Habitat-specific breeding performance and cavity dynamics of Lewis’s Woodpeckers (*Melanerpes lewis*) in British Columbia

by

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Abstract

Lewis’s Woodpeckers (*Melanerpes lewis*) are Threatened in Canada and rely on pre-existing cavities for nesting. I studied how cavity density, competition, and predators influence Lewis’s Woodpecker breeding performance across three habitats in British Columbia, and investigated the broad-scale patterns of nest tree persistence and reuse over time. I found that Lewis’s Woodpecker breeding performance was high in riparian cottonwood habitat, moderate in live pine, and lowest in crown-burned pine habitat. Cavity density explained habitat-based breeding performance. Nest tree persistence was generally high, but declined over time, and while nest tree reuse varied dramatically across years, there was no consistent temporal pattern. Our results suggest that 1) resource managers should use regionally-specific data for managing Lewis’s Woodpecker populations, and 2) cavities may be a limiting factor for the recovery of Lewis’s Woodpecker populations in Canada, particularly in regions where nest tree persistence is lower and may not support recruitment.

Keywords: Lewis’s Woodpeckers; cavity limitation; breeding performance; nest tree; persistence
To mom and dad, who always believed in me and gave me every opportunity to follow my heart
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Table of Contents

Approval ................................................................................................................................. ii
Ethics Statement .................................................................................................................... iii
Abstract ................................................................................................................................. iv
Dedication ............................................................................................................................... v
Acknowledgements ............................................................................................................... vi
Table of Contents ................................................................................................................ vii
List of Tables ........................................................................................................................ ix
List of Figures ........................................................................................................................ xi
The Lewis's Woodpecker (Melanerpes lewis) ........................................................................ xii

Chapter 1. General Introduction .......................................................................................... 1
  1.1. Thesis Overview ........................................................................................................... 4
  1.2. References ................................................................................................................... 5

Chapter 2. Factors Influencing Habitat-specific productivity of Lewis's Woodpeckers ............ 9
  2.1. Abstract ......................................................................................................................... 9
  2.2. Introduction .................................................................................................................. 10
  2.3. Methods ....................................................................................................................... 12
      2.3.1. Study Area and Habitat Descriptions ................................................................ 12
      2.3.2. Field Methods .................................................................................................... 13
      2.3.3. Statistics ............................................................................................................. 16
  2.4. Results ......................................................................................................................... 17
      2.4.1. Habitat Differences in Breeding Performance, Cavity and Competitor Density, Predators, and Foraging Behavior ........................................................................... 17
      2.4.2. Factors Influencing Habitat-dependent Breeding Performance ....................... 19
  2.5. Discussion .................................................................................................................... 20
      2.5.1. Conclusion .......................................................................................................... 24
  2.6. References .................................................................................................................... 24
  2.7. Figures ........................................................................................................................ 29
  2.8. Tables .......................................................................................................................... 31

Chapter 3. Nest Tree Persistence and Cavity Dynamics ......................................................... 37
  3.1. Abstract ....................................................................................................................... 37
  3.2. Introduction .................................................................................................................. 37
  3.3. Methods ....................................................................................................................... 41
      3.3.1. Field Methods .................................................................................................... 41
      3.3.2. Statistical Methods ........................................................................................... 43
  3.4. Results ......................................................................................................................... 44
      3.4.1. Broad-scale Nest Tree Persistence and Reuse ................................................... 44
      3.4.2. Local Scale Nest Tree and Cavity Persistence, Reuse and Reasons for Loss .......... 45
  3.5. Discussion .................................................................................................................... 46
3.5.1. Nest Tree Persistence ................................................................. 46
3.5.2. Nest Tree Reuse ................................................................. 48
3.5.3. Conclusions ........................................................................ 49
3.6. References .................................................................................. 50
3.7. Figures ....................................................................................... 51
3.8. Tables ......................................................................................... 56

Chapter 4. General Conclusions ................................................................. 59
4.1. Management Implications ............................................................. 64
4.2. References ................................................................................... 65
Appendix A. Regional variation in Nest Success (the production of ≥1 fledgling) and Productivity per successful nest (number of fledglings) in Burned, Riparian and Live Pine Habitat Types ......................................................... 71
List of Tables

