structure of species. As the climate oscillated and glaciers advanced and receded numerous times across North America and Europe, vegetative composition would change and the fauna associated with it would vary along with the vegetation. During glacial maxima, biota

at higher latitudes would be compressed towards the lower latitudes as the glacier moved across the landscape. During this time, species that currently inhabit boreal forests would have resided in refugia south of the glaciers and permafrost (Hewitt 2000). As the climate warmed, northward range expansion of species occurred rapidly with the aid of north-flowing prevailing winds (Pielou 1991). Species such as white spruce (*Picea glauca*) covered what is now the Great Plains during the last glacial maxima (Wisconsin) and made a rapid advance northward along the western extent of the Laurentide glacier. Species that were associated with boreal habitats would follow the geographic range expansion of the spruce. The constant contraction and expansion of species ranges during the Pleistocene resulted in the loss of alleles and homozygosity within many populations of species (Hewitt 1993). Many bird species in North America show low genetic diversity (Hewitt 1996, 2000), and a plausible explanation may the constriction of the species' ranges during glacial maxima and then the rapid expansion post glaciation.

In addition to using phylogeographic techniques to infer genetic histories, using tools that specifically address microevolutionary questions can provide further insight by focusing on more recent events in explaining the current genetic structures of geographically separated populations. To date, there have been no studies focusing on the population genetics of isolated populations of the American Three-toed Woodpeckers. The Black Hills population is currently considered to be consubpecific with *P.d. dorsalis* in the Rocky Mountains, but their taxonomic classification is not well defined because of their small population size and isolation from other populations residing in the Rocky Mountains. Because of these population characteristics, American Three-toed Woodpeckers in the Black Hills deserve conservation concern and face a

greater probability of suffering the negative effects of inbreeding depression and genetic drift, which could further reduce the population size.

Along with stochastic threats, the Black Hills population is also confronted with deterministic threats such as habitat destruction, which can further exacerbate the genetic effects of small population size making it more vulnerable to extirpitation. The Black Hills is one of the most heavily logged National Forests in the United States (Ball and Schaefer 2000, Wienk et al. 2004), and although the majority of logging for timber sales takes place in the central to southern Black Hills, which are largely ponderosa pine forests, thinning and salvage logging due to fire suppression regimes in the northern Black Hills are likely to impact species dependent upon snags, such as the American Three-toed Woodpecker. Snags and coarse woody debris are created by natural disturbances such as windthrow, fire or insect and pathogen infestations and are an important component of western coniferous ecosystems (Farris et al. 2004). In the past, areas of accumulated woody debris and numerous snags were considered a fire hazard, but today the importance of these structures to wildlife and the community dynamics is well documented (Bull et al. 1997; Murphy and Lenhausen 1998, McComb and Lindenmayer 1999; Rose et al. 2001). Destruction of snag habitats can result in lower population viability due to the synergistic effects of stochastic and deterministic processes. Less available habitat may result in smaller population size, thereby increasing the probability of inbreeding depression.

Today, many species are threatened by reduction in habitat and consequent effects on population size due in part to their restricted current post-glacial geographic ranges and more importantly, to human proclivity towards “progress”. Resolution of the genetic uniqueness of the

Black Hills population may provide insight on how the population may be supported through translocations from donor populations if deemed necessary and may have broader implications by assisting in management planning for the white spruce habitat for which there are no current plans. By providing forest managers with information on an old-growth/mature habitat specialist such as the American Three-toed Woodpecker, many other species and the ecosystem as a whole may benefit from the results of this comprehensive study investigating the ecology and genetic aspects of this unique isolated population.

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Chapter 2: Population Abundance and Distribution of the American Three-toed Woodpecker in the Black Hills, South Dakota

The American Three-toed Woodpecker (*Picoides dorsalis*) is a sedentary species that inhabits boreal forests, but is also irruptive, taking advantage of increases in resource availability caused by various forms of disturbance such as fire (Murphy and Lehnhausen 1998), windfall (Virkkala et al. 1991), and insect infestations (Yunick 1985). Considered an old-growth forest specialist, it is dependent on structural characteristics such as snags that are often found in old-growth and disturbed forests (Short 1974, Murphy and Lenhausen 1998). It is known to be closely associated with spruce forests to such an extent that its geographic range follows that of the southern limit of the geographic range of spruce trees, and can survive in areas in which the only conifers are spruces (Bock and Bock 1974). Because of its rarity and dependence on snags for nesting and foraging, the American Three-toed Woodpecker's population status has become a cause for concern (Hoyt and Hannon 2002, Imbeau and Desrochers 2002). Region 2 of the USDA Forest Service, which encompasses Colorado, Wyoming, South Dakota, Nebraska and Kansas, lists the American Three-toed Woodpecker as a sensitive species due to its rarity. A sensitive species is defined as a population whose current or predicted downward trends in abundance or habitat requirements will reduce its distribution (Wiggins 2004). The Natural Heritage Program in South Dakota lists the American Three-toed Woodpecker as imperiled due to low population size and to other factors that make it vulnerable to extinction throughout its geographic range (Wiggins 2004). In South Dakota the American Three-toed Woodpecker is a rare, permanent resident of the Black Hills. The Black Hills population is at a high risk for

population declines due to rarity, limited distribution of its preferred white spruce habitat and the importance of timber and resource management activities within the Black Hills National Forest.

As a consequence of the American Three-toed Woodpecker's low abundance, elusive nature and preferred habitat of dense conifer forests, few studies focus on its population abundance and distribution across its geographic range, and studies in the Black Hills are fewer still. Results from North American Breeding Bird Surveys (BBS) from 1980-2003 indicate low densities throughout its western North American geographic range, but densities tend to fluctuate regionally (Sauer et al. 2004). Data from Audubon Society Christmas Bird Count (CBC) from 1959-1988 indicate that American Three-toed Woodpecker abundance did not change in the Rocky Mountains in Colorado, but declined slightly in abundance in British Columbia (Wiggins 2004). Reliance solely on BBS and CBC for abundance estimates can be problematic due to low detection probability as a result of the rarity and unobtrusive nature of the American Three-toed Woodpecker in addition to the low number of BBS and CBC survey routes through difficult terrain where this species often occurs (Wiggins 2004, Giroir et al. 2007).

Within the Black Hills National Forest, a forest-wide density survey conducted during 2000-2001 resulted in a total population estimate of 320-440 birds (0.08 birds/km^2) (Mohren 2002). In 2002 and 2003 population surveys conducted only within white spruce habitat yielded density estimates of 1.80 birds/km^2 and 3.64 birds/km^2 respectively (USDA 2005). In addition, the Rocky Mountain Bird Observatory (RMBO) conducted point counts along habitat-stratified transects throughout the Black Hills using standard non-playback methods from 2001-2009 to monitor bird populations. The results indicate that the estimated density (birds/km^2) of the American Three-toed Woodpecker in white spruce habitats in the Black Hills ranged from 0.7 in

2001 to 3.9 in 2003 (White et al. 2010). Overall relative abundance estimates based on corrections for detectability range from 0.02 birds/point in 2001 to 0.10 birds/point in 2005 (White et al. 2010). In the Black Hills, American Three-toed Woodpeckers were almost always found in white spruce habitat, and unlike in other parts of their geographic range they were not found in post- fire ponderosa pine habitat (Giroir et al. 2007). Additionally, spruce in close proximity to aspen is an important habitat characteristic for the American Three-toed Woodpecker (Hill 2001, Mohren 2002) likely due to its susceptibility to heartwood rot rendering it a soft substrate for excavation of nesting and roosting sites (Aitken et al. 2002).

Standard (non-playback) point-count surveys with correction for detectability are thought to be a reliable and robust survey method for most abundant and easily identified bird species (Norvell et al. 2003). However, bird species that are rare and inconspicuous may be missed on non-playback surveys (Allen et al. 2004, Jacob et al. 2010). Due to the elusive behavior of the American Three-toed Woodpecker, I used point count playback methods, which should increase opportunities for observations relative to non-playback point count methods in a time and resource limited study.

The objectives of this study are to 1) provide a relative abundance estimate of the American Three-toed Woodpecker in the Black Hills of South Dakota using playback methods and 2) to compare my results with those from previous studies using non- playback surveys with corrections for detectability from the same transects to determine if the results of two methods differ for a rare and unobtrusive woodpecker species. To my knowledge, this is the first study focusing on a species within the *Picoides* genus comparing the two methods. The estimation of

population abundance is important to provide baseline data for monitoring population trends, setting conservation objectives and guiding management activities. Additionally, by comparing the results of non- playback versus playback survey methods for determining relative abundances, this study should help to elucidate the extent that the playback method increases the likelihood of detecting the American Three-toed Woodpecker.

Study Area and Methods

This study was conducted in the Black Hills, South Dakota. Major geologic regions of the Black Hills include a granite core in the east-central region and the Limestone Plateau and Minnelusa Foothills, which encircle the granite core (Froiland 1978). The Limestone Plateau region varies from 3 km wide in the southeast to 25 km wide in the west with elevations ranging from 1850-2200 m. Due to the relatively high elevations, the climate is cooler and the annual precipitation is often higher than in other regions of the Black Hills, providing conditions suitable for subalpine belts of white spruce (*Picea glauca*), along with the more common ponderosa pine. The Black Hills are one of only a few areas south of the Canadian border where pure populations of white spruce grow (Hoffman and Alexander 1987), and it is the farthest west where a population is located (Shepperd and Battaglia 2002). Aspen habitat dominated by quaking aspen (*Populus tremuloides*) covers close to 5% of the Black Hills and most commonly occurs in the northern Limestone Plateau where white spruce is climax and in areas of destruction within the coniferous forests (Hoffman and Alexander 1987). The varied climate, topography, geology and isolation from other mountain ranges have created a variety of habitats in the Black Hills that are seen as a refuge for biodiversity within the Northern Great Plains (Shepperd and Battaglia 2002).

The population surveys in this study were based on 26 random RMBO transects (390 total points) established by the RMBO, which mostly follows the linear white spruce habitat along north-facing slopes and canyon bottoms throughout the Black Hills, South Dakota (Panjabi 2003, White et al. 2010). Surveys were conducted during the breeding season of 2005, with 20 transects concentrated in the Limestone Plateau of the northwestern Black Hills, as this area contains the primary concentrations of spruce stands within the Black Hills (Figure 2.1). Additionally, four transects were located in the northeast and two in the southern Black Hills, both of which have limited white spruce stands.

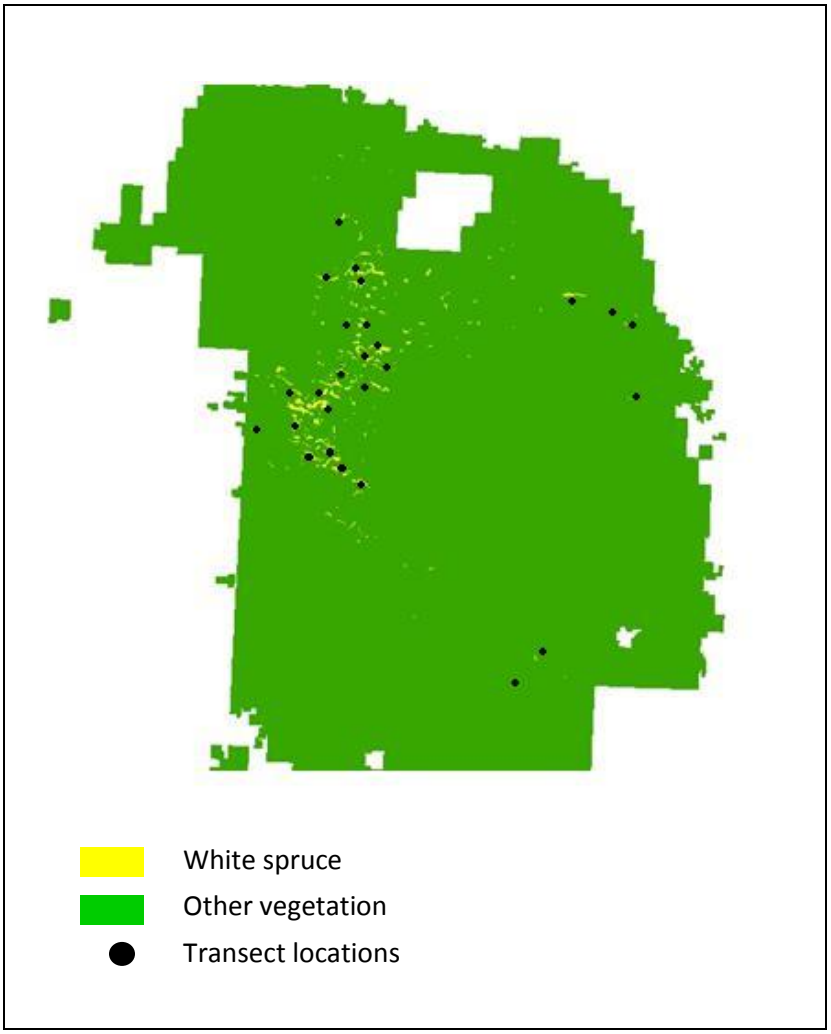

Figure 2.1- 26 transect locations used for the American Three-toed Woodpecker population surveys in the Black Hills, South Dakota.

Each transect consisted of 15 points spaced 250 m apart. Surveys were conducted in the early morning (0445-0930 MST) from late May to early July, which is within the major drumming/calling period (both on a daily and seasonal basis) for the American Three-toed Woodpecker (Leonard 2001). Surveys were not conducted on days with rain or high winds. All woodpeckers seen or heard were counted at each point using a 5-minute survey period with a playback procedure consisting of an initial 1 minute of listening, followed by 30 seconds of playback, followed by 30 seconds of listening. The alternating 30-second playback/listening

periods were repeated until the 5-minute survey period was complete. A Peterson Audio Field Guide was used as the source of the woodpecker drumming and calls, and the sounds were broadcasted from a personal CD player through an electric blowhorn (Radio Shack Model 320-2037). This playback method allowed the drumming/call notes to attract woodpeckers from a considerable distance (>200 m). Relative abundance was defined as the number of responses (the number of American Three-toed Woodpeckers heard calling or drumming, or visually detected in response to the recording) divided by the number of transects or points. To provide conservative estimates of relative abundance, if a bird was observed in the same direction as a previously detected bird at a previous point on the transect, or if visual observation revealed the bird to be a previously detected individual, it was not recorded as a new detection.

Results

A total of 78 American Three-toed Woodpeckers was observed on the 26 transects (Table 2.1). The overall relative abundance using the playback method was 0.20 birds per point (3.0 birds/transect). On two transects, 9-10 individuals were detected yielding an estimate of 0.6 birds/point as the maximum relative abundance for any transect. We detected no American Three-toed Woodpeckers on six transects. Standard (non-playback) point-count surveys (with corrections for detection probability) for the same transects conducted annually or bi-annually by RMBO from 2001-2009 varied from 0.02 birds/point in 2001 to 0.10 birds/point in 2005 (White et al. 2010). Thus, the playback method increased the overall abundance estimates by two to almost 10-fold relative to those for standard non-playback point counts with corrections for probability of detection.

The greatest abundance of American Three-toed Woodpeckers occurred within spruce habitats on the Limestone Plateau in the northwestern Black Hills, where spruce habitat generaaly occurs along north-facing slopes and cool canyon bottoms. Overall relative abundance of American Three-toed Woodpeckers on the Limestone Plateau transects (n=20) was 0.24 birds/point. Similar values for central (n=2) and northwestern (n=4) transects (Figure 2.1), where spruce is more patchily distributed and occurs mostly in thin linear stands following canyon bottoms, were 0.13 and 0.05 birds/point, respectively.

To assess the potential for competitive interactions among woodpecker species in the Black Hills, other woodpecker species observed during the survey periods were also recorded and their relative abundances calculated. Overall relative abundances of other woodpecker species observed on transects included Hairy Woodpecker (*Picoides villosus*) 0.07 birds/point (1.08 birds/transect), Red-naped Sapsucker (*Sphyrapicus nuchalis*) 0.04 birds/point (0.58 birds/transect) and Downy Woodpecker (*Picoides pubescens*) 0.01 birds/point (0.19 birds/transect).

Discussion

Relative Abundances and Distribution

Our results support previous studies that show spruce stands to be important habitat for the American Three-toed Woodpecker (Bock and Bock 1974, Imbeau et al. 1999). The highest densities of American Three-toed Woodpeckers in our study occurred on the Limestone Plateau region of the Black Hills, where spruce habitats are most extensive. Although, the American Three-toed Woodpecker is considered to be a sedentary species, it can be irruptive and will

opportunistically move into recently disturbed areas providing suitable habitat (Yunick 1985, Hoyt and Hannon 2002). Old-growth and mature forests, as well as areas affected by natural disturbances such as fire, wind-throw and disease, harbor wood boring (Cerambycidae) and bark beetles (Scolytinae), which comprise the American Three-toed Woodpecker's primary prey (Murphy and Lehnhausen 1998, Wiggins 2004). The original disturbance event, along with the subsequent damage caused by beetle infestations, increase the number of snags available for nesting and roosting and thus likely increase the abundance of the American Three-toed Woodpecker in these areas.

Forest fires are an important disturbance regime that provide suitable habitat for the American Three-toed Woodpeckers (Murphy and Lehnhausen 1998) in some portions of their range from 0-3 years post burn (Murphy and Lehnhausen 1998, Hoyt and Hannon 2002). Their occupancy of post burn areas declines between 3-8 years most likely due to the increasing desiccation of burned trees and subsequent reduction in wood boring and bark beetles numbers as moisture content in the bark and phloem declines (Hoyt and Hannon 2002). Contrary to results of studies in other parts of their geographic range, the Black Hills population of the American Three-toed Woodpeckers has not responded by an increasing their presence in areas of recent burns (Hoyt and Hannon 2002, Kotliar et al. 2005). For example, in 2000, the Jasper burn in southern Black Hills ponderosa pine forest burned 90,000 acres and later, two fires adjacent to the Jasper burn burned an additional 40,000 acres. A 2001 study in the Jasper burn revealed no American Three-toed Woodpeckers in the burned areas (Mohren 2002). RMBO surveys from 2001-2007 within the Jasper burn also failed to detect American Three-toed Woodpeckers (Girior 2007). Our results also support the lack of presence in recent burns as two of our 26

transects occurred close to and partially within the 2002 Grizzly Gulch burn in the northeastern Black Hills. We detected no American Three-toed Woodpeckers on this transect even though there appeared to be suitable white spruce habitat adjacent to the burned areas.

Many potential explanations exist for why American Three-toed Woodpeckers are not found in post-burn areas in the Black Hills, ranging from their interactions with predators and competitors to the effects of fire dynamics, such as burn severity (Kotliar et al. 2005). Two general explanations for why American Three-toed Woodpeckers avoid burned areas in the Black Hills seem most probable. First, the majority of fires in the Black Hills occur in south-central regions with warmer and drier ponderosa pine. American Three-toed Woodpeckers in our study occurred in highest abundance in spruce habitat on the Limestone Plateau in the northwestern Black Hills. These locations are moister than areas in the southern Black Hills and therefore not as susceptible to forest fires. It is possible that American Three-toed Woodpeckers would increase their densities in areas of recent white spruce burns if they occurred, so they may be limited by dominant tree species within the burn, rather than by presence or absence of burned forest per se (but see Hoyt and Hannon 2002).

Another plausible explanation why American Three-toed Woodpecker do not inhabit post-burn areas in the Black Hills may be due to interspecific competitive exclusion by the closely related Black-backed Woodpecker, which is sympatric with the American Three-toed Woodpecker over much of its range (Bock and Bock 1974). The Black-backed Woodpecker is considered a fire specialist and exploits areas of recent fires, including those in the Black Hills (Saab and Powell 2005, USDA 2005). Forest fires and mountain pine (*Dendroctonus ponderosa*)

outbreaks across the southern and central Black Hills within the past decade have dramatically increased areas of suitable habitat for Black-backed Woodpeckers (USDA 2005) such that their populations have expanded dramatically (Mohren 2002, White et al. 2010). It is possible that competition between these two species in the Black Hills may function to exclude the American Three-toed Woodpecker from recently burned areas although why competitive exclusion would occur in the Black Hills but not other regions of sympatry remains to be investigated.

Sympatric woodpecker species on spruce transects in our study included Hairy Woodpecker and Red-naped Sapsucker and competition with these species might also limit the distribution of American Three-toed Woodpecker in the Black Hills. Hairy Woodpeckers, which are considered generalists, occur throughout North America in a variety of different habitats from conifer to deciduous forests (Jackson et al. 2002). On numerous occasions during the study period we observed Hairy Woodpeckers foraging and nesting in close proximity to American Three-toed Woodpeckers and occasionally engaging in aggressive interspecific behavior (A. Ervin and D. Swanson, unpublished observations). In addition, Red-naped Sapsuckers were relatively common on our transects (0.6 birds/transect), especially when aspen was present and we commonly observed this species nesting and foraging within aspen habitats in which American Three-toed Woodpeckers were also found (A. Ervin and D. Swanson, unpublished observations), suggesting the potential for competitive interactions.

Future studies within the Black Hills focusing on the potential for competition among sympatric woodpeckers, including post-fire population interactions between black-backed and three-toed woodpeckers, are needed to assess the potential for competition as a factor limiting American Three-toed Woodpecker distribution in the Black Hills.

Comparison of Survey Methods

Non-playback point-count survey methods are the standard for obtaining relative abundance indices that are used to monitor population trends and habitat associations of avian species (Rosenstock et al. 2002). However, utilizing passive non-playback methods may not reflect true abundance estimates for elusive species occurring in dense vegetation as they may not be observed using these traditional survey methods (Lor and Malecki 2002, Allen et al. 2004). Use of playback methods maximizes detectability in game and marsh bird species (Allen et al. 2004, Evans et al. 2007) and improves the accuracy of relative abundance estimates by homogenizing the probability of detection among sampling units (Jakob et al. 2010). Standard point-count surveys assume that the probability of detection remains constant throughout the survey period. However, several confounding variables such as observer performance, environmental influences and bird behavior may cause variations in detectability and thus render the results unreliable (Buckland et al. 1993, Rosenstock et al. 2002, Thompson 2002). Methods to standardize detectability, such as playback in addition to standardizing potential confounding factors such as duration of count, distance between stops and weather conditions, are assumed to reduce differences in detection probabilities during point counts (Nichols et al. 2000). Nevertheless, concern over unreliable relative abundance estimates resulting from uncorrected detection probabilities remains and methods to directly estimate detection probabilities such as distance-sampling (Buckland et al. 2001, Thomas et al. 2010), double-observer sampling (Nichols et al. 2000) or count removal analyses (Farnsworth et al. 2002, Alldredge et al. 2007) have become popular in recent years. Distance sampling measures point-to-observation distances

that are used to directly estimate the probability of detection as a function of distance (Thomas et al.2010). The RMBO used this method during their point-count surveys in white spruce habitat in the Black Hills from 2001-2009 (White et al. 2010). We used the same white spruce transects for our point-count playback surveys but did not use the distance method to estimate the probability of detection because playback attracts birds to the observer such that distance data become unstable (Zimmerling and Ankney 2000). The overall relative abundance estimates for three-toed woodpeckers in the current study were 2-10 times greater than RMBO's estimates using standard point-counts, with corrections for probability of detection (White et al. 2010). Because of the American Three-toed Woodpecker's unobtrusive behavior, it is likely that the RMBO results do not reflect true overall abundance because playback increases the detection probability for American Three-toed Woodpeckers. Studies of other elusive bird species also found that using playback methods increased detectability and improved the accuracy of abundance estimates by homogenizing detectability among sampling units (Johnson et al. 1981, Zimmerling and Ankney 2000, allen et al. 2004, Jakob et al. 2010.

The results of this study show that playback surveys increased the overall relative abundance estimates of American Three-toed Woodpeckers in the Black Hills. We recommend using standardized playback point counts for future monitoring of American Three-toed Woodpeckers because their inconspicuous behavior and preference for dense conifer forests may provide unreliable abundance estimates due to low detection probabilities on standard non-playback point counts.

Precise comparisons of bird densities among sites and studies is difficult because of variation in sampling protocols and detectabilities of birds, but such comparisons can still be

instructive for broad-brush comparisons of relative abundances among sites. White et al. (2010) reported American Three-toed Woodpecker density (birds/km^2) in white spruce habitat in the Black Hills ranging from 0.7 in 2001 to 3.9 in 2003 and 2005, with an overall average density of 2.4 during surveys from 2001-2009. The White et al. (2010) density estimate for the Black Hills is lower than reported densities from point-count surveys in the southern Rockies and Colorado Plateau, which averaged 3.15 in 2008 and 2009 (Blakesley et al. 2010). However, our results compare favorably to those from other North American locations (Leonard 2001). In addition, the overall average abundance (birds/point) that White et al. (2010) detected was roughly similar to the average relative abundance at sites in the northern Rocky Mountains. Given that our abundance estimates were at least twice those for White et al. 2010, these data suggest that American Three-toed Woodpeckers in the Black Hills occur at abundances roughly similar to those for other sites in the Rocky Mountains.

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Chapter 3: Foraging Ecology of the American Three-toed Woodpecker in the Black Hills of South Dakota

Introduction

The range of the American Three-toed Woodpecker (*Picoides dorsalis*) is closely associated with high elevation old-growth and mature boreal forests in the United States and Canada (Virkkala 1987, Imbeau et al. 1999). Often referred to as a habitat specialist, it is dependent on characteristics of old growth forests such as large diameter trees and snags. Snags are particularly important for foraging and drumming (Mannan et al. 1980, Aulen 1991). The American Three-toed Woodpecker also occurs in areas of recent natural disturbance caused by fires, insect infestation, drought conditions or wind-throw (West and Speirs 1959, Yunick 1985). Natural disturbances weaken or kill trees, thereby increasing the abundance of beetles, the larvae of which are the primary prey of American Three-toed Woodpeckers. Bark beetle (Scolytidae) larvae are the most consumed prey item (Murphy and Lehnhausen 1998), but three-toed woodpeckers also feed on larvae of wood-boring beetles (Cerambycidae and Buprestidae), moths, caterpillars and ants. Foraging typically consists of flaking and pecking, but can also occasionally involve excavation limited to the bark and cambium (Bull et al. 1986). Natural history differences between bark and wood boring beetles influence prey choice by American Three-toed Woodpeckers. Bark beetles are shallow feeders, occurring just below the surface of the bark on living and dead conifers (Pechacek 2006). They are smaller than wood -boring beetles and short lived. Wood- boring beetles typically feed deeper in the phloem tissue of dead or dying conifer trees and are larger in size, and longer lived than the bark beetles. White spruce

is a thin-barked species (USDA 2005) and the primary foraging mode of American Three-toed Woodpeckers is flaking and scaling off bark, since they are not strong excavators (Spring 1965, Murphy and Lenhausen 1998, Hoyt and Hannon 2002). This may partially explain why American Three-toed Woodpeckers have a closer association with thin-barked species such as white spruce, than with other conifer species with thicker bark, such as ponderosa pine.

Because of the American Three-toed Woodpeckers' low abundance, elusive nature and preferred habitat of dense conifer forests, few studies have been conducted on the species. The few previous foraging ecology studies have focused on foraging behavior and habitat associations in post- fire areas, effects of forest cover on foraging behavior, and local-scale habitat characteristics used for foraging (Goggans et al. 1989, Murphy and Lehnhausen 1998, Hoyt and Hannon 2002, Imbeau and Desrochers 2002). Studies involving the closely related Eurasian Three-toed Woodpecker focused on prey preferences of adult and young woodpeckers (Pechacek and Kristin 2004) and gender and seasonal effects on foraging behavior in alpine forests dominated by Norway spruce in Germany (Pechacek 2006).

American Three-toed Woodpeckers are irruptive and opportunistically exploit areas of recent disturbance (West and Speirs 1959, Yunick 1985) that promote beetle infestations. However, occupancy of these areas declines over time, most likely due to increasing desiccation of damaged trees, which results in reduced prey availability. In post- burn sites, American Three-toed Woodpeckers were more likely to occur in areas with high densities of lightly burned trees for up to three years after the fire occurred. Occupancy of these areas decreased 3-8 years post-fire (Hoyt and Hannon 2002). Interestingly, American Three-toed Woodpeckers in the

Black Hills, are not commonly found in recently burned areas. The majority of fires that occur in the Black Hills are located in the warmer, drier southern portions, whereas fires are not common in the cooler, wetter white spruce forests in the higher elevations on the Limestone Plateau, which is the stronghold of American Three-toed Woodpeckers in the Black Hills. The limited subalpine belt of spruce forests in the northern Black Hills may be providing the American Three-toed Woodpecker with enough prey such that there is less of a need to exploit burned areas (Giroir et al. 2007).

In addition to studies focusing on the specifics of foraging ecology in post-burn habitats, other studies have focused on foraging at more than one spatial scale. In central Oregon, Goggans et al. (1989) observed American Three-toed Woodpeckers foraging (n=493) in unlogged forests 97% of the time. Lodgepole pine was used in 63% of foraging attempts and recently dead trees during 77% of foraging attempts. Overall, mature and old-growth sawtimber was selected and stands with seedlings, saplings or poles and multi-storied stages were selected against. However, the Goggans et al. (1989) study was limited in two aspects. First, 79% of the observations were from only three birds and second, foraging use was not compared to the proportion of substrate that was available. Rather than showing strong support for a preference of foraging substrate characteristics, the results may reflect American Three-toed Woodpeckers' use of foraging substrates based on their local abundance within the study area rather than showing a preference for particular characteristics.

The previous foraging studies on the American Three-toed Woodpecker have focused on populations within contiguous coniferous forests. There are no foraging studies to date that focus

on foraging ecology of American Three-toed Woodpecker in isolated habitats with limited white spruce distribution such as the population that resides in the Black Hills of South Dakota. Rare, small, sedentary and isolated populations that are habitat specialists face unique ecological and genetic challenges not likely to be present in other populations. Competitive interactions with other species in the same foraging guild may have an influence on foraging behavior and limit species distribution. Additionally, the current forest management plan in the Black Hills supports the reduction of fire and insect hazards (USDA 2005), which may have a detrimental effect on the American Three-toed Woodpecker if retention of dead and dying trees is not considered within management objectives.

American Three-toed Woodpecker populations may be negatively affected by fire suppression and salvage logging regimes (Goggans et al. 1989, Murphy and Lenhausen 1998, Kotliar et al. 2008). Although fires rarely occur in the high elevation, patchily distributed spruce habitats where American Three-toed Woodpeckers prefer to forage (Hoyt and Hannon 2002), the negative effects of changes in natural fire regimes in ponderosa pine forests may affect foraging behavior, as three-toed woodpeckers also forage in ponderosa pine and lodgepole pine forests (Goggans et al 1989). In addition, high-severity fires in ponderosa pine forests may provide critically important foraging and nesting sites for American Three-toed Woodpeckers (Kotliar et al. 2008). Typically, forest managers seek to prevent high-intensity fires through fire suppression methods such as prescribed understory burns to reduce fuel loads and forest thinning, which reduces snags that serve as important foraging resources for American Three-toed Woodpeckers (Kotliar et al. 2008).

The purpose of this study is to determine if a relationship exists between habitat characteristics and foraging preferences for the American Three-toed Woodpecker in the Black Hills, South Dakota. In this study I compare use of foraging substrates to their availability within the study area to determine foraging preference and avoidance (Zwicker and Walters 1999). I specifically examined tree characteristics and the duration of foraging bouts to determine if the American Three-toed Woodpecker in the Black Hills shows a preference for specific foraging substrate attributes. Results from this study will assist informed management decisions regarding habitats important to this unique, isolated population and will provide baseline data for additional studies relating to the effects of competition or habitat degradation.

Study Area

We conducted our study in the Black Hills of South Dakota. The American Three-toed Woodpecker is considered a habitat specialist and is closely associated with old growth and mature spruce forests. As such, we focused our foraging data collection efforts on white spruce forests, which occur in greatest abundance on the Limestone Plateau in the northwestern Black Hills.

Methods

Foraging Substrates Used

We collected data on American Three-toed Woodpecker foraging behavior during the breeding seasons (mid-May- early August) from 2006-2008. We focused our searches for foraging American Three-toed Woodpeckers in areas where woodpeckers had been previously

located during population playback surveys or during nest searches within previously located woodpecker territories or in areas where we observed trees with flaked bark typical of three-toed woodpecker foraging. We located woodpeckers by looking and listening as we walked slowly through the search area. American Three-toed Woodpeckers observed opportunistically during the course of our studies were also included in the data set. Once we visually located a woodpecker, we recorded foraging substrate attributes including tree species, status (living or dead), and tree size category (based on diameter at breast height, DBH). Tree size was classified as small (<23 cm DBH) or large (>23 cm DBH), but tree size category was not recorded in 2006. We also recorded the duration of each foraging bout by timing the foraging activity with a stopwatch. Individual woodpeckers were followed until we lost contact with them, and we recorded multiple foraging bouts for individual birds using the sequential observation method of Morrison (1984).

We compared foraging substrate use to availability of the tree characteristic within the study area by conducting vegetation sampling at random locations within white spruce habitats. We determined substrate availability by randomly selecting 30 points from previously established (by the Rocky Mountain Bird Observatory) random transects in white spruce habitat (Panjabi 2003). For vegetation surveys, each random point was considered the survey center and we determined the number and size category of each species of vegetation according to the protocol of Bate and Saab (2005). Vegetation was categorized based on species and size (two categories: small [<23 cm DBH] and large [>23 cm DBH]) of living trees and snags. In addition, we recorded the number and size category of downed logs and the number of shrubs.

Characteristics of living trees, small snags and downed logs were recorded within four 6

m X 50 m strip transects in each of the cardinal directions. The random point was considered the center of the transects. Large snags (>23 cm DBH) were recorded on four 20 X 50 m strip transects centered on the random point. Shrubs that were > 20 cm in height were counted in three 4 m-radius subplots centered on the random point and at 50 m from the random point north and south.

Statistical Analysis

In 2006 we did not include the tree size category; so 2006 data were analyzed separately from the breeding seasons of 2007 and 2008. We pooled foraging data from individual birds for the 2007 and 2008 breeding seasons. For all analyses, male and female data were combined because we had insufficient data for intersexual comparisons (Morrison 1984). To determine if the American Three-toed Woodpecker selects tree species, size or status (living or dead) for foraging according to availability, we used Chi-square Goodness-of-fit tests or Fishers Exact Test to compare use to availability. To mitigate the potential for non-independent samples with repeated observations from individual birds, we used two different observation techniques, each of which was analyzed separately. For the single point observation technique, we included only the individual bird's first foraging bout. For the sequential observations, we analyzed all observed foraging bouts of an individual until the bird flew and could no longer be observed. The point observation method helps to mitigate the issue with non-independent samples, but the sequential observation method captures more rare foraging behaviors (Morrison 1984). Therefore, using both methods should provide a more accurate representation of foraging

selection. For the analyses comparing the mean duration of foraging bouts for each tree species, Kruskal-Wallis one-way ANOVA on ranks was performed.

Results

We recorded a total of 306 foraging observations from 53 birds as follows: 19 individual birds (108 observations) in 2006, 23 individual birds (115 observations) in 2007, and 11 individual birds (83 observations) in 2008. During the 2006 breeding season, 72.2% of total foraging bouts were on spruce trees, 59% of which were on dead spruce and 41% on living spruce (Figure 3.1). Additionally, 19.4% of foraging bouts occurred on living and dead ponderosa pine and 8.3% on aspen. Using the sequential observational method, American Three-toed Woodpeckers foraged on dead spruce in greater proportion than its availability ($P < 0.001$), and foraged on live spruce in lower proportion than its availability ($P < 0.001$). All other trees were used in proportion to their availability. The single observation method analyses only included the categories of dead and living spruce and dead and living pine as these were the only substrates used by birds during single point observations. This method yielded similar results to the sequential observation method; dead spruce was used in greater proportion than its availability ($P = 0.040$), and living spruce was used in lower proportion than its availability ($P = 0.021$).

For the breeding seasons of 2007 and 2008, 33% of total foraging bouts were on snags, 77.5% were on large size trees and 80.1% were on living or dead spruce (Figure 3.1). Sequential observation data revealed large spruce, large spruce snags and large pine were used in greater proportion than their availability ($P < 0.001$ for all comparisons; Figure 3.3). Live small spruce

($P < 0.001$) were used in lower proportion than their availability (Figure 3.3). Small spruce snags were also used in lower proportion than their availability ($P = 0.047$), Foraging use and availability did not differ significantly for any other foraging substrate (Figure 3.3). Single point observations revealed large spruce snags were used in greater proportion than their availability ($P = 0.010$), and living small spruce were used in lower proportion than their availability ($P < 0.001$). Foraging use of other substrates did not differ significantly from their availability.

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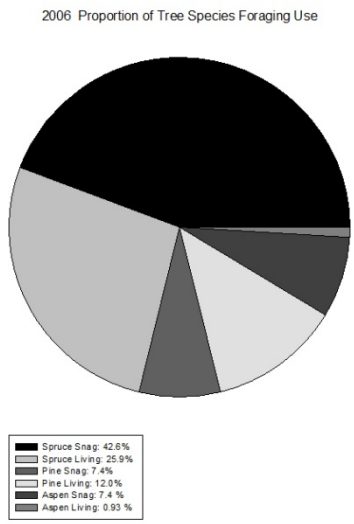

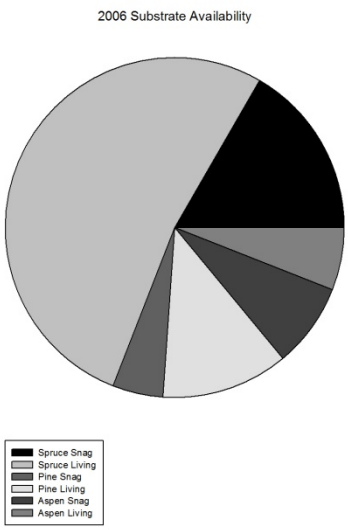

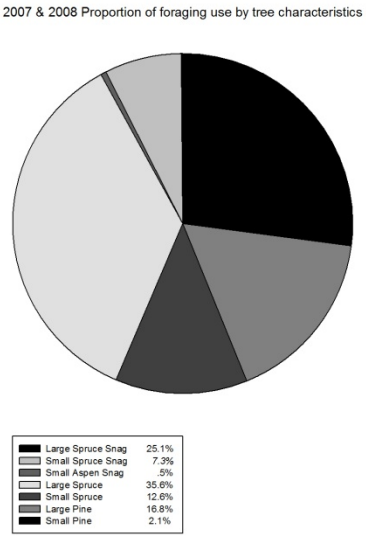

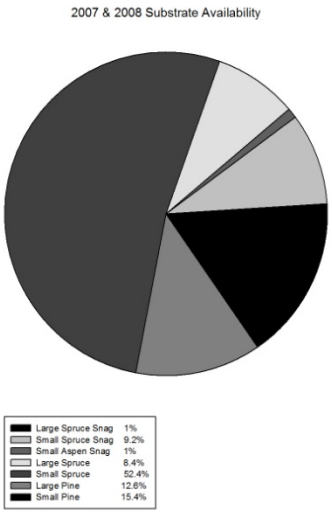

Foraging duration did not differ among the different foraging substrates (Figure 3.2; Kruskal-Wallis, H =3.649, df =3, p =0.302). However, white spruce snags and living ponderosa pine approached significance at P = 0.093, with longer foraging bouts on spruce snags than on living pine. For 2007 and 2008, woodpeckers foraged for significantly longer bouts on large white spruce snags than on living large ponderosa pines (Figures 3.3; Kruskal-Wallis, H = 4.912, df = 1, p = 0.027). All other comparisons were not significant.

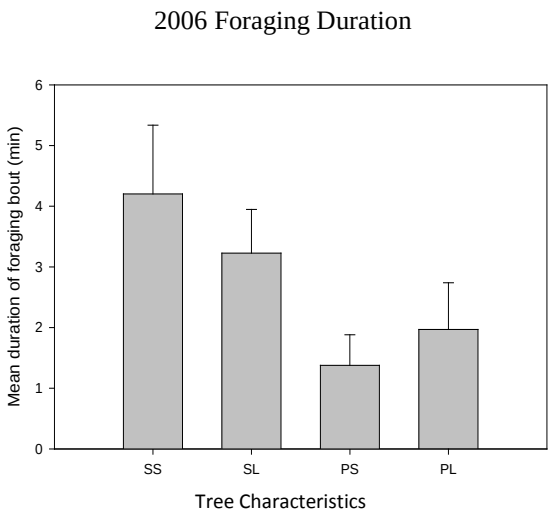

Figure 3.2. 2006 mean ± SE foraging duration on tree characteristics. SS = spruce snag, SL = living spruce, PS = pine snag, PL = living pine.

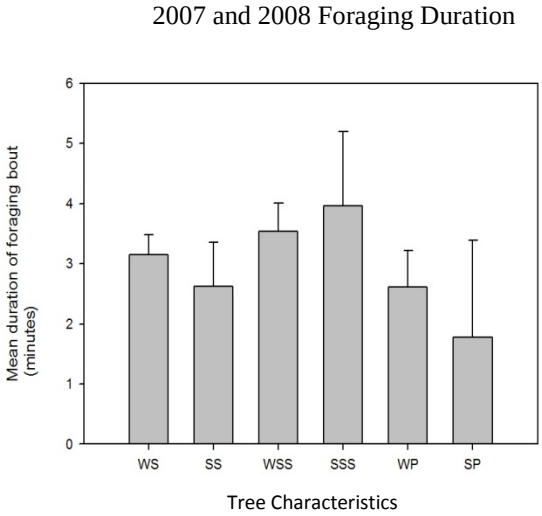

Figure 3.3. 2007 and 2008 mean ± SE foraging duration on different tree characteristics. SS = spruce snag, WS = large spruce, SS = small spruce, WSS = large spruce snag, SSS = small spruce snag, WP = large pine, SP = small pine.

Discussion

Our results suggest that American Three-toed Woodpeckers in the Black Hills, South Dakota, prefer large (> 23 cm dbh) living and dead spruce and large ponderosa pine trees as foraging substrates and select against living small spruce. These data support previous findings for American Three-toed Woodpeckers in the Deschutes National Forest, Oregon, which selected mature and overmature sawtimber and avoided small-sized trees. However, the Oregon birds tended to forage on lodgepole pine (63%) rather than Engelmann spruce (25%) (Goggans et al. 1989), whereas in our study, they selected white spruce for foraging more often than ponderosa pine, although both were used in greater proportion than their availability at our study sites. American Three-toed Woodpeckers are closely associated with white spruce forests (Bock and Bock 1974), and even though ponderosa pine covers almost 95% of the forested area in the Black Hills (Sheppard and Battaglia 2002, Brown and Cook 2006), our results clearly indicate their affinity for large white spruce trees as foraging substrates. White spruce forests are patchily distributed and low in abundance in the northern Black Hills, occurring mostly on north-facing slopes and canyon bottoms (USDA 2005).