Table 2.1. Summary of candidate model sets examining how habitat, cavity density, competitors and predators influences the breeding performance of Lewis’s Woodpeckers in British Columbia, Canada. .......................... 31

Table 2.2. Habitat-specific breeding performance (mean ± 95% CI) of Lewis’s Woodpeckers in British Columbia, Canada. .......................................................... 32

Table 2.3. Variation (mean ± 95% CI) in cavity abundance, competitors, surplus cavities, foraging behaviors and proportion of sites with a high corvid abundance and presence of bears across three habitat types in British Columbia, Canada.............................................. 33

Table 2.4 Summary of candidate model set examining the influence of habitat, cavity density, predators, and competitors on the Hatching Success (the proportion of eggs that hatch) of Lewis’s Woodpeckers in British Columbia, Canada. We used Akaike’s Information Criterion for small sample sizes (AICc). We described model fit by the number of parameters (K), difference in Akaike’s Information Criterion (ΔAICc) and weight of evidence (wi), the likelihood of each model relative to all other models in the candidate set............................................................. 34

Table 2.5. Summary of candidate model set examining the influence of habitat, cavity density, predators, and competitors on the Nest Success (≥1 fledgling) of Lewis’s Woodpeckers in British Columbia, Canada. We used Akaike’s Information Criterion for small sample sizes (AICc). We described model fit by the number of parameters (K), difference in Akaike’s Information Criterion (ΔAICc) and weight of evidence (wi), the likelihood of each model relative to all other models in the candidate set............................................................. 35

Table 2.6. Summary of candidate model set examining the influence of habitat, cavity density, predators, and competitors on the Productivity of Lewis’s Woodpeckers in British Columbia, Canada. We considered productivity to be the number of fledglings from each nest that was able to produce ≥1 fledgling. We used Akaike’s Information Criterion for small sample sizes (AICc). We described model fit by the number of parameters (K), difference in Akaike’s Information Criterion (ΔAICc) and weight of evidence (wi), the likelihood of each model relative to all other models in the candidate set......................................................................... 36

Table 3.1. Model summaries for nest tree persistence in British Columbia. We used Akaike’s Information Criterion for small sample sizes (AICc). We described model fit by the number of parameters (K), difference in Akaike’s Information Criterion (ΔAICc) and weight (wi), the likelihood of each model relative to all other models in the candidate set......................................................................... 56
Table 3.2. Complete model summaries for sequential nest tree reuse by Lewis’s Woodpeckers in British Columbia. We used Akaike’s Information Criterion for small sample sizes (AICc). We described model fit by the number of parameters (K), difference in Akaike’s Information Criterion (ΔAICc) and weight (w_i), the likelihood of each model relative to all other models in the candidate set. ..........................57

Table 3.3. Variation in the reuse of cavities by five species of cavity-nesting birds (no. [%]) in British Columbia in from 2013 to 2014. LEWO=Lewis’s Woodpecker, AMKE=American Kestrel, EUST=European Starling, NOFL=Northern Flicker, WESO=Western Screech-Owl. ........................................................................................................58

Table 4.1. Survival estimates for Melanerpes Woodpeckers .............................................69

Table 4.2 Estimates of population growth (lambda) for Lewis’s Woodpeckers in a) Riparian b) Live Pine and c) Burned habitat types in British Columbia, Canada. Lambda is estimated using all combinations of juvenile survival and adult survival estimates from Table 4.1..................70
List of Figures

Figure 2.1. Relationship between a) cavity density and b) surplus cavities and hatching success (the proportion of eggs in a clutch that hatched) of Lewis’s Woodpeckers in British Columbia, Canada in 2013 and 2014............................................................ 29

Figure 2.2. Relationship between a) cavity density and b) surplus cavities and fledging success (the number of fledglings produced per successful nest) of Lewis’s Woodpeckers in British Columbia, Canada in 2013 and 2014................................................................. 30