Tree size appears to be an important foraging selection attribute of the American Three-toed Woodpecker in the Black Hills. Previous studies also indicate that trees with large DBH ranging from 23-28 cm (Bull et al. 1986) are most often chosen as foraging substrates (Mohren 2002). A previous study conducted in the Black Hills concluded that the average DBH of foraging trees was 22.9 cm. However, this average was smaller than the average DBH of trees at random sites within the study area (Mohren 2002). Beetle infestations typically occur in snags

and larger diameter trees (USDA 1996, Mohren 2002), so increased prey availability in larger trees is a probable explanation for selecting these trees for foraging use.

Similar to other woodpecker species, the preference for snags is an important characteristic for American Three-toed Woodpecker habitat for foraging, nesting, roosting and drumming (Goggans et al. 1989, Leonard 2001, Imbeau & Desrochers 2002). Three-toed woodpeckers often respond opportunistically to insect infestations resulting from recent disturbances such as fire (Murphy & Lehnhausen 1998, Hoyt & Hannon 2002) and windthrow (Leonard 2001). When compared to previous reports of 78-93% (Imbeau & Desrochers 2002) and 88% (Goggans et al. 1989) of foraging bouts on snags, our results show lower use of snags for foraging, with only 41.5% of the foraging bouts occuring on snags. A possible explanation for the relatively low degree of foraging on snags by three-toed woodpeckers in the Black Hills may be the fire patterns within the Black Hills National Forest. In contrast to other populations, the Black Hills population does not seem to shift its distribution in response to recent fires (Murphy & Lehnhausen 1998, Kotliar et al. 2008). The majority of fires in the Black Hills occur in warmer and drier areas typical of ponderosa pine forests in the southern Black Hills (USDA 2005). The American Three-toed Woodpecker has a close association with the patchily distributed white spruce forests which primarily occur in the cooler, moister, higher elevations in the northern Black Hills, and consequently they do not experience fires as often as the southern Black Hills (USDA 2005). Therefore, the Black Hills American three-toed Woodpecker population does not respond to fire disturbance in a similar manner to other populations and the increased abundance of post-fire snags are not utilized to the extent that they are in other portions of the range.

Most studies of American Three-toed Woodpecker foraging ecology, with the exception of the Imbeau and Desrocher (2002), have not compared foraging substrate use to availability as our study did. Such studies can demonstrate a preference of woodpeckers for a particular foraging substrate rather than imply choice based on substrate availability. Our study focused on foraging use during the breeding season, and because foraging preferences may vary seasonally, we cannot necessarily extrapolate foraging preferences during the breeding season to other periods of the year. However, as weak excavators, the primary foraging method of American Three-toed Woodpeckers is flaking bark to find prey rather than excavating. Therefore, it likely prefers thin-barked species such as white spruce rather than thicker-barked species such as ponderosa pine. The significantly greater mean foraging duration on large spruce snags compared to living ponderosa pine in this study is consistent with differences in tree bark thickness and primary foraging methods for American Three-toed Woodpeckers. Thus, it seems likely that the foraging preferences we documented during the breeding season do extend to other seasons.

Conservation Implications

The preference of American Three-toed Woodpeckers for foraging on large living and snag spruce in this study underscores the importance of mature spruce habitat containing large trees to this species.The low abundance, elusive nature and dependence on mature white spruce habitat of American Three-toed Woodpeckers combine to make it a key species of conservation concern. Greater concern should be extended to the Black Hills population due to its isolation from other populations as well as the low abundance and patchy distribution of its preferred

white spruce habitat within the Black Hills National Forest. Because of the low incidence of fires occurring within the spruce habitat, post burn salvage logging is not as much of a direct threat within white spruce habitat as other management activities such as insect hazard reduction or timber management operations that have the potential to further limit mature spruce forests, which are preferred foraging habitats for the American Three-toed Woodpecker. Approximately 90% of the white spruce habitat in the Black Hills is considered late successsional mature forest (USDA 2005). It is often this category of forest structure that is under threat of aggressive forest management due to timber operations and fire and insect hazard reduction regimes.

Although American Three-toed Woodpeckers are primarily associated with white spruce forests in the Black Hills and large spruce trees and snags serve as the primary foraging substrates, the importance of other habitat types shouldn't be discounted. The Black Hills population is also associated with mixed forests types consisting of ponderosa pine, white spruce and aspen (Mohren 2002). Resource management within mixed forests adjacent to white spruce forest would likely affect the habitat suitability of the American Three-toed Woodpecker population in the Black Hills. Current forest management plans in the Black Hills focus on reducing fire and insect hazards which threaten mature forests (USDA 2005).

Based on our results, mature white spruce forests, including standing snags, are important American Three-toed Woodpecker foraging habitats within the Black Hills National Forest and therefore should be an important conservation consideration included in future forest management plans. Additionally, management activities adjacent to white spruce forests should

be carefully considered as this species has been known to utilize the edges of ponderosa pine, white spruce and aspen habitat for foraging and nesting (Mohren 2002, Chapter 4).

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Chapter 4: Nest-site selection and nesting success of American Three-toed Woodpeckers in the Black Hills of South Dakota

The American Three-toed Woodpecker (*Picoides dorsalis*) is considered to be an old-growth forest specialist due to its dependence on structural characteristics such as snags that are often found in old-growth and disturbed forests (Short 1974, Murphy and Lenhausen 1998). It is known to be closely associated with spruce forests to such an extent that its geographic range follows that of southern limit of the geographic range of spruce trees and can survive in areas in which the only conifers are spruces (Bock and Bock 1974). Because of its rarity and dependence on snags for nesting and foraging, its population status has become a cause for concern (Hoyt and Hannon 2002, Imbeau and Desrochers 2002). In South Dakota, the American Three-toed Woodpecker is a rare, permanent resident of the Black Hills. In region 2 of the USDA Forest Service, the Black Hills population is listed as a sensitive species defined as a population whose current or predicted downward trends in abundance or habitat requirements will reduce its distribution (Wiggins 2004). The Natural Heritage Program in South Dakota has listed it as a species that is imperiled due to low population size and/or because of factors making it vulnerable to extinction throughout its geographic range (Wiggins 2004). In addition, because of its specialized habitat, the limited distribution of white spruce and the importance of timber management within the Black Hills National Forest, the Black Hills population of American Three-toed Woodpecker is at relatively high risk for population declines.

Due to the American Three-toed Woodpecker's low abundance, elusive nature and preferred habitat in dense conifer forests, few studies focus on habitat characteristics important

for nest site selection or reproductive success. In different portions of its range in western North America, the American Three-toed Woodpecker nests in mature/old growth lodgepole pine (*Pinus contorta*) stands and in wet areas (Hoffman 1997), lodgepole pine snags in mature and unlogged forests (Goggans et al. 1989), old growth, mixed conifer forests close to wet areas (Short 1974) and in quaking aspen (*Populus tremuloides*) (Steeger and Dulisse 1997). In addition to utilizing old growth forests for nest site locations, the American Three-toed Woodpecker exploits ephemeral resources such as recently burned forests (Hutto and Young 1999, Murphy and Lehnhausen 1998, Hoyt and Hannon 2002). In portions of its range, the abundance of American Three-toed Woodpeckers increases significantly in recently burned areas (Koplin 1969) due to the increase in their preferred prey, bark beetle larvae (Scolytidae) (Kreisel and Stein 1999, Murphy and Lehnhausen 1998) and occurrence of large numbers of snags that may be used for nesting, roosting and drumming sites. Although nest site selection is variable, overall this species exhibits a pattern of nest habitat preference for old growth conifer forests that have been affected by some form of disturbance.

The importance of snags to wildlife (Davis 1983, McComb and Lindenmayer 1999), and especially to cavity nesting bird species (Nappi et al. 2003, Spiering and Knight 2005), is well documented and has become an important consideration in numerous conservation management plans. As a primary nest excavator, the American Three-toed Woodpecker creates a new nest cavity each breeding season. Although creating a new cavity is energetically expensive when compared to choosing a pre-existing cavity, it may help mitigate low reproductive success caused by parasite infestations and increased susceptibility to predation that is often seen in secondary cavity nesters (Nilsson et al. 1991). Primary excavators are often considered keystone

species because they provide cavities that can be utilized by other wildlife for many years post excavation. Secondary cavity nesting avian species such as White-breasted Nuthatch (*Sitta carolinensis*) and Mountain Bluebird (*Sialia currucoides*) (DeGraaf et al. 1991) and mammals such as red squirrels (*Tamiascurus hudsonicus*), northern flying squirrels (*Glaucomys sabrinus*) and deer mice (*Peromyscus maniculatus*) (Aitken et al. 2002) depend upon the primary excavators to provide nesting and roosting cavities. As an integral component of the forest community, the population status of species belonging to the primary cavity excavator guild can be cause for concern if their reproductive rates become low.

Various factors influence nest site selection and nesting success including proximity to food resources (Virkkala 1991), available suitable nesting habitat (Misenhelter and Rotenberry 2000) and presence of predators (Nilsson 1984, Martin 1993). Predation is the most common source of nest mortality of cavity nesting birds (Nilsson 1984). Common predators in coniferous forests are small mammals such as red squirrels, chipmunks, northern flying squirrels and pine martens (Martin 1988, Gentry and Vierling 2007). Increased nest predation as a consequence of forest fragmentation has been well documented (Andrén 1995, Donovan et al. 1995, Robinson 1995) and is an important concern for species that often require disturbed areas for suitable nesting sites. Historically, these species depended on fire maintained habitats or small and short-lived natural openings that occurred within the forest (Weldon and Haddad 2005), but today due to the increasing rates of anthropogenic changes, fragmented forests can offer similar attributes to naturally disturbed forests. However, edge habitats that have been created unnaturally may increase nest predation at edges edges to levels greater than those in naturally fragmented areas (Paton 1994, Weldon and Haddad 2005).

The Black Hills National Forest is largely managed for timber production (Mills et al. 2000) and is one of the most heavily logged National Forests in the United States, with almost every hectare cut at least once within the last 125 years (Ball and Schaefer 2000, Wienk et al. 2004). Natural disturbances such as insect infestations, fire, disease and wind create snags that are utilized at various stages of deterioration by wildlife. Snags are often viewed as problematic for the timber industry and forest managers as they can increase the likelihood of beetle infestations of healthy trees in the vicinity of snags. In addition, snags and coarse woody debris often found in old growth and disturbed forests increase the fuel load and thereby increase the probability of high intensity crown fires.

Although pre-settlement historical fire regimes in the Black Hills included recurrent low intensity surface fires and occasional high intensity crown fires (Brown and Cook 2006), today fire suppression regimes are largely the consequence of the concerns relating to wildland-urban interface problems (Benson and Murphy 2003). Indeed, 46% of the land in the Black Hills ecoregion is privately owned (Benson and Murphy 2003) and therefore, forest fires are a legitimate concern for forest managers. Managers often reduce the threat of high intensity burns by reducing fuel loads via prescribed burns or by implementing timber harvests, both of which can negatively impact cavity-nesting birds by reducing the number of large sized snags and downed wood that are used for nesting, roosting and foraging (Machmer 2002, Bull et al. 2005), but also see Saab et al. 2005). The few studies focusing on woodpecker response to burned habitats in the Black Hills (Vierling and Lentile 2006, Gentry and Vierling 2007) have been confined to the relatively arid southern Black Hills which are largely vegetated by homogenous ponderosa pine forest. However, the consequences of different fire regimes within and in close

proximity to white spruce forests in the cooler and moister northern Black Hills have not been studied and this lack of information may hinder implementation of management plans that would be beneficial for cavity-nesting bird species such as the American Three-toed Woodpecker.

Under current forest management plans, the American Three-toed Woodpecker population could be at risk as a consequence of sanitation or salvage logging of snags that is conducted to help prevent the spread of insect infestation and occurrence of high intensity crown fires. The American Three-toed Woodpecker has been cited as the most likely boreal bird species to be negatively affected by forestry (Imbeau et al. 2001) and therefore, a critical need exists for studying the nesting ecology of this species. In addition, there is special concern for isolated populations such as that in the Black Hills, due to their rarity and dependence on limited forest habitat attributes, such as white spruce stands, for which there are no current management plans, and snags, whose presence may conflict with current forest management plans.

Monitoring habitat characteristics important for nest site selection and nesting success can provide insights into possible causes underlying population trends (Martin and Geupel 1993) and thus, is the rationale behind this study. Overall, the purpose of the study is to provide crucial nesting ecology data and to elucidate possible factors affecting populations of American Three-toed Woodpeckers in the Black Hills. The two specific objectives of this study are to 1) describe habitat characteristics that are associated with nest site selection by the American Three-toed Woodpecker by comparing habitat use to habitat availability and to 2) estimate reproductive success of the Black Hills population and elucidate what factors may be limiting to nesting success. Based on previous studies, we predict that the Black Hills population of American

Three-toed Woodpeckers will prefer to nest in conifer snags in disturbed areas and that their nesting success will be comparable to that of other woodpecker cavity nesters in western conifer forests, which generally exceed 75% (Li and Martin 1991).

Study Area and Methods

Study Area

We conducted our study in the Black Hills of South Dakota, a mountain range situated in the Northern Great Plains, often referred to as a forested island in a grassland sea (USDA 2005). The highest peak rises over 2215 m above sea-level and they span 200km from north to south and 100km east to west (Froiland 1978). Ponderosa pine (*Pinus ponderosa*) is the dominant overstory tree species in the Black Hills, covering almost 95% of the forested area, but white spruce (*Picea glauca*) and aspen (*Populus tremuloides*) are also important canopy tree species (Sheppard and Battaglia 2002, Brown and Cook 2006).The Black Hills are one of only a few areas south of the Canadian border where pure populations of white spruce grow (Hoffman and Alexander 1987) and it is the farthest west where a population is located (Shepperd and Battaglia 2002). White spruce covers 2% of the Black Hills and aspen covers approximately 3% of the Black Hills and both species commonly occur in the northern Limestone Plateau region (Hoffman and Alexander 1987). The American Three-toed Woodpecker is considered a habitat specialist and is closely associated with old growth and mature spruce forests. As such, we focused our nest search efforts in white spruce forests which largely occur on the Limestone Plateau in the northwestern Black Hills at elevations of 1,800 to 2,150 m.

Locating and Monitoring Nests

We focused nest site searches in areas where we had previously located woodpecker territories based on results of population playback surveys conducted in 2005 in which we used random Rocky Mountain Bird Observatory (RMBO) transects that mainly transversed white spruce habitats (Panjabi 2003, Chapter 2).

During the breeding seasons of 2005-2008 we searched for nests following the techniques of Martin and Geupel (1993) from end of May through early July as this covers the main nesting period for three-toed woodpeckers (Leonard 2001). We focused our efforts on known woodpecker territories or in areas with scaled trees typical of three-toed woodpecker foraging and systematically searched for potential nest sites in snags because these substrates have been documented to be used for nest sites by other populations (Wiggins 2004). Additionally, we tracked any American Three-toed Woodpecker observed opportunistically. We followed birds until we lost them from view, we located a nest cavity or we determined that they were not nesting in the area. For any location that appeared to be a potential nest site, a Universal Transverse Mercator (UTM) coordinate was recorded using a handheld Garmin (Model Vista) GPS unit and nests that were difficult to relocate were marked by flagging placed >5 m from the site in order to avoid attracting predators (Martin and Geupel 1993). Once a nest was located, we checked and recorded the status of the nest every 3-4 days using a Sandpiper Technologies Wireless TreeTop Peeper 4 Video Monitor System until fledging or failure. For each nest we recorded the date, the number of eggs or nestlings and the approximate age of the nestlings. Nests that were inaccessible were monitored by observing adult behavior and all data with the

exception of egg and nestling number were recorded. In 2007 and 2008, some of the periods between successive nest checks were greater than four days due to equipment failure. We considered nests that fledged at least one bird as successful and we considered empty nests to be successful if on the previous visit we observed nestlings to be close to fledging or if we found fledglings close to the nest location. We considered nests abandoned if neither adult was attending the nest and predated if nestlings or eggs were no longer in the nest prior to expected fledge dates or if eggs shells were crushed. For breeding seasons 2007 and 2008 we installed a Cuddeback Excite 2.0 heat/motion activated remote digital game camera at three nest locations in order to detect potential nest predators and/or potential causes for nest failure.

Vegetation Surveys

For each nest site location we recorded tree species, stage of decay (living or dead), tree size (as diameter-at-breast-height, dbh), approximate height of tree, cavity orientation and UTM location. At the conclusion of the nesting attempt, we conducted a vegetation survey around the nest tree in order to determine local habitat features around the nest site according to the protocol of Bate and Saab (2005).We considered the nest site as the center point and we counted the number, size (small [<23 cm dbh] and large [> 23 cm dbh]) and status (living trees or snags) of each tree species. In addition, we recorded the number and size of downed logs and the number and species of shrubs. Numbers of living trees, small snags and downed logs were recorded within four 6 m X 50 m strip transects in each of the cardinal directions from the nest site. Large snags (>23 cm dbh) were recorded on four 20 X 50 m strip transects centered on the nest site

location. Shrubs that were >20 cm in height were counted in three 4 m-radius subplots centered on the nest site and at 50 m from the nest site north and south.

To determine whether American Three-toed Woodpeckers were selecting particular habitat features, we compared habitat characteristics at the nest site location with habitat characteristics at 30 random points from the RMBO white spruce transects. Each random point was considered the survey center and we counted the number and size of each species of tree and shrub. Vegetation measurements were recorded using an identical protocol to the nest site locations (see above).

Statistical Analyses

Nesting success was determined by calculating apparent nest success and by Mayfield daily nest survival estimates (Mayfield, 1961, 1975) in order to compare our results to other studies. Additionally, we used maximum-likelihood estimators in Program MARK, Version 6.0 (White and Burnham 1999, Dinsmore et al. 2002, Shaffer 2004) to determine daily survival rate (DSR) and to model nest survival as a function of potentially influential covariates (Jehle et al. 2004). I evaluated 12 models in an *a priori* candidate model set for nest survival (Table 4.1). The models included combinations of categorical and continuous covariates as outlined below.

1. Species (i.e., nest tree species either white spruce, quaking aspen or ponderosa pine). American Three-toed Woodpeckers typically nest in conifers such as pine, spruce or firs. They rarely nest in deciduous trees such as aspens (Wiggins 2004). Little support was found for tree species along with distance to habitat edge as an important predictor in nesting success for the

Black-backed Woodpecker in the Black Hills (Bonnot et al. 2008). We predict that tree species is not an important predictor of nesting success.

2. Age (i.e., nest age from excavation to success or failure date). Bonnot et al. (2008) suggested that nest age was one of the most important predictors of nesting success for the closely related Black-backed Woodpecker. As the nest age increases, the more exposed the young are to predators due to increases in begging calls and the number of foraging trips the adults make to feed the young (Martin et al. 2000). We predict that nesting success decreases with nest age.

3. Cavity Height. Studies focusing on other cavity nesting birds have documented decreases in nesting success with lower nest cavity placement (Nilsson 1984, Li and Martin 1991, Albano 1992, Christman and Dhondt 1997). We hypothesize that nests with a low cavity height will experience a lower nest success.

4. Tree status (i.e., nest in snag or living tree). Li and Martin (1991) found that cavity nesting birds used snags for nest sites in higher proportion than their availability. Living trees have more consistent cavity temperatures and are warmer at night (Hooge et al.1999, Wiebe 2001), which may enhance the survival of the brood for some cavity nesting species. However, Wiebe (2001) did not find that this increased nesting success. We predict that tree status will not influence nest success.

5. Date (i.e., to determine if nest survival declines as the nesting season progresses). Bonnot et al. (2002) documented date to be a strong predictor of nest survival for Black-backed Woodpeckers. Suggestions for lower nesting success as the season progresses range from late

egg-laying to predator influences (Fisher and Wiebe 2006). Late egg-laying may be the result of renesting attempts and as such, the energetically expensive task of a second nesting attempt may reduce the parental care and thereby result in increased nesting failures later in the breeding season (Bonnot 2002, Fisher and Weibe 2006).

6. DBH (i.e., small = <23cm dbh, large = ≥ 23 cm dbh). American Three-toed Woodpeckers typically excavate cavities in mature conifer trees. Goggans et al. (1989) documented the mean dbh of nest trees as 27.5 cm. Large diameter nesting trees may provide better insulation against cool temperatures in high elevation conifer forests (Joy 2000). Additionally, a nest placed in a tree with a large dbh may be more protected from predators due to the thicker cavity walls (Harestad and Keisker, 1989) and thus, may enhance nest success.

7. Year (i.e., 2005, 2006, 2007, 2008). We hypothesized that yearly variation such as weather patterns (i.e. temperature and precipitation) may cause differences in daily nest survival rates.

All candidate models were compared to a null model S (.) of constant nest DSR using Akaike's information criterion for small samples (AIC_c) (White and Burnham 1999). The model with the lowest AIC_c was considered to be the model that best fit the nest survival data. AIC_c weight was used for support.