Figure 3.1. The six regions that Lewis's Woodpeckers currently occupy in British Columbia................................................................. 51

Figure 3.2. Variation in the probability of Lewis’s Woodpecker nest tree persistence across 11 years (2004-2014) in British Columbia, Canada................................................................. 52

Figure 3.3. Variation in the probability of Lewis’s Woodpecker nest tree persistence across four broad regions in British Columbia, Canada. ................................................................. 53

Figure 3.4. Variation in the probability of Lewis’s Woodpecker nest tree reuse from one year to the next in British Columbia, Canada from 2004-2014................................................................. 54

Figure 3.5. Variation in the probability of Lewis’s Woodpecker nest tree reuse from one year to the next across four regions in British Columbia, Canada. ................................................................. 55
The Lewis’s Woodpecker (*Melanerpes lewis*)

photo credit: Philina English

xii
Chapter 1.

General Introduction

Lewis’s Woodpecker (Melanerpes lewis) populations across western North America have declined dramatically since breeding bird surveys were started 40 years ago (Sauer et al. 2014). Small populations and suspected declines of populations in Canada based on regional monitoring led to their designation as a Threatened species under the Species at Risk Act (SARA) in 2010 (Environment and Climate Change Canada 2016). The Committee of Endangered Wildlife in Canada (COSEWIC) has identified western pine beetle (Dendroctonus ponderosae) infestations, urban encroachment, suppression of wildfire, and competition with the invasive European Starlings (Sturnus vulgaris) as the primary threats to the species, since they alter the suitability of nesting habitat and/or reduce insect (prey) abundance (Environment and Climate Change Canada 2016). The same factors are thought to threaten populations in the United States (Abele et al. 2004). Lewis’s Woodpeckers in Canada are currently restricted to patches of live ponderosa pine, burned coniferous forest and riparian black cottonwood habitat (hereafter called “live pine”, “burned” and “riparian” habitats), in the south-central and southern interior of British Columbia. All of these habitats contain an open canopy cover conducive for their characteristic flycatching behavior and also a dense understory shrub layer that allows for insect production (Bock 1970). The Lewis’s Woodpecker occurs within six distinct regions: Cariboo-Chilcotin, Thompson-Nicola, Okanagan-Similkameen, Boundary, West and East Kootenay.

The Okanagan Valley of the southern interior of British Columbia has undergone substantial habitat loss and degradation mostly due to urbanization, agriculture, and flood control (Lea 2005). The area occupied by live pine, the most abundant of the three habitats, has decreased by 53% since the late 1800s, and the area of riparian habitat has decreased by 63% (Lea 2005). Fire suppression has also reduced the amount of burned
habitat available for Lewis’s Woodpeckers (Ohmart 1994). Nesting and roosting holes are often a limited resource in modified landscapes (Newton 1994). The substantial loss of suitable habitat means that nesting and roosting cavities may be a limiting resource. Lewis’s Woodpeckers may be particularly vulnerable to loss of nesting cavities because they are weak excavators, meaning that they generally do not excavate for themselves. Instead they rely on primary cavity-nesting species, such as other woodpeckers to create nesting holes (Martin and Eadie 1999, Martin et al. 2004).

If high quality cavities are required to reproduce successfully, cavity availability may limit populations of cavity-nesting species even if cavities do not appear to be in short supply. Cavities with proper insulation (Wiebe 2001), shape (Zhu et al. 2012) or height (Rendell and Robertson 1989, Li and Martin 1991, Kaliński 2014) can protect nests against predators and severe weather. Cornelius et al. (2008) suggested that high quality cavities may be limiting in Argentinian Atlantic forest because although there were many cavities present, few were used. Cockle et al. (2008) found that cavities that were used differed from those that were not used in being ≥ 20cm in cavity depth with a cavity entrance of ≤ 14cm and that cavities with these features were rare. These deeper cavities with smaller entrances may provide greater protection from both weather and other animals. Sufficient numbers of high quality cavities may be especially important to cavity selection in the presence of predators (Li and Martin 1991), or when competitor species are aggressive (Koch et al. 2012). Lewis’s Woodpeckers are known to prefer nesting in deep cavities with small entrances (Zhu et al. 2012). Substantial tree cutting due to urban sprawl, agriculture (Lea 2005), and/or salvage operations after western pine beetle infestations may have decreased the number of suitable cavities available for Lewis’s Woodpeckers (Environment and Climate Change Canada 2016) in British Columbia.