Table 4.1. Descriptions of variables used in candidate models in Program MARK for evaluating factors influencing nesting success in 2005-2008.

Variable	Description
Species	Nest tree species
Age	Age (days) from first day of active nest status
Cavity Height	Height from ground to cavity entrance (m)
Condition	Nest tree status, living or snag
Date	Progression of the nesting season
DBH	Diameter breast height of the nesting tree (cm)
Year	2005, 2006, 2007 or 2008

To determine what habitat characteristics are important for nest site selection, we compared the proportion of use (based on nest site location) to availability (based on the 30 random point vegetation analyses). We compared microhabitat characteristics of the nest tree (tree species, size category [either large or small] and status [either live or snag] and macrohabitat characteristics surrounding the nest site (density, size categories, and status of tree species) by Student's *t*-tests or Mann-Whitney *U*-tests (if parametric assumptions were not met). Descriptive statistics and statistical analyses were performed using Sigma Stat 3.5. All statistical tests were conducted at alpha = 0.05.

Results

We found and monitored 28 American Three-toed Woodpecker nests in the northern Black Hills (Figure. 4.1) during the 2005-2008 breeding seasons for a total of 305.5 exposure days. Nests were constructed in living spruce (n=2), spruce snag (n=6), living aspen (n=10), aspen snag (n=7), living pine (n=1) and pine snag (n=2) trees. Twelve nests were successful and apparent nest success by nest tree was 62.5% in spruce, 35.3% in aspen and 33.3% in pine. Apparent nest success was 33.3% for live trees and 50% for snags. Average (±SE) clutch size for

completed clutches was 3.42 ± 0.23 (*n*=12). The average (± SE) number of young fledged from the 12 successful nests was 2.33 ± 0.19.

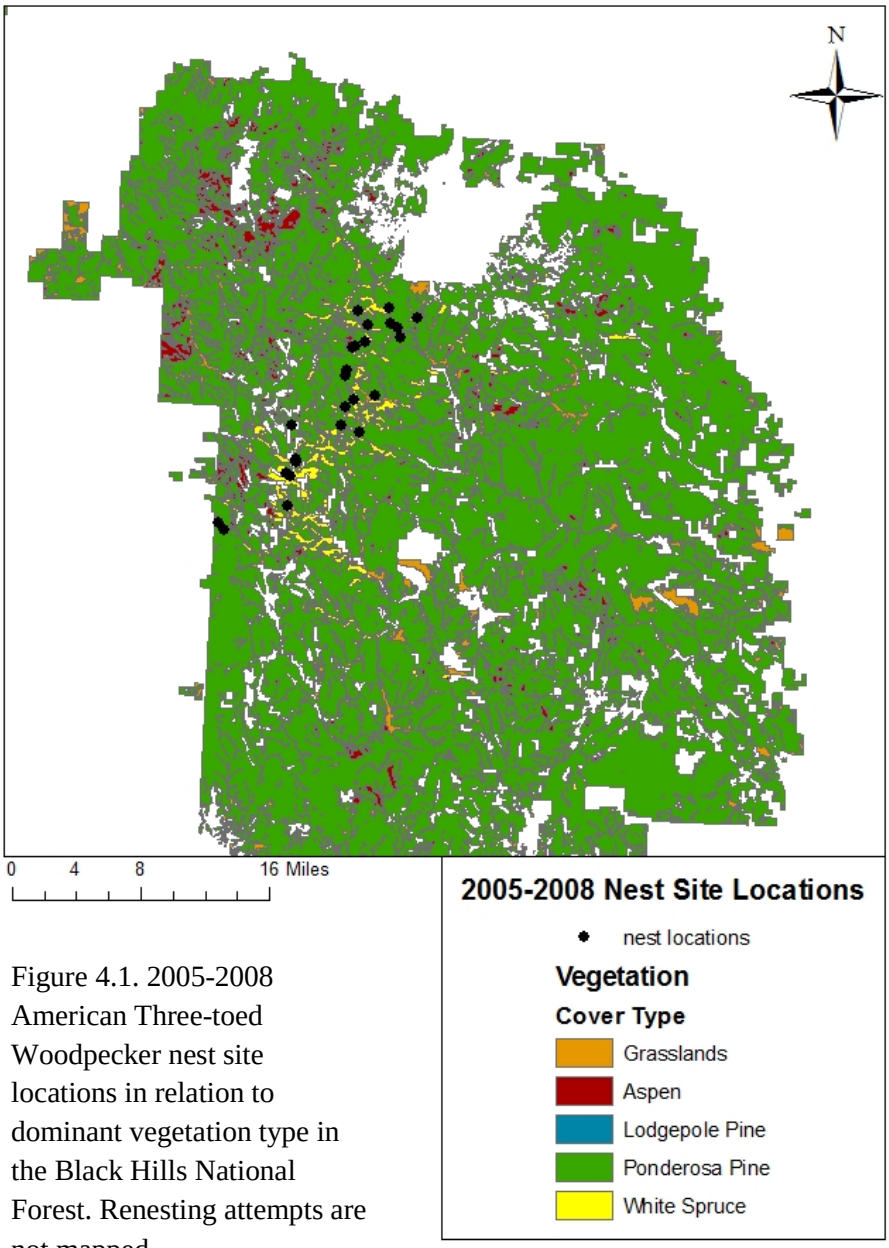

Figure 4.1. 2005-2008 American Three-toed Woodpecker nest site locations in relation to dominant vegetation type in the Black Hills National Forest. Renesting attempts are not mapped.

Nest-site selection- Significantly fewer live trees (P=0.029) occurred around nest locations than around random sites. Numbers of snags and combined numbers of small and large trees and snags did not differ significantly between nest and random sites (Table 4.2). Large living and snag aspens were significantly more common around nest sites than around random sites (P = 0.007 and P = 0.019, for living trees and snags respectively; Appendix A). Large living ponderosa pine were significantly more common around random sites than nest sites. Abundance of other tree species or snags did not differ significantly between nest and random sites (Appendix A). Shrub surveys revealed that snowberry (*Symphoricarpos occidentalis*) (P = 0.008) and gooseberry (*Ribes oxyacanthoides*) (P < 0.003) were significantly less abundant around nest sites than around random sites. Abundances of other shrub species did not differ significantly between nest and random sites (Appendix A).

Table 4.2. Comparison of tree size and status of nest sites (n=28) of the American Three-toed Woodpecker versus random sites (n=30) in the Black Hills, South Dakota with two-tailed Student's t-tests. Mann-Whitney U tests were performed when parametric assumptions were not met. Significant results are in bold.

		Nest site	Random site	*t*	*P*	*U*	*P*
Attribute		mean ± SE	mean ± SE				
Status							
	Live	120.45 ± 13.12	157.33 ± 9.98	2.247	0.029		
	Snag	48.41 ± 8.68	45.13 ± 6.22	0.309	0.759	437	0.982
Size[a]							
	Small	123.90 ± 14.18	149.57 ± 11.87	1.392	0.169		
	Large	43.21 ± 28.43	50.90 ± 4.98	1.061	0.293	526	0.17

[a] Small is dbh < 23cm, Large is dbh > 23 cm

Nest cavity heights ranged from 1.12 m to 11.28 m with a mean ± SE of 4.08 ± .39 m (n=28). Dbh measures of nest trees ranged from 13.3-47 cm with a mean ± SE of 29.21 ±2.17 cm (*n*=22). DBH (*P* > .4367) and cavity height (*P* >.9523) did not vary significantly between nest trees with successful or failed nests (Table 4.3).

Table 4.3. Comparisons of nest tree characteristics based on nest failure or success.

		Failure mean±SE	Success mean±SE	*P*
Tree status				
Snag				
	DBH (cm)	32.8 ± 5.894 (*n*=5)	32.66 ± 3.62 (*n*=8)	0.983
	Cavity Height (m)	5.06 ± 0.95 (*n*=8)	4.10 ± 0.56 (*n*=8)	0.397
Live				
	DBH (cm)	21.75 ± 2.50 (*n*=5)	27.15 ± 3.69 (*n*=4)	0.250
	Cavity Height (m)	3.14 ± 0.47 (*n*=8)	3.97 ± 1.24 (*n*=4)	0.461
Overall				
	DBH (cm)	27.28 ± 3.53 (*n*=10)	30.82 ± 2.72 (*n*=12)	0.4367
	Cavity Height (m)	4.10 ± 0.57 (*n*=16)	4.05 ± 0.52(*n*=12)	0.9523

Notes: Field technicians failed to record DBH for 2008 field season

Nest survival- Apparent nest success (successful nests/total nests) ranged from 0% in 2008 to 62.5% in 2006. The overall apparent nest success for 2005-2008 was 42.9%. Mayfield

daily survival rate (DSR) was 0.947 and this rate extrapolated over the entire nesting period of 38 days (13 days of incubation and 25-day nestling period) yields a nest survival of 13.0%. The DSR in the simple (assuming constant DSR over the entire nesting period) maximum-likelihood model in Program MARK was 0.955 with a 95% confidence interval (CI) of 0.927-0.975. The estimated nest success from this model, based on a nest exposure period of 38 days, was 17.4% (95% CI, 5.6%-38.2%).

The maximum-likelihood model from Program MARK that best fit the data was the nest tree status model (Table 4.4). Several other models also received substantial support ($\Delta AIC_c < 2$). These included models incorporating, in addition to tree status, cavity height, tree species, nest age and year (Table 4.4). The null constant survival model also received substantial support. The model that included all variables received the least support.

In the nest survival analysis using Program MARK to determine if various factors affect nest survival, the model that best fit the data was the nest tree condition model (Table 4.4). Additionally, the condition + cavity height and nest tree species models were within 1 AIC_c units of the best model and the nest age + nest tree condition model were within 2 AIC_c units of the best model. The model that included all variables received the least support.

Table 4.4. Maximum liklihood models of Daily Survival Rate (DSR) from Program MARK for American Three-toed Woodpecker nests in the Black Hills, South Dakota during 2005-2008. The covariates in bold received the most support.

Model	K[a]	ΔAIC_c	AIC_c weight[b]
Condition	2	0.000	0.105
Condition + Cavity height	3	0.247	0.093
Species	2	0.647	0.076
Age + Condition	3	1.301	0.055
Constant Survival S (.)	1	1.766	0.043
Year	4	1.816	0.042
Age	2	2.101	0.037
Age + DBH	3	2.471	0.031
Cavity Height	2	2.551	0.029
DBH	2	2.898	0.024
Date	2	3.27	0.021
Age + Year	5	3.762	0.016
Condition + Cavity height + Age + Species + Year + Date + DBH	11	11.52	0.000

[a] The number of parameters estimated in each model

[b] Difference in AIC_c between listed model and top model

The majority of nest failures were attributed to predation based on evidence from crushed eggs in nest cavities along with photographic images captured during presumed predation attempts. The remote digital game camera at three nest site locations documented several mammalian predators including northern flying squirrels (*Glaucomys sabrinus*), red squirrels (*Tamiasciurus hudsonicus*) and least chipmunks (*Tamias minimus*). At one nest location a red squirrel was photographed pulling a nestling out of a nest located in an aspen tree (Figure. 4.2). Indeed, throughout our four- year study we noted many observations of red squirrels within the vicinity of American Three-toed Woodpecker nests and several acts of aggression by parent woodpeckers against red squirrels near the nest cavity. In addition, we recorded two occasions of northern flying squirrels evicting American Three-toed Woodpeckers from completed cavities, apparently before eggs were deposited, and both cavities were in aspen trees within white spruce forests.

a. b.

Figure. 4.2. Photographic evidence for red squirrel predation on American Three-toed Woodpecker nests in the Black Hills, South Dakota. These are two photos from a sequence of 26 min where the squirrel was present at the nest cavity. Panel (a) shows a red squirrel entering an American Three-toed Woodpecker nest cavity.
Panel (b) shows the same red squirrel pulling an American Three-toed Woodpecker nestling out of the same nest cavity.

Discussion

Nest-site selection- American Three-toed Woodpeckers in the Black Hills appear to select nest sites within or in close proximity to aspen groves. Nest sites had significantly more wildlife-sized living and snag aspens than did random sites. Additionally, 61% of nests were located in aspens. These results are consistent with earlier studies that showed cavity-nesting woodpecker species (although not American Three-toed Woodpeckers) select nest patches with high numbers of living and snag aspens when compared to random sites (Li and Martin, 1991). However, the finding that aspen appears to be an important characteristic for nest site selection in American Three-toed Woodpeckers was unexpected, as most previous studies indicate that they select nest sites within conifer and mixed conifer and hardwood habitats and use a variety of tree species

such as western larch, lodgepole pine, Douglas fir and Engelmann spruce, with only limited use of aspen (Goggans et al. 1989, Wiggins 2004).

American Three-toed Woodpeckers are considered weak excavators (Spring 1965) and as such, they may be more likely to excavate trees that are susceptible to heartwood rot such as aspen or damaged conifers. Another possible explanation for the high incidence of aspen use for nest sites in this study may be that woodpeckers are selecting aspen because they are often found on moist, north facing slopes on the edges of disturbed habitats (Shepperd and Battaglia, 2002). Thus, American Three-toed Woodpeckers may be selecting for edge habitats rather than tree species. The lower numbers of living trees around nest sites than around random sites in this study is consistent with use of open, edge habitats by American Three-toed Woodpeckers. Indeed, most of the nests located in this study occurred in recently disturbed open stands, on the edges of meadows or roads or near an opening in the forest (personal observation). Our results support previous findings from other studies conducted in mixed conifer forests in the Deschutes National Forest in Oregon and the Black Hills. The Deschutes study determined that 60% of nests were located on edges, roads, parking lots or trails (Goggans et al.1989) whereas the Black Hills study concluded that the American Three-toed Woodpecker selects edge habitats of ponderosa pine, white spruce and aspen (Mohren 2002). The Black Hills are penetrated by an extensive road system, developed in part for access to past timber harvest (Alexander 1987). Therefore, areas of undisturbed continuous forests are rare within the Black Hills. Between the high densities of forest service roads, numerous mountain meadows and areas of recent disturbance, edge habitats in the Black Hills are prevalent. However, aspen dominates only a

small portion of the Black Hills landscape and therefore management plans affecting aspen may negatively impact American Three-toed Woodpeckers.

Wildlife-sized ponderosa pine, snowberry and gooseberry were all significantly more numerous at random sites than at nest sites. These results may be a reflection of the woodpecker's selection for nest site characteristics such as close proximity to edge habitats and specific foraging substrates. The moist conditions in the northern Black Hills are conducive to production of white spruce and aspen forests and although ponderosa pine occurs, it does so in lower density as it prefers more arid conditions (USDA 2005). The American Three-toed Woodpeckers preference for white spruce for foraging (Chapter 3) in addition to its selection of nests within or in close association to edge-associated aspen groves, may make these habitat types, which are often found adjacent to each other, attractive as nest site locations.

Ponderosa pine with a snowberry understory is the most common pine habitat type in the Black Hills (Hoffman and Alexander 1987). Snowberry prefers open, warm sites that are well drained and is typically found in climax communities. Gooseberry also prefers open sites, but is most often located in clearings in moist areas and thickets in lowland boreal forests (Carey 1995). The greater numbers of these shrub species at random locations compared to nest sites is unexpected, but the difference in gooseberry abundance may be related to woodpecker selection of nest site locations along edge habitats where conditions are warmer and drier than in the forest interior and, therefore less favorable to gooseberry. The higher numbers of snowberry, which prefer open, warm habitats, at random locations is more difficult to explain, but these differences

may relate to the selection against ponderosa pine at nesting locations by American Three-toed Woodpecker, given that snowberry and ponderosa pine often co-occur.

It is interesting that our study does not support previous research indicating the importance of snags for nesting substrates (Anderson 2003, USDA 2005). Only 57% of the trees selected for nesting sites in this study were snags. Damaged trees have softer phloem and weak excavators such as the American Three-toed Woodpecker are thought to prefer building nests in softer substrates such as snags or live aspens rather than in living conifers (Leonard 2001). Our results do not support a preference for utilizing snags for nesting sites, therefore, American Three-toed Woodpeckers may be choosing nest site locations based on other attributes, such as aspen abundance and proximity to habitat edges, rather than to tree status.

Nest Survival—Nesting success estimates in this study varied with the method of estimation used. Overall apparent nesting success was 42.9%, the Mayfield nest survival estimate was 13.0% and the simple-model maximum-likelihood estimate was 17.4%, all of which were lower than expected based on results from previous studies. Goggans et al. (1989) determined that apparent nest success for twenty American Three-toed Woodpecker nests in Oregon conifer forests was 53%. Mayfield nesting success rate for five different woodpecker species in the Coconino National Forest in Arizona ranged from 74%- 100% (Martin and Li 1991). On a local level, a recent of the closely related Black-backed Woodpecker nesting within standing dead forests resulting from mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the central and northern Black Hills documented maximum-liklihood nesting success of 41%-

78%. Predation was identified as the main cause of nest loses in that study (89%) (Bonnot et al. 2008).

Consistent with this and other nesting success studies focusing on cavity nesting birds (Li and Martin 1991), we also found that most nest failures were attributed to predation. We documented northern flying squirrels usurping American Three-toed Woodpecker cavities in addition to a red squirrel dragging a nestling out of the nesting cavity. Throughout their range, northern flying squirrels are associated with mixed conifer- hardwood forests due to their use of hardwoods such as aspen and birch for denning and conifer patches for foraging (Menzel 2006). Indeed, a recent telemetry study in the Black Hills confirmed this pattern by documenting northern flying squirrels using aspen and birch for denning during the day and ponderosa pine at higher elevations during the night when foraging (Hough and Dieter 2009). Although white spruce may be important habitat for nesting and foraging throughout northern flying squirrels' geographic range (Hough 2008), no study has focused on the abundance of northern flying squirrels in the patchily distributed white spruce forests in the Black Hills. Future research should explicitly address flying squirrel and American Three-toed Woodpecker interactions and should be directed towards the flying squirrel population that resides within white spruce habitat.

Similar to northern flying squirrels, mixed-hardwood-conifer habitat is considered important habitat for red squirrels. The Rocky Mountain Bird Observatory (RMBO) conducted a 9- year habitat-based bird monitoring program in the Black Hills and they noted that the numbers of red squirrels throughout the Black Hills increased from 2001- 2007. In white spruce habitat the density of red squirrels recorded in 2001 was 37.9 (squirrels/km^2) and in 2007 it was 107.0.

The increase in density recorded in aspen habitat was even more dramatic from 12.9 in 2001 to 70.0 in 2007 (Giroir et al. 2007). In comparison, the RMBO also conducted a study throughout Wyoming, but focused on the national forests which included the Big Horn National Forest. In aspen habitats the estimated density ranged from a low of 16.5 squirrels/km^2 in 2005 to 29.9 squirrels/km^2 in 2008. In mid-elevational conifer forests red squirrel estimated densities ranged from 15.1 squirrels/km^2 in 2002 to 35.8 squirrels/km^2 in 2003 (Hanni et al. 2009). Another study in western North American forests has documented greater densities of red squirrels in forested landscapes and a decline in density with increasing fragmentation (Tewksbury et al. 1998). Why the red squirrel population appears to be increasing rapidly in the Black Hills is perplexing. Nonetheless, our results indicate that mammalian predators may be an important factor in nesting failure rates of the American Three-toed Woodpeckers. Therefore, future studies focusing on predators of cavity nesting birds within the Black Hills may be beneficial for implementing appropriate conservation and resource management strategies relating to American Three-toed Woodpeckers and other cavity nesting species.

Candidate models in program MARK assessed factors that may influence nest survival and were compared to the constant DSR model S (.). The model that showed the most support was nest tree status (live or snag). Apparent nest success was 50% for snags, whereas apparent nest success in living trees was only 33.3%. Additionally, cavity height and tree status were supported as important variables for nesting success. Only 36% of successful nests were located at a height < 3.7m. Overall, cavities in living trees that were < 3.7 m. high experienced the greatest nest failure. This result compares favorably with other studies focusing on nesting success of cavity nesting birds which found that low nests failed more often than high nests

(Nilsson 1984, Li and Martin 1991, Albano, 1992, Christman and Dhondt 1997). A recent study in the Black Hills focusing on the Lewis's Woodpecker in post-burn habitats concluded an exceptionally high nesting success of 90% and the mean of nest height was 8.5 m (Gentry and Vierling 2007). Mammalian predators may be able to enter nest cavities more easily at lower nest sites because parent woodpeckers may not be able to detect predators as effectively around lower nests because these nests are more commonly concealed by foliage (Li and Martin 1991).

The year covariate was also supported as an important predictor of nesting success. Failures and successes were nearly equal for 2006 and 2007. However, during the 2005 season, only 33% of nests survived, a result that may be an effect of small sample size (n=3). In addition, a 100% nesting failure was documented for the 2008 breeding season. Out of the six nests located, two pairs excavated a second cavity after the first nest failed and both of these re-nesting attempts also failed. Re-nesting is energetically expensive (Fisher and Wiebe 2006) and the increased demands placed on the re-nesting parents (2 of 6 total nests in 2008) may have contributed to the high nest failure in 2008.

Implications for management

Overall, the low reproductive success of the Black Hills American Three-toed Woodpecker is suggestive that this population may be functioning as a population sink. In order for a population to persist in a sink habitat, a surplus of individuals produced in a source population would need to compensate for the loss of individuals in the sink habitat (Pulliam 1988). This is a conservation concern for the American Three-toed Woodpecker as previous genetic research suggests extremely low migration rates from proximate populations residing in

Montana and Alberta Canada (Chapter 5). If low nesting success continues, resulting in long-term population declines, then augmenting the Black Hills population with individuals from other populations may be necessary in order to sustain the population. Future monitoring of the Black Hills population is necessary to determine if this population is declining over the long-term.

American Three-toed Woodpeckers appear to prefer living and snag aspens for nesting sites in the Black Hills. In addition, close proximity of nesting sites to spruce stands, which are used for foraging also appears to be an important habitat characteristic (Chapter 3). Northern flying squirrels, red squirrels and least chipmunks share similar habitat associations and consequently, American Three-toed Woodpecker productivity may be limited more by predation than habitat suitability.The importance of aspen/spruce habitat for American Three-toed Woodpeckers and population dynamics for potential mammalian predators in this habitat should be considered in future resource management decisions in the northern Black Hills.

Additionally, future research on juvenile mortality and dispersal distances and the effects of different fire regimes on American Three-toed Woodpeckers in the northern Black Hills in necessary. The high nesting success of the Lewis's Woodpecker in post-burn habitats in the southern Black Hills may be the result of low predation rates associated with reduced cover for mesopredators such as the red squirrel (Gentry and Vierling 2007). Indeed, overall nesting success in these post-burn habitat was 90%. Although prescribed burns have been documented to negatively impact cavity nesting birds (Bull et al.2005), other studies have suggested that prescribed burns may be beneficial (Hutto, 1995, Bateman and O'Connell, 2006, Saab et al.

2005). In portions of its geographic range, American Three-toed Woodpeckers occupy moderately burned sites (Hoyt and Hannon 2002) and are less common in unburned areas and in large, high-intensity burns (Kotliar et al. 2008).Therefore, research focusing on the effects of different fire regimes on three-toed woodpecker nesting success in the northern Black Hills would be beneficial by management of this species.

If the Black Hills is in fact a sink for three-toed woodpecker populations, long term conservation goals should be directed towards identifying potential source populations for the Black Hills. Although the American Three-toed Woodpecker is considered to be a sedentary species, they are irruptive in areas that have suffered some form of disturbance such as fires (Murphy and Lehnhausen 1998), beetle infestations (Yunick 1985) or windfall (Virkkala et al. 1991) and they occasionally travel far distances to reach these ephemeral resources. The Big Horn Mountains in northern Wyoming and the northern Rocky Mountains in Montana are likely the closest populations of American Three-toed Woodpeckers and may be providing the Black Hills with a few immigrants (Chapter 5). Therefore, it is important that breeding biology and genetic research be conducted on Rocky Mountain populations as they may be source populations that are helping to maintain the Black Hills population. Any conservation efforts focused on the Black Hills population might be thwarted by negative events impacting potential source populations. As a consequence, identifying and maintaining source populations providing immigrant individuals to the Black Hills should be an important management strategy.

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Chapter 5: Microsatellite and mitochondrial analyses of the American Three-toed Woodpecker (*Picoides dorsalis*) in the Black Hills of South Dakota

Introduction

Species are often subdivided into clusters of individuals that breed in separate local random mating units (demes), but that also exchange individuals between demes and other populations (Allendorf and Luikart 2007). Small amounts of gene flow between demes and populations can sustain the genetic cohesion of the species and provide partially isolated populations with genetic variation that may help prevent extirpation (Allendorf and Luikart, 2007). However, if cohesive gene flow is cut off, the population becomes a separate evolutionary unit (Moritz, 1995, Lomolino et al.2006) and genetic divergence may led to speciation. Small populations that are completely isolated are at an increased risk of extirpation due to genetic drift and inbreeding which can further exacerbate already reduced population size caused by habitat modifications and climatic changes (Frankham 1996, Frankham et al. 2002). These changes may subsequently produce alterations in predator communities (Angelstram 1986, Keyser 2002), resulting in greater detrimental impacts on small isolated populations. Elucidating the genetic structure within and between populations is important for the determination of which demes and populations are the most salient targets for conservation concerns.

The Black Hills, South Dakota are an isolated mountain range considered to be an eastern outlier of the Rocky Mountains. The nearest mountain ranges are the BigHorns to the west and the Laramies to the southwest, each of which are 240-320 km from the Black Hills (Froiland 1978). Often cited as an “island on the plains” (USDA Forest Service, 2005), the varied climate,

topography, geology and isolation from other mountain ranges have created a variety of habitats in the Black Hills that are considered a refuge for biodiversity within the Northern Great Plains (Shepperd and Battaglia 2002). Additionally, historical influences of the Pleistocene have also shaped species composition and genetic structures within the Black Hills (Turner, 1974,Wilson et al. 2005). The constant contraction and expansion of species ranges during the climatic oscillations of the Pleistocene resulted in the loss of alleles and increase in homozygosity within many populations of species (Hewitt 1993). Many bird species in North America possess low genetic diversity (Hewitt 1996, Hewitt 2000), and a plausible explanation may be the constriction of the species ranges during glacial maximas and the subsequent rapid expansion in post-glacial periods.

Although the Black Hills remained an unglaciated pocket during the Pleistocene, the composition and distribution of taxa were strongly affected by the cool, moist climate during the glacial maxima (Froiland 1978). It is likely that the boreal type coniferous forests, which included white spruce, expanded from the higher elevations in the Black Hills to the lower elevations, and those areas around the Black Hills became contiguous montane/boreal coniferous forests (Turner 1974). When the glaciers receded, the climate became warmer and dryer, and, therefore, the boreal type coniferous forests became isolated to higher elevations in the Black Hills (Froiland 1978). Biota dependent upon features of boreal forests became isolated on these boreal caps. The Black Hills are one of only a few areas south of the Canadian border where pure populations of white spruce grow (Hoffman and Alexander 1987), and it is the farthest west where a population is located (Shepperd and Battaglia 2002).

Rare, sedentary and habitat specialist species that are geographically isolated from mainland populations which reside in contiguous forests, may be cause for conservation concern due genetic erosion and subsequent extirpation (Wright 1978, Srikwan and Woodruff 2000). The American Three-toed Woodpecker (*Picoides dorsalis*) is considered to be a habitat specialist closely associated with spruce forests. Limited genetic studies have been conducted because of its rarity, unobtrusive behavior and inhabitation of high elevation, dense conifer forests. The only previous genetics study focused exclusively on three-toed woodpeckers' phylogeographic patterns and documented a 4% mtDNA sequence divergence between the currently named Eurasian Three-toed Woodpecker and American Three-toed Woodpecker. Zink et al. (2002) suggested that the difference was great enough to warrant a species-level taxonomic split. Additionally, the study determined that there was a lack of genetic variation across the North American continent; however, the study was limited to a small sample size (n=8) and sampled only within contiguous forests (Zink et al. 2002). American Three-toed Woodpeckers typically are associated with naturally fragmented habitats, and it is unknown if populations in isolated habitats, such as the Black Hills, have become genetically differentiated from the contiguous populations (Wiggins 2004).

A recent study of the closely related Black-backed Woodpecker (*Picoides arcticus*), a fire dependent species which also inhabits the Black Hills, determined that there is little current gene flow between the Black Hills population and the continuously distributed population from Rocky Mountains to Quebec. Furthermore, the gene flow was determined to be male-mediated and the unforested prairies surrounding the Black Hills appear to be impeding female dispersal (Pierson et al. 2010).

A genetic study focused on a rare, sedentary species inhabiting an isolated mountain range can provide important insights into the historic and contemporary processes that have shaped the population genetic structure and thus help to elucidate if particular populations are in jeopardy of extirpation. In addition to ecological and behavioral data, genetics data complete the comprehensive picture of the overall population status, which is critical for implementation of effective conservation plans. In this study I assess patterns of variation in both mitochondrial cytochrome b sequences and microsatellite loci of the American Three-toed Woodpecker with a special focus on the Black Hills population. More specifically, my objectives were (1) to assess the amount of genetic variation within and between the Black Hills, Montana, Alaska, Washington and Alberta, Canada populations (2) determine if there is recent gene flow among the populations (3) determine if the populations are structured geographically, and (4) assess historical biogeographical patterns of the populations.

Study Area and Methods

Sampling

Blood or tissue samples were collected from 41 American Three-toed Woodpeckers in five sampling locations: Black Hills, South Dakota (*n*=20), Western Montana (*n*=11) Okanogan County, Washington (*n*=3), Alaska (*n*=3) and Alberta (*n*=4) (See Appendix B). Tissue samples from Washington and Alaska were obtained from the Burke Museum in Washington. Tissue samples from Alberta were obtained from the Museum of Alberta in Alberta, Canada. Blood samples from Montana were obtained from Jenny Woolf at the University of Montana.

Sampling protocols for all samples obtained within the Black Hills from 2006-2007 consisted of capturing birds entering or leaving their nest cavities by erecting mist nests in front of their cavity entrance or using a hand-held hoop net placed over their cavity entrance. Birds were banded and weight, sex, wing length, tail length, tarsus length and bill depth were recorded. Blood samples were obtained from the brachial vein of each bird and stored at room temperature in a lysis buffer (Longmire et al. 1988). DNA from blood was extracted using an AquaPure Genomic DNA Kit (Bio-Rad). Tissue samples obtained from museums were first frozen with liquid nitrogen and ground by using a mortar and pestle. The samples were then placed in a lysis solution and incubated at 55°F for 12 hours. DNA was extracted by using ChargeSwitch® gDNA Tissue Kit (Invitrogen).

Sequencing

Initial analyses of mtDNA from 41 American Three-toed Woodpecker samples involved using 1,936bp from four genes: (COI 424bp, CytB 398bp, ND2 820bp, ND3 218bp) using five screener samples: (2 Black Hills, 2 Montana, 1 Alberta, and 1 Alaska). MtDNA was amplified by polymerase chain reaction (PCR) (See Appendix C and D for primers used and amplification programs). PCR products were purified by ethanol precipitation and Pellet Paint® NF Co-Precipitant (Novagen) was used during the cleaning process for some samples. Amplified products were stained with SYBR® Green (Invitrogen) and visualized on a 1.2% agarose gel. The samples were cycle sequenced by using Big Dye III (ABI) or DYEnamic ET Terminator cycle sequencing kit (GE Healthcare). All Programs were performed on the Bio-Rad MJ Mini thermocycler or MJ Research PTC-200 themocycler. The forward and reverse strands of each of

the samples were aligned using Sequencher 4.5 (Fuchs et al. 2004) in order to produce a double stranded copy.

Genotyping

For microsatellite analyses we initially used 14 polymorphic loci: Ptri3, Ptri5, Ptri8, Ptri13, Ptri14, Ptri18, Ptri20, Ptri22, Ptri24,Ptri30, Ptri31, Ptri36, Ptri37 and Ptri38 (Välimäki et al. 2008) (Table 5.1).Eleven loci were successful amplified and three were excluded from the analysis due to non-specific amplification or failure to amplify. One locus was later determined to be a null allele and was excluded from analyses. Loci were analyzed in two multiplex reactions. Preparation of the primer mix consisted of 1µl of each forward primer, 4µl of each reverse primer and 1µl of the fluorescently labeled tags FAM™, VIC™, NED™ or PET™. PCR amplifications took place in 10µL reactions which consisted of 3µl ddH20, 1µl primer mix, 5µl QIAGEN Multiplex PCR kit (QIAGEN) and 1ul DNA . Samples were amplified with the following protocol: initial denature at 95° for 15 minutes followed by 35 cycles of 94° for 30 sec, 57° for 1 min 30 sec, 72° for 1 min followed by a final elongation step of 15 minutes. The amplification product was confirmed by staining the sample with SYBR® Green (Invitrogen) and analyzing it on a 1.5% agarose gel.

Table 5.1. Microsatellite loci, number of alleles, length range and primer sequences used in multiplexed PCR reactions and in analyses. 'GTTTCTT' was added to the 5' end of all the reverse primers. All primer sequences are as reported by Valimaki et al. (2008).

Locus	No.Alleles	Length	Primer Sequence (5'-3')
ptri5	9	178-230	F: VIC-GCACACTCCTCATCTCTATCCA
			R: TAGCTTTGGTTTGTTCCCATCT
ptri8	3	217-225	F: NED-GATCCAAGTTACAGCTATCCTCG
			R: TAGCTTTGGTTTGTTCCCATCT
ptri13	10	144-180	F: FAM-ACCAGAGCAGAGGAGAGGGTA
			R: AAGGTCCCTATTTATGCAGGGT
ptri18	3	220-228	F: PET-GATCCAAGTTACAGCTATCCTCG
			R: CAAAGAGCCACAAAGATGAATG
ptri20	4	230-245	F: NED-GCTGTGCATATTGTGTAGGCAT
			R: AGATGGCAGAGGATGAAACATT
ptri22	9	236-272	F: PET-TAGAACAGGACTCAAAGGCAGAG
			R: CCAGTAAACTTGGTGGAACACA
ptri24	6	256-276	F: FAM-GCATGGGAAATGCTTATGTAT
			R: CTTCTTGAACCAAAACCCAAAG
ptri31	8	317-345	F: NED-GGTCCTGTGCTGTTGTTATGAG
			R: GTTTAGCCCACATTCCTGAACT
ptri36	8	329-373	F: FAM-AGTGAAGGGACAGATGCAAAAT
			R: AAACACTGATACAAAGGCTGGC
ptri38	6	385-417	F: VIC-ATTTTGCTGTTCTTTCAGGTGC
			R: ACGCTTTCTGTTATTGATGCCT

After PCR, 1:5, 1:10, 1:15, 1:20 or 1:75 dilution plates were prepared. Preparation of ABI plates consisted of 10µl 500LIZ® and 1µl diluted product in each well. Samples were denatured at 90° for 2 min and then placed directly on ice. Analysis was performed on an ABI PRISM sequencer (Applied Biosystems, Inc.). ABI GeneScan™500LIZ® Size Standard was used to determine the size of alleles, and chromatograms were viewed and analyzed with GeneMapper (Applied Biosystems, Inc.). Any samples with questionable allele scores were

rechecked by a second or third individual and if scoring among individuals varied, the sample was reanalyzed.

Statistical Analyses

Genetic Variation

Microsatellite markers were tested for deviations from Hardy-Weinberg equilibrium (HWE), and linkage disequilibrium (LD) between pairs of loci were tested in GENEPOP (version 1.2; Raymond and Rousset 1995). The mean number of alleles/locus, observed and expected heterozygosity were assessed in GENETIC DATA ANALYSIS (GDA, Lewis and Zaykin 2000). Allelic richness, which measures the number of alleles corrected for sample size and $F_{IS,}$ which measures departure from Hardy-Weinberg proportions within local demes, was calculated in FSTAT. MICRO-CHECKER (Van Oosterhout et al.2004) was used to identify genotyping errors such as null alleles, allele dropouts and erroneous scores as a result of stutter peaks.

Individual and Population analysis

Genotypic data were used to identify genetic structure through both nonspatial and spatial Bayesian-clustering methods in the programs STRUCTURE (Pritchard et al. 2000) and GENELAND (Guillot et al. 2005), respectively. STRUCTURE uses the genotypes to statistically assign individuals to a number of anonymous genetic clusters (K) defined by the user. This membership assignment method may help to elucidate population structures that are obscure. I used the admixture ancestry model with an initial burn-in of 10,000 and 50,000 replications to run the program seven independent times with K=1-7 for each run. Comparison of Ln and alpha levels

were used to determine the best estimate of the number of populations (Evanno et al. 2005). After the number of populations (K) was estimated, the program was set to a burn-in of 100,000 and 400,000 replications.

The spatial Bayseian clustering program GENELAND is part of an R package that estimates the number of populations and assigns individuals according to their population of origin (Chen et al. 2007). In addition, it uses geographic coordinates of individuals to spatially plot population membership and correlates genetic differences with landscape features. Data analysis parameters consisted of the number of populations varying from 1-7, 100,000 iterations with thinning at every 100th iteration and 2km uncertainty of geographic coordinates. Twenty independent runs were performed.

Population genetic structure via hierarchical analysis was performed by conducting an analysis of molecular variance (AMOVA) in ARLEQUIN 3.11 (Exocoffier et al. 2005) on total population, groups and individual populations. In order to visualize correlations of allele frequencies across populations, a principal components analysis (PCA) was conducted using PCA-GEN software (J. Goudet, www2.unil.ch/popgen/softwares/pcagen.htm).

Recent migration rates were assessed by using Bayesian multilocus genotyping methods in BAYESASS 1.3 (Wilson and Rannala, 2003) with the number of iterations for the MCMC set at 300,000, sampling frequency of 2,000 and burn-in period set at 999,999. A delta value for allele frequency was set at 15. A Mantel test was used in IBD web service (Jensen et al. 2005) to test for association of genetic distance between pairs (Rousset 1997) and geographic distance.

Sequence analyses

The program SEQUENCHER was used to align 398bp for cytochrome b. To test for population change or selection, I estimated Tajima's D and Fu's F and calculated mismatch distributions. Significance was tested in coalescent simulations. In order to access sequence variability, haplotype diversity (*h*) and nucleotide diversity (π) were calculated. All analyses were performed in DnaSP (Rozas et al. 2003). Haplotype median-joining networks were calculated in NETWORK 4.5 (http://www.fluxus-engineering.com).

Results

Estimates of genetic variation

The allele frequencies of 10 microsatellite loci analyzed in 41 American Three-toed Woodpeckers from five sampling locations revealed a total of 72 alleles across all loci. The number of alleles in each population ranged from a low of 32 in Washington to a high of 55 in Montana. Nine alleles were unique to individual populations (Black Hills, two; Montana, two; Alberta, two; Washington, two; Alaska, one).

Exact tests (Guo and Thompson 1992) for deviations of Hardy-Weinberg equilibrium at each locus revealed one locus, ptri3, approaching significance at P= 0.05799. Upon further testing, the null allele estimated frequency was .281 which supports the likelihood that this locus is a null allele and therefore, ptri3 was excluded from subsequent analyses. H-W tests performed across all loci for each population resulted in no populations deviating from H-W proportions. However, the Black Hills population was the closest to approaching significance at p= 0.1526,

while other populations ranged from *P*= 0.5742 (Montana) to *P*=1 (Alberta and Alaska). Significant linkage disequilibrium across all populations (after Bonferroni correction $P < 0.05$) was found between two pairs: locus ptri18 and ptri8; and ptri36 and ptri8. With the exception of the Washington population, most inbreeding coefficients (F_{IS}) were low, ranging from -0.200 to -0.044 (Table 5.2).

Table 5.2 Genetic diversity statistics for five American Three-toed populations based on (a) 11 microsatellite loci and (b) mtDNA cytochrome b region sequences. Nc= no calculation due to sample size

Population	sample (n)	mean alleles/locus	AR	H_o	H_e	F_{IS}
(a) microsatellites						
BH	20	5.2 ± 2.0	1.66 ± 0.18	0.95	0.82	-0.159
MT	11	5.5 ± 1.9	1.69 ± 0.22	0.91	0.83	-0.099
AL	4	4.4 ± 1.8	1.74 ± 0.22	1	0.96	-0.044
WA	3	3.2 ± 1.0	1.74 ± 0.21	0.67	0.87	0.273
AK	3	3.3 ± 0.9	1.77 ± 0.14	1	0.87	-0.2
(b) mtDNA		No. of haplotypes	h	π	Fu's Fs	Tajima's D
BH	19	7	0.854 (0.050)	0.01787	2.165	0.9031
MT	11	9	0.945 (0.066)	0.02183	-1.638	0.63549
AL	3	3	1.000 (0.272)	0.00342	-1.216	nc
WA	4	3	0.833 (0.222)	0.02464	2.479	-0.6784
AK	2	2	1.000 (0.500)	0.04749	2.89	nc

A total of 12 variable sites comprising 17 haplotypes were observed among mtDNA cytochrome b sequences (398bp) for 39 American Three-toed Woodpeckers. Nucleotide diversity ranged from .00342 to .04749, and haplotype diversity ranged from 0.833 to 1.0 (Table 5.2). Overall haplotype diversity was 0.9231. Nucleotide and haplotype diversity was highest in the Alaska population and lowest in the Washington and Black Hills populations.

Genetic structure of populations

I assessed genetic variation by AMOVA for both microsatellite and mtDNA markers based on two hierarchical levels: groups (based on regional proximity or inferred from STRUCTURE and GENELAND clusters) and populations (based on proximity of sample sites). Results for microsatellites indicate that for each grouping, the majority allele frequency variance is found among individuals within the population which ranged from 91.47% to 92.47% (Table 5.3). Variation due to differences among the regional groupings ranged from 5.22% to 7.91%. The grouping which excluded the Black Hills population from the other populations explained most of the among-group variance in the mtDNA analysis.

Table 5.3 Summary of analysis of molecular variance (AMOVA) for ten microsatellite loci and cytb mtDNA region in different groupings of the American Three-toed Woodpecker.