In addition to cavity availability, many other factors contribute to low nest success and productivity of cavity nesting birds. Predation is considered to be the major cause of nest failure in birds (Martin 1993). Common nest predators of cavity-nesting birds in British Columbia include a variety of mammals, such as mice, squirrels, raccoons, and bears (Walters and Miller 2001). Snakes and predatory or opportunistic birds, such as accipiters, corvids or other woodpeckers may also prey on cavity-nests (Walters and Miller 2001, Paclik et al. 2009). Food availability is another important factor in determining timing and
nest success of birds (Lyons 2005). Lewis’s Woodpeckers are primarily aerial foragers that feed on adult stage riparian insects, beetles and moths, but also opportunistically feed on other seasonally abundant sources of food such as grasshoppers or fruit (Bock 1970). Competition for nest cavities can either directly interfere with nesting, if competitors eject eggs or nestlings (Finch 1990), or can limit the number of cavities that are available. When cavities are limiting, some individuals are forced to use lower quality cavities, which can increase exposure to both the weather and predators (Rendell and Robertson 1989, Fisher and Wiebe 2006, Goodenough et al. 2009, Koch et al. 2012). Northern Flickers (Colaptes auratus), American Kestrels (Falco sparverius) and European Starlings are frequent users of Lewis’s Woodpecker cavities in the southern interior of British Columbia (Zhu et al. 2012, pers. observ.).

Invasive European Starlings have been identified as a possible contributor to the declining populations of Lewis’s Woodpeckers in Canada (COSEWIC 2010). Cavity usurpation is a well-documented practice between members of cavity-nesting communities (Short 1979). As particularly aggressive secondary cavity-nesters, European Starlings are known to commonly usurp nests from other cavity-nesting birds, including other Melanerpes woodpeckers (Acorn Woodpecker Melanerpes formicivorus, Troetschler 1976; Red-bellied Woodpecker Melanerpes carolinus, Ingold 1989; Gila Woodpecker Melanerpes uropygialis, Kerpez and Smith 1990). Zhu et al (2012) noted that European Starlings took over multiple Lewis’s Woodpecker cavities during 2004 and 2005 in British Columbia, and so posited that European Starlings may be negatively impacting breeding Lewis’s Woodpeckers. However, others have noted that Lewis’s Woodpeckers appear to be strong competitors (Bock 1970, MacRoberts and MacRoberts 1976), and by documenting interactions during the breeding season, Vierling (1998) concluded that there was little competition between nesting European Starlings and Lewis’s Woodpeckers.

Environment and Climate Change Canada has identified knowledge of Lewis’s Woodpecker breeding performance across habitats in Canada as crucial for managers planning recovery actions. Research focused on habitat-based differences in Lewis's Woodpecker breeding performance in other parts of the Lewis’s Woodpecker range have found contrasting patterns. For instance, 89% of nests were successful in riparian habitats in Montana (Fylling 2013), but Saab and Vierling (2001) found that only 46% were
successful in Idaho. Generally, burned habitat is considered to be highly productive (Gentry and Vierling 2007, Saab and Vierling 2001), although a study within British Columbia showed that nest success in live pine and burned habitat combined was as low as 52% (Zhu et al. 2012). A comparative study of these three habitat types used by Lewis’s Woodpeckers in British Columbia has not yet been carried out, even though identifying habitat features that allow for productive populations is important for species’ recovery (Vierling and Saab 2001).