Group	Variance	% variation microsatellite	% variation mtDNA
[Black Hills] ; [Montana + Alberta + Washington+ Alaska]	Among groups	6.32	14.35
	Among populations within groups	2.20	13.29
	Within populations	91.47	72.36
[Black Hills]; [Montana + Alberta]; [Washington + Alaska]	Among groups	5.22	7.85
	Among populations within groups	2.32	17.61
	Within populations	92.47	74.54
[Black Hills]; [Montana + Alberta + Washington]; [Alaska]	Among groups	7.91	4.51
	Among populations within groups	0.29	21.06
	Within populations	91.79	74.42

Bayesian clustering algorithm in STRUCTURE suggests that there are two clusters of populations (Figure 5.2, Table 5.4); however, GENELAND revealed three population clusters (Black Hills, Montana +Alberta+Wasington, Alaska). For both programs the results supporting the chosen number of estimated populations of each was strongly similar to the alternative suggestions of three clusters in STRUCTURE and two clusters in GENELAND.

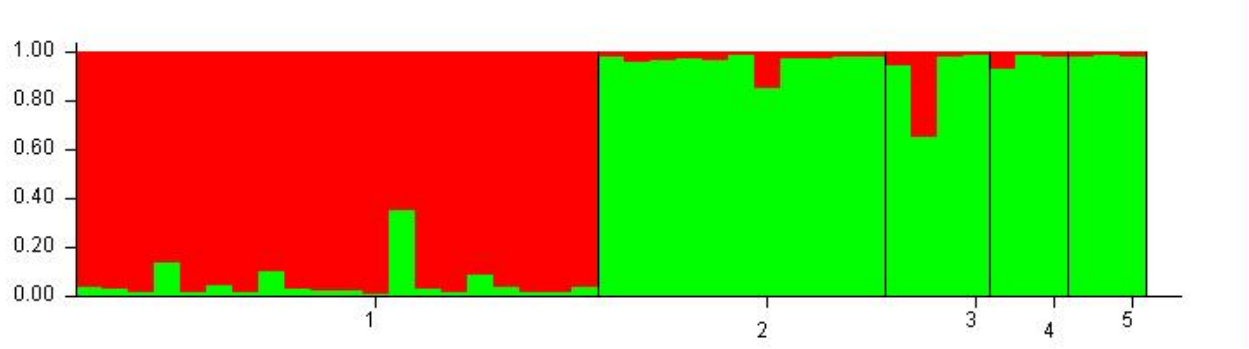


Figure 5.2. Cluster assignment based on K=2 in STRUCTURE. 1=Black Hills, 2=Montana, 3=Alberta,4=Washington and 5=Alaska.

Table 5.4. Proportion of membership of each pre-defined population in each cluster

	1	2
South Dakota	94.40%	5.60%
Montana	3.50%	96.50%
Alberta	10.90%	89.10%
Washington	3.30%	98.70%
Alaska	1.70%	98.30%

The first two principal components explained 21.31% of variation (PCA1, 12.43%, PCA2, 8.88%) in genetic structure among American Three-toed Woodpecker populations (Figure 5.3). This plot shows a distinct separation between the Black Hills population and the other populations.

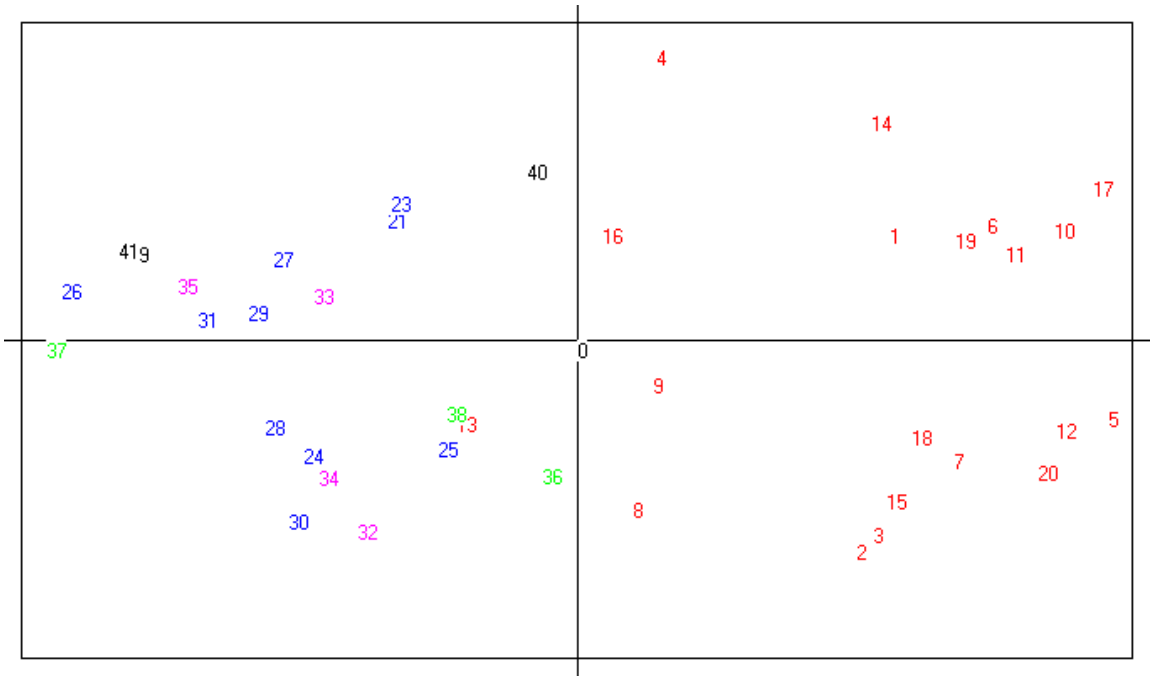


Figure 5.3. Principal component analysis based on microsatellite genotypes of American Three-toed Woodpeckers. Black Hills = (1-20, red); Montana = (21-31, blue); Alberta = (32-35, pink); Washington = (36-38, green) and Alaska = (39-41, black).

Contemporary migration rates as calculated in BAYESASS resulted in estimates ranging from *m*=0.004 to 0.123 (table 5.5). The Black Hills had the lowest migration rates into the population while Montana provided the greatest number of migrants for all populations except for the Black Hills. Gene flow based on the mean frequency of private alleles (Barton and Slatkin, 1986) was Nm=0.64. Overall, the estimated migration rates suggest some gene flow between populations and a general movement in the southeast to northwest orientation.

Table 5.5. BAYESASS migration rates among American Three-toed Woodpecker populations					
	Recipient population				
	Black Hills	Montana	Alberta	Washington	Alaska
Source population					
Black Hills	0.984	0.013	0.05	0.04	0.039
Montana	0.004	0.878	0.123	0.114	0.115
Alberta	0.004	0.026	0.734	0.041	0.042
Washington	0.004	0.053	0.05	0.768	0.049
Alaska	0.004	0.03	0.042	0.037	0.755

Although nonsignificant (P= 0.1950), Mantel results did suggest moderate isolation by distance (R^2 =0.259; Figure 5.4).

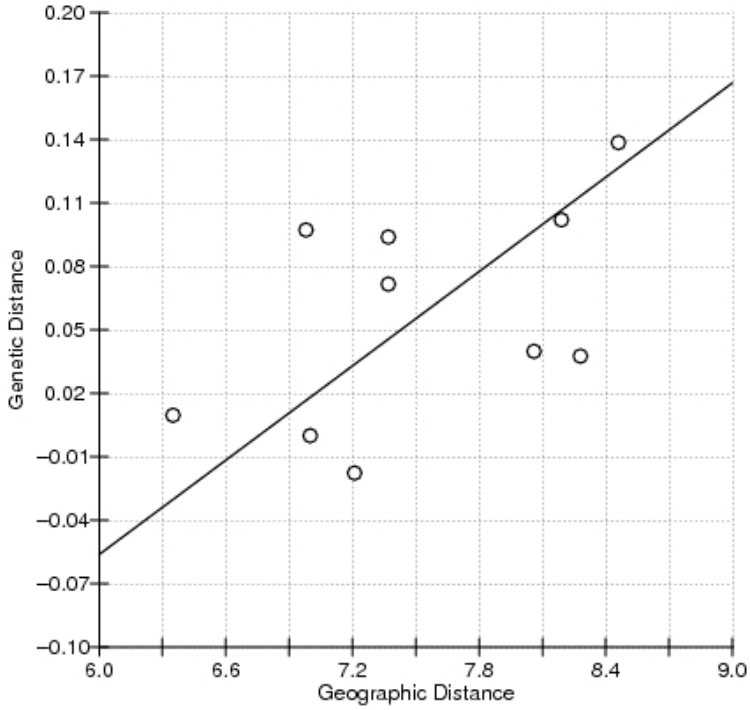


Figure 5.4. Pairwise estimates of $F_{ST}/(1-F_{ST})$ plotted against geographic distance (ln-km) over all populations.

Phylogeographic analyses.

A median-joining network of all haplotypes revealed one haplotype common to the Montana and Black Hills population and one haplotype common to the Alberta, Washington and Alaska populations. Several rare haplotypes within individual populations were revealed (Figure 5.5).

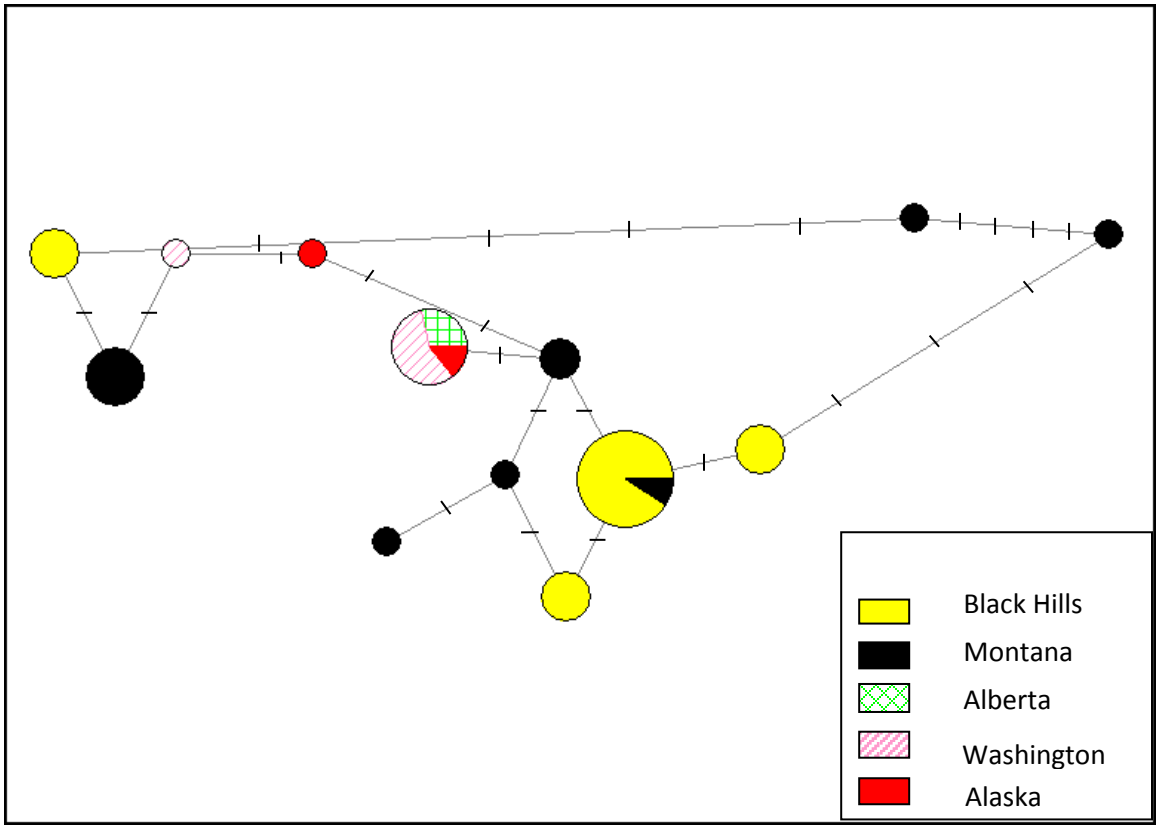
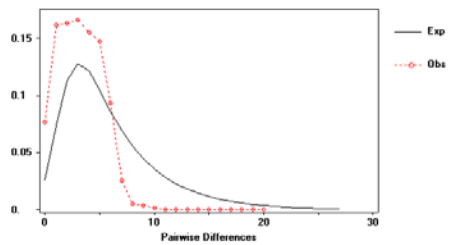


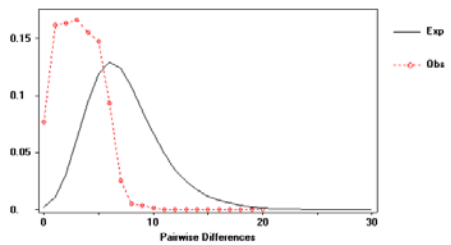
Figure 5.5. Haplotype Median-joining network from 398 bp of cytochrome b. 41 American Three-toed Woodpecker samples from five geographic locations were used for construction of the network. The size of each circle is proportional to the haplotype frequency. Each pie slice represents the number of birds that share a haplotype in each of the sample locations. Tic marks indicate the number of mutational steps. A preprocessing star contraction algorithm was used to identify a historic demographic expansion and therefore, only 13 of the 17 haplotypes are displayed.

The Fu's F_S and Tajima's D tests for neutral evolution revealed that the Black Hills had positive values for both tests which are indicative of a recent bottleneck event and a decrease in population size. Pairwise mismatch distribution for Black Hills, Montana and Alberta and all populations together resulted in a unimodal distribution which is suggestive of recent exponential growth (Fig 5.6 a-f) (Slatkin and Hudson 1991).

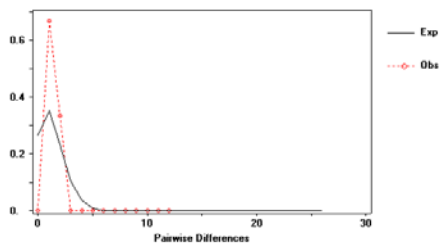
(a) Black Hills



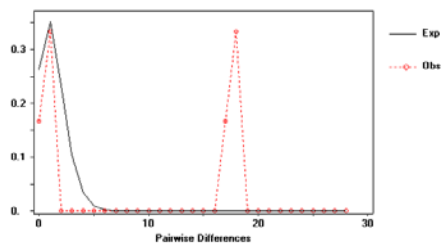
(b) Montana



(c) Alberta



(d) Washington



(e) Alaska

(f) All populations

Figure 5.6. Pairwise mismatch distribution for the American Three-toed Woodpecker. Graphs show the observed (dotted line) and expected (solid line) frequencies for number of pairwise differences in the cytochrome b mitochondrial region.

Discussion

Overall, genetic variation is high in populations of American Three-toed Woodpeckers according to H_E and the number of alleles in 10 microsatellite loci and haplotype diversity (h) values in sequence analysis. Our results agree with previous results from eight individual American Three-toed woodpeckers sampled across North America, which revealed high haplotype diversity (h=0.96) (Zink et al. 2002b.). However, most of the H_E and (h) values are almost two-fold what was reported for the Black-backed Woodpeckers (Pierson et al. 2010), which is a close relative to the American Three-toed Woodpecker. The estimates of high genetic variation are unexpected based on the American Three-toed Woodpecker's life history characteristics such as its sedentary nature and dependence on white spruce which is limited in distribution. Results from the Black Hills population are especially interesting due to its geographic isolation from other populations residing in contiguous boreal/montane forests. Indeed, the nearest known American Three-toed population is located in montane coniferous forests in the Big Horn mountain range of Wyoming, which is 240 km west of the Black Hills

(Froiland 1978). These results suggest a probable scenario that may explain the lack of current genetic differentiation and phylogeographic patterning observed.

The high haplotype diversity and low nucleotide diversity are indicative of a recent range expansion of the American Three-toed Woodpecker. Additionally, the unimodal distribution for the Black Hills, Montana and Alberta populations and all the populations combined suggests a single recent population expansion (Rogers and Harpending, 1992). Although the median joining haplotype network found in the NETWORK analysis did not reveal the typical star-like phylogeny often seen in a recent population expansion, this may be due to low sample sizes from Alberta, Washington and Alaska populations. A common haplotype (H2) shared between the Black Hills and Montana population along with several rare haplotypes found within single populations may provide further support for a recent population expansion. The evidence of a lack of phylogeographic structure compare favorably with other studies focusing on birds with limited distributions (Ball and Avise 1992, Zink et al. 2002a, Zink et al. 2002b, Davis et al.2006).

Post –Pleistocene rapid range expansion from boreal forest south of the ice sheets may explain the lack of phylogeographic structure of the American Three-toed Woodpecker. Past genetic research has often focused on the effects that the Pleistocene had on genetic diversification of taxa within North America and Europe (Hewitt 1996, 2000; Avis and Walker, 1998; Knowles, 2001). During the Pleistocene epoch, glaciers advanced and retreated across the landscape, resulting in the contraction of populations towards the equator during glacial advances and subsequent expansion northward during glacial retreats. This period of oscillation caused changes in population distribution and composition which is evident within population

genetic structure. During the most recent glacial advance, which occurred in the late Pleistocene, the Wisconsin ice sheet came within 150 miles to the east of the Black Hills when it paralleled the Missouri River and the Continental ice sheets reached the Big Horns 150 miles to the west (Froiland 1978); thus, creating an unglaciated pocket around the Black Hills. During glacial maximas, boreal/montane forests moved from higher elevations to lower elevations resulting in contiguous boreal/montane forests surrounding the Black Hills. Species dependent on these forests types moved to lower elevations and southward. Once the climate warmed and the glaciers receded, taxa expanded their ranges northward and sedentary boreal dependent species became restricted to high elevation isolated mountain ranges (Lomolino et al. 2006) such as the Black Hills. However, highly vagile species, such as birds, have been documented to have low genetic diversity across their range which has been attributed to rapid postglacial range expansion (Hewitt 2000).

Lack of substantial population structure was also evident in the results from nuclear genetic analyses. There is evidence of limited recent gene flow between populations based on high heterozygosity values, migration rate estimates from MCMC methods and mean frequency of private alleles in addition to support from Isolation By Distance (IBD) tests including Mantel tests of significant correlation. Although nonsignificant (P= 0.1950), Mantel results did suggest moderate isolation by distance (R^2 =0.259). The number of populations included in IBD tests are inversely related to Mantel P values; thus, with smaller numbers of populations, the less probability of significance. A recent meta-analysis on the sensitivity of study methods on IBD results revealed in order to have a >90% of probability of significance, a study would need a sample of 23 populations (Jenkins et al. 2010). Nonetheless, a significant IBD result does not

guarantee uniform gene flow among populations as significant IBD values can occur even if there are barriers to geneflow (Bossart and Prowell 1998; Lugon-Moulin and Hausser 2002; Garnier et al. 2004). Often clustering methods, such as the Bayesian-clustering methods used in this study, coupled with IBD methods can elucidate barriers to gene flow (Garnier et al. 2004).

In the present study, STRUCTURE and GENELAND recovered two and three individual populations, respectively. In both, the Black Hills population was differentiated from the other populations. Additionally, PCA also revealed a distinct separation between the Black Hills population and other populations. It is likely that the prairie surrounding the Black Hills is at least a partial barrier to gene flow. A comparison of recent migration rates between populations suggests that there is very little gene flow into the Black Hills population, but there is greater gene flow from the Black Hills population into the other populations, particularly into the Alberta population. Among all populations, the Montana population appears to be providing the most migrants.

Although results indicate gene flow among American Three-toed Woodpecker populations, the majority of genetic variation is contained within individuals in populations with only 5-8% of the variation explained among populations based on the microsatellite AMOVA. Considering that 90% of the genetic variation is contained within the population, geographically isolated populations with little gene flow into the population, such as the Black Hills, may be a conservation concern.

Overall, our results along with estimates of nesting success (Chapter 4) suggest that the American Three-toed Woodpecker population structure may be characterized by source-sink

dynamics and that that the Black Hills population may be currently serving as a sink population. Source populations are defined as populations that inhabit high quality habitats that produce a surplus of individuals that migrate to other populations (Gaggiotti 1996, Range et al. 2006) whereas sink populations are those in lower quality habitat that require immigrants from other populations in order to remain a viable population (Pulliam 1988). Although high rates of heterozygosity may be explained by sex-based dispersal (Prout, 1981), small population size (Pudovkin et al. 1996) or effects of mating system (Luikart and Cornuet, 1999), it may also be indicative of metapopulation dynamics due to the fluctuation in genetic composition (Segelbacher and Storch, 2002).

Along with other woodpecker species', the American Three-toed Woodpecker is known to be sedentary (Zink et al. 2002b), although it has been documented to be irruptive during times of habitat disturbance (Wiggins 2004). Indeed, the American Three-toed Woodpecker has been documented 200 km south of its geographic range when it responded to an outbreak in Dutch elm disease in the 1950s (Yunick 1985). The irruptions into areas of increased prey availability appear to be irregular with long lapses between irruptions (Yunick 1985). Pulses of long-distance dispersal may explain the evidence of contemporary genetic diversity within the American Three-toed Woodpecker populations and may be maintaining the species as a metapopulation.

Conservation Implications

Based on our results, conservation of the Black Hills population should be a priority in resource management planning for the species. In addition to the geographic isolation and limited gene flow into the Black Hills population, the natural history characteristics of American

Three-toed Woodpecker also contribute to population status concern. This species is closely associated with white spruce forests, and in the Black Hills, white spruce is limited in distribution often found in patches on north facing slopes or cool canyon bottoms (USDA 2005). Conservation planning should first focus on the retention of white spruce forests adjacent to aspen stands with old-growth characteristics such as those with substantial numbers of snags that can be used for foraging and nesting sites (see chapters 2 and 3). Additionally, low levels of nesting success may be attributed to predation and nest kleptoparisitism by red squirrels, (*Tamiasciurus hudsonicus*), least chipmunks (*Tamias minimus*), and northern flying squirrels (*Glaucomys sabrinus*). Installation of aluminum flashing above and below the nest cavity may assist in deterring predation as this has proven beneficial for Red-cockaded Woodpckers (Neal et al. 1993). Lastly, although genetic variation is large within all populations, the Black Hills populations has negligible amounts of gene flow into the population. Currently, the Black Hills population is listed as a "sensitive species" by the USDA, Forest Service. Although it is not considered endangered, the small population size and geographic isolation make it susceptible to the detrimental effects of genetic drift.

If, in the future, augmentation should be necessary for the Black Hills population, mangers should be cognizant of the important attributes the donor population should possess before the movement of individuals into the Black Hills occurs (Storfer 1999). First, in order to prevent outbreeding depression caused by breaking co-adapted gene complexes and population local adaptations, the donor population should be the closest geographically to the Black Hills and have similar habitats. Based on our results, the Montana or Alberta populations would probably be the best donor population. The Montana population appears to be the closest

genetically, while the Alberta population is the closest population that resides within boreal (i.e., spruce) forest habitat. Introducing new genetic variation is important to the survival of a small isolated population, but too much variation may increase the likelihood of outbreeding depression (Frankham et al. 2002). Second, the donor population should have a high reproductive rate, nearly equal sex ratio and high numbers of juveniles within the population. The juveniles could be donated to the Black Hills population before territories are established within the donor population.

The results of this study offer insights into the historical phylogeographic patterns and current genetic status of five geographically separated populations with special emphasis on the Black Hills population. Using both nuclear and mtDNA markers provided a more comprehensive picture of the genetic health of the American Three-toed Woodpeckers that conservation and resource managers can use before making management decisions that affect the future population status of American Three-toed Woodpeckers.

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Chapter 6: Home Range Size and Habitat Associations of The American Three-toed Woodpecker (*Picoides dorsalis*) in the Black Hills of South Dakota.

Introduction

Increases in habitat degradation have resulted in resource selection studies becoming an important component of conservation management plans because they provide quantitative information regarding long-term resource requirements for populations (Manly et al. 2002). Resource selection occurs at different hierarchical levels: geographic range, landscape, home range, patch and selection of particular food items (Johnson 1980).Two levels within this hierarchy are often used concurrently in studies and one of the most common pairings are landscape and home range levels (Katnik and Wielgus 2005). Home range studies are frequently a component of larger ecological studies because they incorporate important necessary resource requirements for activities such as feeding, mating and production of offspring (Burt 1943). The size, configuration in relation to landscape attributes and vegetative composition within and near home ranges are often the focus of these studies. Delineation of home range characteristics may be affected by competition within and among species, population density, predation, topography, heredity, and vegetative composition and structure (Manly et al. 2002). Additionally, heterogeneity within the home range itself contributes to the disproportionate use of particular areas over others (Samuel et al. 1985). These core areas of concentrated use should be identified and conserved as they may be crucial for the continued persistence of populations. This may be especially true for populations that are dependent on habitat characteristics that are rare, patchily distributed and likely to be negatively affected by forest management plans.

The American Three-toed Woodpecker is a rare, sedentary species that is closely associated with white spruce habitat (Leonard 2001). Because of its use of dense, high elevation conifer forests, only a few published studies have focused on the home range requirements of this species. Goggans et al. (1989) determined that the minimum convex polygon (MCP) breeding-season home range for the American Three-toed Woodpeckers (n=3) in the Deschutes National Forest, Oregon, was mean (±SE) 166±73 ha. This analysis was largely based on the post-nesting period. The habitat selection within the home range indicated selection for single-storied mature/over-mature sawtimber and selection against single-storied saplings, seedlings and poles.

The Eurasian Three-toed Woodpecker (*Picoides tridactylus*) was recently acknowledged as a separate species from the American Three-toed Woodpecker based on a phylogeographic study that determined a 4% mtDNA sequence divergence (Zink 2002). A home range study of the Eurasian Three-toed Woodpecker (n=24) in Berchtesgaden National Park, Germany, during the nesting period determined a mean home range size (± SE) of 86.4 ± 23.4 ha using the (ADK) method (Pechacek 2004). Additionally, the size of the home range increased significantly in forests with low tree density and in areas with higher diversity of tree species, leading to the suggestion that the birds adjust their home range size to the amount of forest present and that higher tree diversity produces a more stable environment not conducive for arthropods requiring large amounts of dead wood (Pechacek and d'Oleire-Oltmanns 2004).

The American Three-toed Woodpecker population in the Black Hills is of particular conservation concern because of its low population size, geographical isolation from other

populations and dependence on white spruce forests which are limited and patchily distributed within the Black Hills. In the Black Hills, white spruce is restricted to the higher elevations on the Limestone Plateau which is located in the north-central Black Hills. Typically located on north-facing slopes and cool canyon bottoms, it often occurs in linear patches parallel to canyons (USDA 2005).The objectives of this study were to (1) determine the Black Hills population breeding period (pre-nesting, nesting and post-nesting, combined) home range size by using minimum convex polygon (MCP), fixed (FK) and adaptive kernel (ADK) estimation methods and to (2) determine if a relationship exists between home range and vegetative characteristics. The FK method was the principal method used to analyze the habitat associations because the FK with least squares cross validation produces less bias than the ADK method when sample sizes are small (Seaman and Powell 1996, Seaman et al. 1999) and MCP is more sensitive to sample size and outlier locations. MCP and ADK home range size estimates were calculated for comparison purposes to other populations.

Study Area and Methods

Study Area

We conducted our study in the Black Hills of South Dakota. The Black Hills are a mountain range situated in the Northern Great Plains and are often referred to as a forested island in a grassland sea (USDA 2005). The varied climate, topography, geology and isolation from other mountain ranges have created a variety of habitats in the Black Hills, which are seen as a refuge for biodiversity within the Northern Great Plains (Sheppard and Battaglia 2002). Because the American Three-toed Woodpecker is considered a habitat specialist and is closely associated with old growth and mature spruce forests (Wiggins 2004), we focused our study on white

spruce forests, which are largely located on the Limestone Plateau region in the northwestern Black Hills. White spruce covers 2% of the Black Hills and aspen (*Populus tremuloides)* covers approximately 3% of the Black Hills, and most commonly occurs in the northwest section of the Limestone Plateau, where white spruce is climax, and in areas of disturbance within coniferous forests (Hoffman and Alexander 1987). Most of the remaining 95% of forest cover within the Black Hills consists of ponderosa pine (*Pinus ponderosa*) (Shepperd and Battaglia 2002, Brown and Cook 2006).

Methods

Capture and Marking

All birds in this study were captured at their nesting cavity. We focused nest site searches in areas of known woodpecker occurrence determined from playback surveys in white spruce forests conducted in 2005 (Chapter 2) in areas where we opportunistically observed woodpeckers, and in areas where trees with flaked bark typical of three-toed woodpecker foraging were located. We systematically searched these areas for nesting sites by observing bird behavior and /or by checking available snags and aspen within the study area for active cavities.

American Three-toed Woodpeckers were captured within the breeding period from late May to mid-July in 2005-2008 by using either a mist nest or hoop net placed in front of the nesting cavity entrance. Once captured, birds were banded with a U.S. Fish and Wildlife Service aluminum leg band and weight, gender, wing length, tail length, tarsus length and bill depth were recorded. A 1.2-g Advanced Telemetry Systems(ATS Model A2455) radio transmitter (<3% of body mass) was attached to either the back (2005) or base of the central retrix (2006-2008) using

cyanoacrylate glue. Braided nylon ties were used to secure the antennae along the length of the central retrix.

Radio transmitters were attached to a total of 27 birds. However, we encountered problems with the retention of the transmitters on several of the birds, so we were unable to obtain the minimum threshold of ≥ 20 locations (see below) from 14 of these birds. Of these 14 birds, seven transmitters were recovered after they were pulled free by the bird, five birds abandoned their territories after nest failure and could not be re-located, and one bird carcass was found with the transmitter still attached. Thus, we obtained sufficient locations for 13birds and only these birds were used in the study. Although we have telemetry data from pre-nesting, incubation and brooding and post-fledging periods, we lack the minimum 20 locations from each period to compare home ranges among the different periods. Therefore, telemetry locations throughout the entire breeding period were pooled together for each bird.

Radio-tracking

Individuals were tracked with Yagi 3-element handheld antennas and ATS receivers (Model R4000) several times each week by triangulation. In order to decrease autocorrelation among locations, a minimum of 1 hour between each recorded bearing was obtained (White and Garrott, 1990). UTM locations were obtained with a Garmin etrax Vista GPS unit. Because of the dense conifer forests and mountainous topography in which the American Three-toed Woodpecker resides, distortion of signal direction was likely introduced (Lee et al.1985). In order to minimize the amount of signal distortion error, several steps were taken. First, whenever possible signals were obtained at least 50 m from the forest edge (Kenward 1987) in order to obtain the most accurate bearing of the signal. Second, if there was inconsistency with location

of the signal or contradiction among field technicians, both technicians would move to higher ground and would attempt to obtain a consistent consensus of the signal location. Third, questionable signals were often verified by homing techniques in which visual observation of the individual validated or refuted the triangulation signal. The precise UTM location of an individual located by homing was recorded as the location of the individual for future analyses. Finally, during triangulation, each technician recorded at least three, and occasionally greater than five, location bearings in order to mitigate problems with imprecise antenna directionality (Mech 2002).

Data Analyses

Home Range- Home range estimates were generated using the program LOAS (Location of a signal, Ecological Software Solutions, Sacramento, California, USA). Locations with an error area larger than 0.04 ha were not used for home range calculations due to an increased risk of Type II error (Conner and Plowman 2001). An area-observation curve was calculated in BIOTAS (Ecological Software Solutions, Sacramento, California, USA) to determine the minimum sample size required for accurate home range estimation. Based on this analysis, the threshold sample size was 20. This result is consistent with the results of a previous home range study of the Eurasian Three-toed woodpecker, in which the threshold sample size requirement for home range analysis was 21 (Jäger and Pechacek, 2002; Pechacek and d'Oleire-Oltmanns, 2004). The triangulated locations for each bird with a minimum of 20 locations were exported to ArcGIS 9.3. The Home Range Extension (HRE) and Hawth's Tools were used to calculate 95% and 50% ADK and FK for home range size estimates and 100% and 50% MCP home range estimates.

Habitat Associations- Telemetry locations were clipped to a vegetation layer of the Black Hills National Forest map in ArcGIS 9.3. To determine habitat use, habitat attributes considered included dominant cover type (ponderosa pine, white spruce, aspen, grasslands), habitat structural stage (open/grass, shrub/seedling, sapling/ pole cover < 40%, sapling/pole cover 40%-70%, sapling/pole cover > 70%, mature tree cover < 40%, mature tree cover 40%-70%, mature tree cover > 70%, over-mature tree), the number of sound (hard) standing snags and non-sound (rotten) standing snags per acre with dbh of ≥ 60cm and lastly, the distance of telemetry locations to roads. These habitat attribute categories were chosen because they were deemed important habitat characteristics in other populations of American Three-toed Woodpeckers (Goggans et al. 1989, Wiggins 2004).

The Euclidean distance-based analysis (DA) method was used to conduct the habitat association analysis. The DA method was used because of its ability to incorporate edge and patchy habitats into the analysis (Conner and Plowman 2001, Conner et al. 2003) and it reduces Type I and telemetry error unlike other analysis methods such as compositional analysis (Bingham and Brennan 2004). The DA method compares minimum distances of known locations to habitat types to expected distances based on random points. Habitat associations were measured at two scales: 1) within-home range scale in which the individuals actual locations within the home range were compared to random points within the home range, and 2) landscape scale in which random points within the home range were compared to random points throughout the study area. The 95% fixed kernel home range estimate polygon and known telemetry locations were layered onto existing vegetation layer of the Black Hills National Forest in ArcGIS 9.3. To determine non-random habitat use, the Hawth's tools extension random point

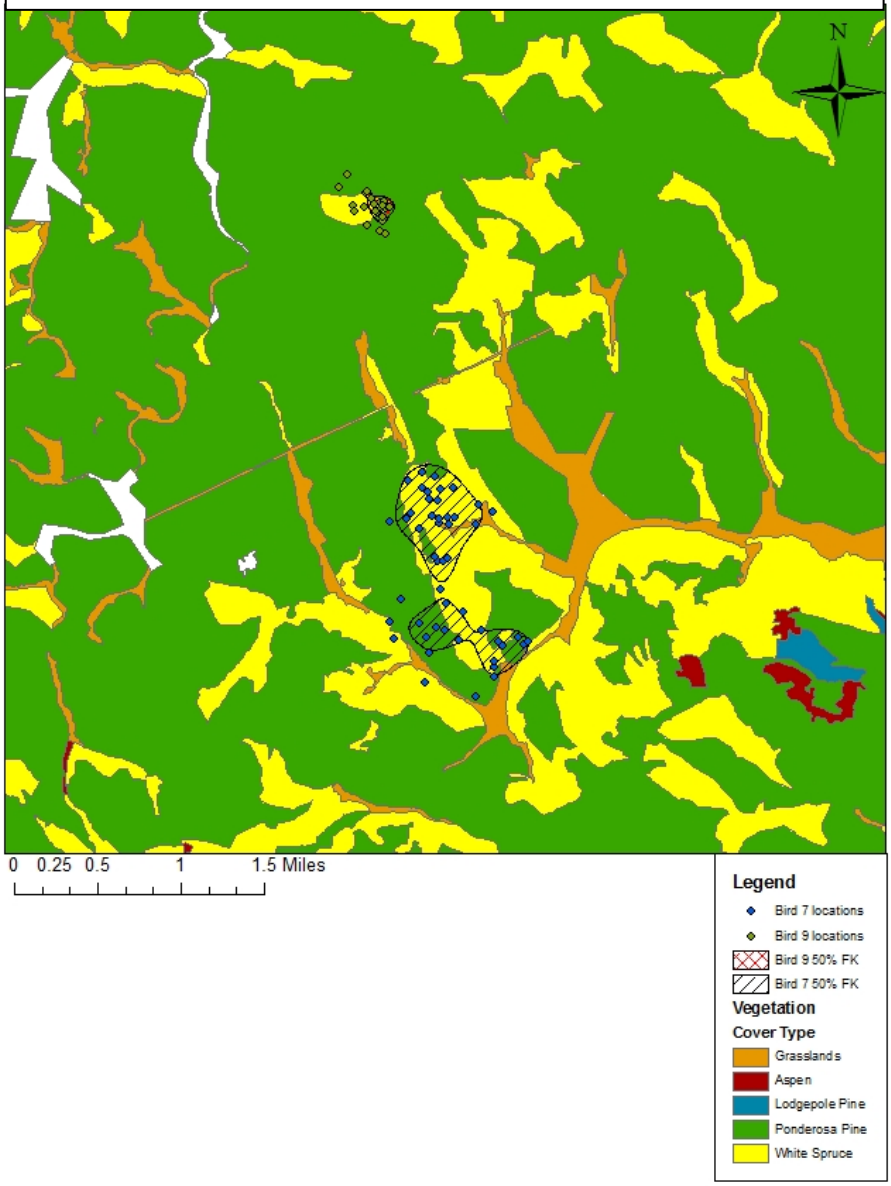
generator was used to distribute 50 random points within the 95% fixed kernel home range polygon for each individual for the within home-range scale analysis and 500 random points within the study area for the landscape level scale. For each bird, we calculated the distance from each random point to the nearest representative habitat attribute of interest. The average distance from the random points to each habitat attribute created a vector of mean distances (r_i) for each bird. The same procedure was used to generate (u_i) for each bird based on the actual locations. A vector of ratios (d_i) for each bird was created by dividing u_i by r_i. Under the null hypothesis of no selection, the expected value of d_i is 1.0. MANOVA was used to determine if ratios differed which would indicate habitat selection. Paired t-tests were used to determine habitat attributes that were used disproportionately to their availability at the home range and landscape levels. All statistical analyses were conducted in SigmaStat 3.5 or JMP 9.Results are presented as means ± SE. We accepted significance at $P \leq 0.05$.

Results

Home range size

We tracked and determined the home range and habitat associations of seven female and six male American Three-toed Woodpeckers. There was no significant difference between male and female home range size for each of the three home range estimates ($t_{12} = 0.807$, $P = 0.437$ FK 95%, $t_{12} = 1.483$, $P = .166$ ADK 95%, $t_{12} = 0.730$, $P = 0.481$ MCP 100%). Intensely used core areas (50% use distribution for each method) comprised 13-23% of the overall home range area (Figure 6.1)

Figure 6.1. FK 50% (core area) home range of two American Three- toed woodpeckers in the Black Hills, South Dakota.



The FK 95% use distribution home range size ranged from 5.7 to 158.9 ha with a mean of 91.1 ± 25.5 ha (n = 13) (Table 6.1). The ADK 95% use distribution estimated the largest mean home range size at 144.73 ± 36.12 (ha) with a range of 8.1 to 386 ha. The ADK 95% result was double the MCP 100% use distribution at 70.88 ± 15.28 ha, with a range of 4.7 to 205.4 ha.

Table 6.1 American Three-toed Woodpecker home range size (ha) using 50% and 100% Minimum Convex Polygon (MCP), and 50% and 95% Fixed Kernel (FK) and Adaptive Kernel (ADK) estimation methods.

		MCP		FK		ADK	
Bird ID							
	n	50%	100%	50%	95%	50%	95%
1	32	0.5	4.7	1.5	7.3	1.1	9.6
2	31	0.6	5.9	1.1	5.7	1.3	8.1
3	42	1.6	17.3	2.4	13.9	2	20
6	43	1.5	99.9	3.1	17.8	2.8	27.3
7	50	84.3	205.4	91.7	336	79	386
9	27	1.8	110.9	5.3	32.6	4.2	43.6
13	48	2.2	19.5	12	69	4	377
20	32	34.1	101.1	46.5	158.9	43.4	172.1
21	32	6.6	72.7	22.5	139.1	17	237.6
23	29	13.7	59.8	27.2	106.1	24.1	125.9
24	26	5	73.8	10.6	71.3	8	106
25	25	4.6	56.5	15.5	95.2	15.9	167.7
26	31	30	93.9	30.1	131.4	46.2	200.6
mean		14.35	70.88	20.73	91.1	19.15	144.73
SE		6.59	15.28	7.01	25.15	6.56	36.12

Habitat associations

Significant habitat associations within home ranges were detected (Λ 0.26, P = 0.044). Mean distances from bird locations to roads and habitats with 9-32 rotten standing snags per acre with a dbh of $\geq$ 60cm were closer than expected (t_{12}= 2.731, P= 0.018; t_{12} = 3.270, P =.007, respectively). No other results were significant. Significant habitat associations were also detected at the landscape level (Λ 0.31, P = 0.036). Aspen cover type (t_{12} = 3.020, P = 0.019) was farther away from bird locations than expected. Mature tree cover < 40% (t_{12} = 3.276, P = 0.014) and roads (t_{12} = 2.907, P = 0.016) were closer than expected to bird locations.

Table 6.2 Habitat Associations of Within Home Range and Within Landscape Locations using paired t-tests. Significant results are in bold. [a]Number of snags per acre with dbh > 60cm.

	Within Home Range		**Within Landscape**	
	t	*P*	t	*P*
Cover Type				
Ponderosa Pine	-1.687	0.117	0.103	0.921
Grassland	-0.844	0.415	0.0434	0.967
Aspen	1.46	0.17	**-3.02**	**0.019**
White Spruce	-0.794	0.442	2.323	0.053
Structural Stage				
Open/Grass	-0.863	0.405	2.66	0.204
Shrub/Seedling	-0.116	0.91	1.439	0.193
Sapling/Pole Cover < 40%	1.681	0.119	0.818	0.44
Sapling/Pole Cover 40-70%	-0.89	0.391	0.255	0.806
Sapling/Pole Cover >70%	0.973	0.35	-0.743	0.481
Mature Tree Cover < 40%	-1.376	0.194	**3.2761**	**0.014**
Mature Tree Cover 40-70%	1.747	0.106	4.356	0.133
Mature Tree Cover > 70%	-0.307	0.764	1.092	0.311
Over-Mature Tree	-1.772	0.102	-2.582	0.349
Snags Soft[a]				
0-8	-1.112	0.288	-1.177	0.278
9-32	**3.27**	**0.007**	0.495	0.636
33-82	-0.677	0.511	1.909	0.098
82-152	1.134	0.279	2.39	0.062
Snags Hard[a]				
0-16	-0.239	0.815	**-3.719**	**0.02**
17-94	-1.518	0.155	1.048	0.329
Roads	**2.731**	**0.018**	**2.907**	**0.016**

Discussion

Home range size

Home range size estimates varied greatly between individuals and estimation methods. Compared to other studies, the 100% MCP home range sizes were less than half as large as those documented by Goggans et al. (1989) study in the Deschutes National Forest, Oregon (This study: 70.88 ± 15.28 ha, n =13; Oregon: 166 ± 73.47 ha, n = 3. Our ADK home range estimates were almost double those of the Eurasian Three-toed Woodpecker during the nesting period in Germany (Pechacek 2004) (This study: 144.73 ± 36.12 ha, n = 13; Germany: 86.4 ± 23.4 ha, n =24). However, Pechacek (2004) also documented pre-nesting (115.8 ± 23 ha) and post-nesting (153.7 ± 17.1 ha) home range sizes that were larger and more comparable to our results. Comparison of home range sizes among different studies should be interpreted cautiously because of differences in study locations, study periods or estimation methods. Indeed, the majority of telemetry locations collected by Goggans et al. (1989) were from the post-fledging period or from failed nesting attempts whereas our locations were from pre-nesting, incubation and post-fledging periods. Because of the energetic demands placed on the parents during the nesting period, home range sizes are often smaller than the pre- and post-nesting periods (Pechacek 2004). Although our sample sizes were not large enough to calculate pre-nesting, incubation and post-nesting separately, the telemetry locations of the birds with the two lowest home range sizes using the FK 95% method (Bird 2 = 5.7 ha, Bird 1 = 7.3 ha) were almost entirely obtained during the incubation stage. In contrast, all the telemetry locations of the bird

with the largest home range size (Bird 7 = 336 ha) were obtained during the post-nesting period. Since the Eurasian Three-toed Woodpecker study (Pechacek 2004) was also conducted during the pre-nesting, nesting and post-nesting periods in habitats dominated by spruce, this allows for a more reliable home range size comparison to our study.