Across habitat types the presence of cavities is likely be important to Lewis’s Woodpeckers. Trees containing cavities are known as wildlife trees, and their persistence through time is one factor in the overall availability of cavities. Wildlife trees may persist for long periods (Yamasaki and Leak 2006), but our understanding of the factors that influence how wildlife trees persist on the landscape is limited (Cooper 1998). Assessment of how wildlife trees persist on the landscape is crucial knowledge that we are currently lacking in British Columbia (Cooper 1998). If the likelihood that Lewis’s Woodpecker nest trees will persist is reduced over time, then cavity availability may further limit Lewis’s Woodpecker populations and contribute to continued population declines in Canada. Edworthy (2012) found that the decay class was the most influential factor in the survival of tree cavities, and live trees were found to persist longer than dead ones. Other factors can contribute to lower persistence of wildlife trees, such as proximity to urban areas, or extreme flooding and weather events (Blewett and Marzluff 2005).

1.1. Thesis Overview

This thesis addresses four of the knowledge gaps identified in the federal Recovery Strategy for Lewis’s Woodpeckers by 1) determining how the breeding performance of Lewis’s Woodpeckers may differ across riparian, burned and live pine habitat types in British Columbia, 2) examining hypotheses for any observed habitat-based differences in breeding performance 3) assessing the impact of a cavity-nest competitor, the invasive European Starling 4) determining patterns of wildlife tree persistence in Canada.

In Chapter 2 I assess how Lewis’s Woodpecker breeding performance differs across three habitat types in British Columbia by monitoring nests over a two-year period.
We subsequently investigate the role of cavity density, competitors and predators on habitat-based variation in breeding performance.

In Chapter 3 I focus on the persistence and reuse of Lewis’s Woodpecker nest trees at the landscape scale and explore how time, region, tree species, and general habitat type influence persistence and re-use of nest trees over 11 years. In addition, I investigate nest tree and cavity persistence at the local scale and assess how nest-site competition by European Starlings may impact Lewis’s Woodpeckers in British Columbia.

Chapter 4 summarizes the previous chapters and also discusses management implications and possible directions for further research in this field.

1.2. References


Chapter 2.

Factors Influencing Habitat-specific productivity of Lewis’s Woodpeckers

2.1. Abstract

High quality tree cavities are a critical resource for cavity-nesting animals. An ideal cavity will provide proper insulation for incubating eggs and developing nestlings, and have the adequate dimensions or height to prevent predator entry. Securing a high quality cavity may be particularly important in areas with more predators. We studied habitat-specific reproductive success of the Lewis’s Woodpecker (Melanerpes lewis), a cavity-nesting species that is listed as Threatened in Canada. We then assessed whether cavity limitation, nesting competitors, foraging behaviors, or the relative abundance of predators influenced the variation in habitat-specific breeding performance. We found that hatching success (the proportion of eggs that hatch) was highest in riparian and burned habitat and lowest in live pine habitat (mean ± 95% CI, riparian = 0.80 ± 0.07, burned = 0.77 ± 0.19, live pine = 0.59 ± 0.09 95% CI). Nest success (the production of ≥1 fledgling) was highest in riparian and live pine habitat and lowest in burned habitat (riparian = 0.78 ± 0.12, live pine = 0.80 ± 0.13, burned = 0.42 ± 0.23). Lewis’s Woodpeckers nesting in riparian habitat produced the most fledglings per successful nest, and those in live pine and burned habitat produced the fewest (riparian = 2.61 ± 0.45, live pine = 1.86 ± 0.31, burned = 1.88 ± 0.59). Habitats differed in the number of nesting competitors surrounding active Lewis’s Woodpecker nests, the number of suitable cavities in these same areas, and showed slight variation in the relative abundance of nest predators. Our results showed that breeding performance differences were best explained by the variation in cavity density, suggesting that the reproductive success of Lewis’s Woodpeckers in British Columbia may be limited by the number of high quality cavities. Since our work identifies that habitat differences in breeding performance in British Columbia are not consistent with those in other regions, we show that acquiring regionally-specific demographic data is important for managing species at risk.
2.2. Introduction