Overall, although our home range size results compare favorably with those of the Eurasian Three-toed Woodpecker, they are much smaller than home range sizes for Black-backed Woodpeckers (*Picoides arcticus*) in western North American conifer forests (Dudley and Saab 2007). The Black-backed Woodpecker post-fledging FK 95% home range size ranged from 115.6 to 420.9 ha and MCP 100% ranged from 150.4 to 766.1 ha (Dudley and Saab 2007). This difference may be due to the use of only post-fledging telemetry locations, as well as the large numbers of isolated areas of concentrated use, which increase MCP estimates. In addition, because Black-backed Woodpeckers are recent burn specialists, habitat differences likely also play a role in the differences in home range size compared to American Three-toed Woodpeckers in our study.

Core areas of home ranges are areas of concentrated use (Samuel et al. 1985) and are often priority habitat for species at risk of local extirpation. The American Three-toed Woodpecker in the Black Hills utilized 13- 23% of the home range as core area. This estimate is similar to the Eurasian Three-toed Woodpecker estimates of 25.5% to 28.4% (Pechacek 2004). Based on the FK 95% method, most home ranges resulted in one to three areas of concentrated use (Figure 6.1). This number of areas of concentrated use within the home range is relatively low for woodpeckers generally (Dudley and Saab 2007).The low numbers of core areas and the

moderate home range size in this study suggest that the American Three-toed Woodpecker in the Black Hills resides in high quality habitat. Three-toed woodpeckers are known to be closely associated with white spruce habitats and in the Black Hills, white spruce habitats are often located along north facing slopes and canyon bottoms (USDA 2005). The narrow, linear, spruce habitats is likely meeting the needs of the Black Hills population such that the home range size remains small to moderate.

Habitat Associations

For both home-range and landscape level habitat associations, telemetry locations were closer than expected to roads. American Three-toed Woodpeckers use edge habitats (Goggans et al. 1989, Mohren 2002) and based on nest site selection data in this study (Chapter 4) many nest sites were located along edges, such as those produced by roads. Because our study was conducted during the breeding season, when most activities are largely focused on the nest site, the importance of edges, such as roads, for activities that define the breeding season home range is corroborated by both telemetry and nest site selection data.

Within the home range, small to moderate numbers of large sized (≥ 60 cm dbh) rotten standing snags were closer to telemetry locations than expected. American Three-toed Woodpeckers often use habitats of recent disturbances because of increased foraging and nesting opportunities in snags (Murphy and Lenhausen 1998, Wiggins 2004). However, three-toed woodpeckers typically occupy areas of dying or recently dead trees (Goggans et al. 1989, Murphy and Lenhausen 1998, Imbeau et al. 1999, Hoyt and Hannon 2002) instead of areas of old dead stands. Unsound (rotten) snags are less likely to have bark beetles (which is the American

Three-toed Woodpeckers prey) because as dead trees dry out, the moisture content of the phloem and bark decreases and consequently bark beetle survival decreases (Werner and Post 1985, Hoyt and Hannon 2002). Therefore, the results that rotten standing snags appear to be an important habitat association within the home range is somewhat surprising. Perhaps such snags are important for territorial drumming sites, as we observed three-toed woodpeckers drumming from such snags on numerous occasions throughout the study period.

At the landscape level, < 40% mature tree cover was closer to telemetry locations than expected. Old-growth and mature forests have been documented to be important foraging and nesting habitats for American Three-toed Woodpeckers (Goggans et al. 1989, Leonard 2001, Wiggins 2004). Because of intensive management in the Black Hills over the past 100 years, most of the forest consists of young to medium-aged stands (Hoffman and Alexander 1987). However, mature and old-growth white spruce is primarily located on the Limestone Plateau in the northern Black Hills which is within our study area. High percentages of mature tree cover was expected based on previous studies (Goggans et al. 1989), however, the Black Hills American Three-toed population is known to use edge habitats (Mohren 2002) and this preference for edge-related habitats may explain why telemetry locations were closer to more open areas, rather than in dense forests.

At the landscape level, telemetry locations were significantly farther from aspen cover than expected. Although American Three-toed Woodpeckers in the Black Hills often select aspen for nest site locations (Chapter 4), dominant aspen cover does not appear important at the landscape scale. In the Black Hills, aspen is primarily located northwest of the Limestone

Plateau, but also occurs in areas of recent disturbance and where white spruce is climax on the Limestone Plateau (Hoffman and Alexander 1987). American Three-toed Woodpeckers may be selecting against the more open aspen cover surrounding their home range because of the decrease in foraging opportunities as American Three-toed Woodpeckers are not known to use aspen as foraging substrates. Conversely, the result may also be a result of the limited amount of aspen located within white spruce forests when compared to the study area which also includes upper north west portions of the Limestone Plateau where aspen typically occurs.

Overall, our results indicate the importance of linear, edge-related, features such as roads. The small to moderately sized home range suggests that the American Three-toed Woodpecker in the Black Hills occupies high quality habitats sufficient to meet its breeding requirements. Management implications include the importance of conserving open areas and large diameter snags. By providing these habitat types, the American Three-toed Woodpecker will likely have greater nesting and foraging opportunities which will help to maintain their small to moderate home range size in narrow and limited spruce forests in the Black Hills.

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Chapter 7: Conclusions and Management Implications

This study addressed questions regarding resource requirements and provided baseline data for future studies focusing on the Black Hills population of the American Three-toed Woodpecker. The unobstrusive behavior , close association with dense conifer forests and rarity have resulted in an absence of basic life history and genetics information pertaining to this species. The population in the Black Hills is likely the most salient conservation concern due to its isolation from other populations. To effectively evaluate the status of the American Three-toed Woodpecker in the Black Hills, data on population density, habitat associations and genetics data were needed. Therefore, this comprehensive study provides a wholistic view of the status of the Black Hills population and provides necessary information in order to effectively manage this population.

The results for the population survey, using playback method with no corrections for probability of detection, yielded abundance estimates at .20 birds/point, 3.0 birds/transect based on 26 transects with 15 points each. On one transect 10 individuals were detected which yields the maximum relative abundance at 0.6 birds/point. Overall, these results compare favorably to American Three-toed Woodpecker populations in the Rocky Mountains (Leonard 2001). By utilizing the playback survey method with no corrections for probability, the abundance estimates increased by 2-10-fold compared to the RMBO using non-playback survey method with corrections for probability of detection (White et al.2010). Due to the difficulty in locating this species, it is recommended that future population surveys use the playback survey method with no corrections for probability.

A large portion of this project was devoted to foraging, nesting and home range habitat associations of the Black Hills population. This study suggests that wildlife size (≥ 23 cm dbh) trees, and especially wildlife spruce snags, were important foraging substrates. In general, small size (< 23 cm dbh) living and snag trees were used in lower proportion to their availability. These results concur with other studies that also propose that wildlife size snags are the primary foraging substrate for the American Three-toed Woodpecker (Goggans et al. 1989). However, unlike other populations in contiguous conifer habitats, the Black Hills population did not exploit recently burned areas for foraging use (Murphy and Lehnhausen 1998, Leonard 2001). Although considered a sedentary species, the American Three-toed Woodpecker is known to be irruptive in areas of recent disturbance due to the increases in prey availability (Yunick 1985). As such, in other areas of its geographic range, it is often found in light (Hoyt and Hannon 2002) to moderately burned forests (Kotliar et al. 2008). The absence of the Black Hills population in areas of recent burns is likely explained by the limited numbers of fires occurring in or near the northern Black Hills spruce forests and/or competitive exclusion by woodpecker fire specialist such as the closely related Black-backed Woodpecker.

The breeding ecology section of this study documented that the nesting success rate of the Black Hills population of the American Three-toed Woodpecker was much lower than other populations and other woodpecker species. The results suggest that the Black Hills population may be functioning as a population sink. Nesting success was highest in spruce snags with cavity heights above > 3.7m. However, 61% of the nest sites were located within aspen trees. The high failure rate, especially in aspen trees, is most likely due to predation. In this study, I documented two instances of flying squirrels usurping American Three-toed Woodpecker nests, a red squirrel

dragging a nestling out of a nest cavity and numerous records of crushed eggs within nest cavities. Mammalian predators such as the northern flying squirrel and red squirrel use aspen trees and conifers for foraging and nesting (Willson et al. 2003, Hough and Dieter 2009). A recent study documented northern flying squirrels residing in the Black Hills used habitats with higher precipitation, aspen and basal area of snags (Hough and Dieter 2009). Other studies have suggested that the American Three-toed Woodpecker also select habitats that are moist (Leonard 2001) and have large numbers of snags (Goggans et al. 1989, Murphy and Lehnhausen 1998). In this study, I documented high selection for aspen trees for nesting substrates and the greater numbers of wildlife size ($\geq$ 23cm dbh) living and snag aspen trees around nest site locations when compared to random sites. Additionally, the majority of nests were located on edge habitats which may affect the predation rate. The selection for similar habitat types and the low nesting success rate demonstrates the urgent need for additional studies focusing on American Three-toed Woodpecker predator population dynamics, juvenile mortality, dispersal distances, edge habitat use and the effects of different fire regimes in aspen/spruce forests.

The home range size of the Black Hills population was close in comparison to the Eurasian Three-toed Woodpecker, but much smaller when compared to the closely related Black-backed Woodpecker. The close association between individual telemetry locations and roads suggest the importance of edge habitat within home range and landscape.

Long term conservation goals should be aimed at identifying potential source populations for genetic augmentation of the Black Hills population. Based on the results from the genetics study, there is very little immigration into the Black Hills population. The Big Horn Mountains

in Montana may be providing the Black Hills population with limited migrants and therefore genetics studies focusing on this population is warranted. Identifying and maintaining potential source populations may be necessary for sustaining the isolated Black Hills population if the nesting success rate doesn't meet or exceed the mortality rate.

Overall, spruce/aspen habitats appear to be important attributes for this population. Large numbers of wildlife sized spruce snags are important for foraging as well as large numbers of aspen trees and spruce snags for nesting. Due to the limited amount of immigration into the Black Hills population and the low reproductive success, effective management plans will be crucial for the long term survival of the Black Hills population .Wise management planning within the aspen/white spruce habitats will likely benefit other mature forest specialist species and help to sustain the Black Hills unique wildlife heritage.

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Appendix A. Comparison of habitat attributes of 2005-2008 American Three-toed Woodpecker nest sites (n=28) and random sites (n=30) in the Black Hills, South Dakota. 2-tailed , independent t-tests. Mann-Whitney U tests were performed when t-tests failed. Significant results are in bold. [a] 2005-2007 nests only.

		Nest site	Random site				
	Attribute	mean ± SE	mean ± SE	t	p	U	p
live							
	White spruce wildlife	20.41 ± 3.16	29.33 ± 3.44	1.9	0.062		
	White spruce small	70.24 ± 10.67	95.17 ± 9.05	1.786	0.079	560.5	0.058
	Ponderosa pine wildlife	5.14 ± 1.27	10.77 ± 2.28	755	0.08	550	0.037
	Ponderosa pine small	9.14 ± 3.16	12.2 ± 2.30	0.786	0.435	538	0.116
	Quaking aspen wildlife	5.14 ± 1.81	.433 ± .17	2.14	0.037	277.5	0.007
	Quaking aspen small	7.10 ± 1.81	8.9 ± 3.19	-0.403	0.688	361	0.248
snag							
	White spruce wildlife	7.14 ± 1.62	6.3 ± 1.65	0.362	0.719	425	0.885
	White spruce small	27.24 ± 6.98	28.6 ± 5.63	-0.152	0.88	493.5	0.379
	Ponderosa pine wildlife	2.48 ± .83	3.5 ± .84	-0.863	0.392	519	0.19
	Ponderosa pine small	2.97 ± 1.79	3.97 ± 1.37	-0.416	0.679	518	0.182
	Quaking aspen wildlife	2.59 ± 1.39	0.4 ± .19	1.533	0.131	304.5	0.019
	Quaking aspen small	5.89 ± 1.66	3.27 ± 1.17	1.299	0.199	348	0.174
Woody debris [a]							
	Small logs	130.0 ± 22.09	87.6 ± 12.65	1.76	0.084	270.5	0.184
	Wildlife logs	29.65 ± 4.55	24.53 ± 3.32	0.84	0.405		
Subplot (5-meter radius)							
	Spruce saplings	6.24 ± 1.33	9.6 ± 1.79	1.502	0.139	549	0.083
	Aspen saplings	18.31 ± 5.59	4 ± 1.24	-2.317	0.03	332	0.106
	Juniper	17.69 ± 5.70	21.93 ± 4.07	1.327	0.19	527	0.16
	Raspberry	3.86 ± 2.49	8.83 ± 4.44	-1.09	0.28	458	0.631
	Snowberry	3.24 ± 2.66	3.8 ± 1.16	-0.195	0.846	578	0.008
	Gooseberry	0.10±.10	3.5 ± 1.23	-3.008	0.004	569	0.003

Appendix B. Genetics sample information

ID	Date collected	Collection Location	Tissue Type	Museum/Accession No.
BH1	2006	Black Hills, SD	Blood	
BH2	2006	Black Hills, SD	Blood	
BH3	2006	Black Hills, SD	Blood	
BH20	2007	Black Hills, SD	Blood	
BH21	2007	Black Hills, SD	Blood	
BH22	2007	Black Hills, SD	Blood	
BH23	2007	Black Hills, SD	Blood	
BH24	2007	Black Hills, SD	Blood	
BH25	2007	Black Hills, SD	Blood	
BH26	2007	Black Hills, SD	Blood	
BH27	2007	Black Hills, SD	Blood	
BH28	2007	Black Hills, SD	Blood	
BH29	2007	Black Hills, SD	Blood	
BH30	2007	Black Hills, SD	Blood	
BH31	2007	Black Hills, SD	Blood	
BH32	2007	Black Hills, SD	Blood	
BH33	2007	Black Hills, SD	Blood	
M11	2006	Western, MO	Blood	
M12	2006	Western, MO	Blood	
M13	2006	Western, MO	Blood	
M14	2006	Western, MO	Blood	
M15	2006	Western, MO	Blood	
M40	2007	Western, MO	Blood	
M41	2007	Western, MO	Blood	
M42	2007	Western, MO	Blood	
M43	2007	Western, MO	Blood	
M44	2007	Western, MO	Blood	
M45	2007	Western, MO	Blood	
B1	1997	Okanogan Co, WA	Muscle/organ	UWBM 58518
B2	1997	Okanogan Co, WA	Muscle/organ	UWBM 58536
B3	1996	Okanogan Co, WA	Muscle/organ	UWBM 62647
B4	1997	Okanogan Co, WA	Muscle/organ	UWBM 58532
B5	1995	Houston, AK	Muscle/organ	UWBM 53993
B6	1995	Lake Louise SR, AK	Muscle/organ	UWBM 53863
B7	1995	Houston, AK	Muscle/organ	UWBM 53987
AB266	1995	Alberta, Canada	Pectoral muscle	Z95.15.4
AB943	1995	Alberta, Canada	Pectoral muscle	Z95.1.3
AB240	1999	Alberta, Canada	Pectoral muscle	Z95.2.1
AB242	1999	Alberta, Canada	Pectoral muscle	Z99.8.18

Appendix B. Genetics sample information

ID	Date collected	Collection Location	Tissue Type	Museum/Accession No.
BH1	2006	Black Hills, SD	Blood	
BH2	2006	Black Hills, SD	Blood	
BH3	2006	Black Hills, SD	Blood	
BH20	2007	Black Hills, SD	Blood	
BH21	2007	Black Hills, SD	Blood	
BH22	2007	Black Hills, SD	Blood	
BH23	2007	Black Hills, SD	Blood	
BH24	2007	Black Hills, SD	Blood	
BH25	2007	Black Hills, SD	Blood	
BH26	2007	Black Hills, SD	Blood	
BH27	2007	Black Hills, SD	Blood	
BH28	2007	Black Hills, SD	Blood	
BH29	2007	Black Hills, SD	Blood	
BH30	2007	Black Hills, SD	Blood	
BH31	2007	Black Hills, SD	Blood	
BH32	2007	Black Hills, SD	Blood	
BH33	2007	Black Hills, SD	Blood	
M11	2006	Western, MO	Blood	
M12	2006	Western, MO	Blood	
M13	2006	Western, MO	Blood	
M14	2006	Western, MO	Blood	
M15	2006	Western, MO	Blood	
M40	2007	Western, MO	Blood	
M41	2007	Western, MO	Blood	
M42	2007	Western, MO	Blood	
M43	2007	Western, MO	Blood	
M44	2007	Western, MO	Blood	
M45	2007	Western, MO	Blood	
B1	1997	Okanogan Co, WA	Muscle/organ	UWBM 58518
B2	1997	Okanogan Co, WA	Muscle/organ	UWBM 58536
B3	1996	Okanogan Co, WA	Muscle/organ	UWBM 62647
B4	1997	Okanogan Co, WA	Muscle/organ	UWBM 58532
B5	1995	Houston, AK	Muscle/organ	UWBM 53993
B6	1995	Lake Louise SR, AK	Muscle/organ	UWBM 53863
B7	1995	Houston, AK	Muscle/organ	UWBM 53987
AB266	1995	Alberta, Canada	Pectoral muscle	Z95.15.4
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AB240	1999	Alberta, Canada	Pectoral muscle	Z95.2.1
AB242	1999	Alberta, Canada	Pectoral muscle	Z99.8.18

Appendix C. mtDNA genes, primers and sources for primers.

Gene	Primer	Sequence	Source
COI	BirdF1	5'-TTCTCCAACCACAAAGACATTGGCAC-3'	Kerr et al. 2007
	BirdR1	5'-ACGTGGGAGATAATTCCAAATCCTG-3'	Kerr et al. 2007
	BirdR3	5'-AGGAGTTTGCTAGTACGATGCC-3'	Kerr et al. 2007
CytB	L14841	5'-GCTTCCATCCAACATCTCAGCATGATG-3'	Kocher et al. 1989
	Cytb_WpIN_H	5'-CCTGATTCGTGGAGGAAGGTGAAGTGGATT-3'	Benz et al. 2006
ND2	H1064	5'-CTTTGAAGGCCTTCGGTTTA-3'	Designed by S. Drovetski, cited in Barber et al. 2004
	L5215	5'-TATCGGGCCCATACCCCGAATAT-3'	Hackett 1996
	L347	5'-CCATTCCACTTCTGATTCCC-3'	Designed by S. Drovetski, cited in Barber et al. 2004
	PtR1	5'-GGGTTAGAAGGGAGGGATTG-3'	Designed by A.Ervin for this study
ND3	H11151	5'-GATTTGTTGAGCCGAAATCAAC-3'	Zink et al.2002
	L10918	5'-TGCGGATTTGACCCACTAGGATCAGC-3'	Zink et al.2002
	H10974	5'-GGAAGGAGTAGGGCGATTTCTAGGTC-3'	Zink et al.2002
	L10755	5'-GACTTCCAATCTTTAAAATCTGG-3'	Zink et al.2002

Appendix D. mtDNA PCR Programs	
	PCR Program
COI	94° for 1 min
	94° for 1 min
	45° for 1 min, 30 sec
	72° for 1 min, 30 sec
	Repeat 2-4, 5X
	94° for 1 min
	51° for 1 min, 30 sec
	72° for 1 min, 30 sec
	Repeat 6-8, 30X
	72° for 5 min
CytB	94° for 3 min
	94° for 20 sec
	59.2° for 45 sec
	72° for 1 min
	Repeat steps 2-4, 35X
	72° for 7 min
ND2	94° for 1 min
	94° for 1 min
	45° for 1 min, 30 sec
	72° for 1 min, 30 sec
	Repeat steps 2-4, 5X
	94° for 1 min
	58° for 1 min, 30 sec
	72° for 1 min, 30 sec
	Repeat steps 6-8, 30X
	72° for 5 min
ND3	94° for 1 min, 30 sec
	94° for 30 sec
	54.1° for 30 sec
	72° for 1 min, 10 sec
	Repeat steps2-4, 35X
	72° for 10 min