Tree cavities provide critical breeding habitat for a large number of vertebrates (Bunnell et al. 1999, Martin et al. 2004, Fokidis and Risch 2005). The quality of these cavities affects the reproductive success of many cavity-nesting species because cavity size and entrance height, shape and orientation can all influence the impact of extreme weather events and predation (Li and Martin 1991, Goodenough et al 2008, Zhu et al. 2012, Isaac et al. 2008, Rico and Sandovol 2014). Cavity availability has consequently been argued to be a limiting factor for some populations of mammals (Carvalho et al. 2014), birds (Newton 1994), and even amphibians (Seshadri et al. 2014). Tree cavities may be formed naturally by rot fungi and bacteria, or by excavating animals (primarily woodpeckers) (Martin and Eadie 1999, Jackson and Jackson 2004). In northern temperate forests, the community of cavity-nesting species has been described as a “nest web”, composed of primary cavity-nesters that excavate the majority of cavities, weak cavity-nesters that rarely excavate and secondary cavity-nesters that do not excavate and rely on cavities created by others or natural decay processes (Martin and Eadie 1999, Martin et al. 2004).

The extent to which competition for high quality nest cavities regulates populations of weak and secondary cavity-nesting birds may vary across habitat types depending on the abundance of primary cavity-nesters and outcomes of competitive interactions among other species in the nest web. Competition for high quality nest sites may be less important in habitats with abundant dead or decaying trees, which provide the raw material for the creation of cavity nests, or when primary cavity-nesters are abundant (Robles and Martin 2014). The abundance of particular species of primary cavity-nesters may be more important than the total abundance of primary cavity-nesters, because each species creates holes that can be used by a specific group of weak or secondary cavity-nesting species. For example, in continuous mixed forests of British Columbia, presence of nesting Tree Swallows (Tachycineta bicolor), a secondary cavity-nester, was influenced by the density of cavities excavated by Hairy Woodpeckers (Leuconotopicus villosus) and Red-breasted Sapsuckers (Sphyrapicus ruber) (Robles and Martin 2014). Competition for high quality cavities may be more important when weak and secondary cavity-nesters are
forced to interact with interspecific competitors that aggressively compete for nesting cavities, like the European Starling (*Sturnus vulgaris*) (Ingold 1994, 1996).

The importance of securing a high quality cavity may also depend on the predator community and the abundance of predators within a habitat. In areas with predators, cavity-nesting species may choose taller cavities or smaller cavity entrance sizes (i.e. higher quality cavities) to avoid predation (Soler and Soler 1983, Kaliński et al. 2014). Predators of cavity-nesting species in northern temperate forests include mammals such as mice, weasels, squirrels and bears (Walters and Miller 2001, Paclik et al. 2009, Kozma 2011), birds such as corvids, accipiters or other woodpeckers (Walters and Miller 2001, Paclik et al. 2009), and climbing snakes (Paclik et al. 2009). Predation is the largest cause of nest failure in birds (Martin 1993, Bosque and Bosque 1995). However, the timing and severity of predation varies with predator species. For example, when mice are present they tend to consume eggs. Corvids, in contrast, may be more likely to prey on nestlings. Bears are also known to prey on nestlings, but tend to cause complete nest failure (Kozma 2011). The impact of predators on nestling survival may also be greater when food is scarce, if parents provision less because they are investing more time in vigilance and/or avoid foraging areas where predators are present (Sonke et al. 2004). Thus, the breeding success of weak or secondary cavity-nesters depends upon interactions involving a complex community of excavators, competitors, predators, nest trees and adequate food resources.

Lewis’s Woodpeckers (*Melanerpes lewis*) are weak cavity-nesting birds whose populations are declining across their range in western North America (-2.7%/yr between 1966 and 2010, Sauer et al. 2014). In 2012, Lewis’s Woodpeckers were listed as a Threatened species in Canada (Environment and Climate Change Canada 2016). In British Columbia, Lewis’s Woodpeckers currently only occupy areas within the south-central and southern interior of British Columbia where they nest in riparian black cottonwood (*Populus trichocarpa*), live ponderosa pine (*Pinus ponderosa*) and crown-burned habitat (hereafter ‘riparian’, ‘live pine’ and ‘burned’ habitat). This region has experienced significant loss and degradation of primary breeding habitat for Lewis’s Woodpeckers since pre-European settlement times (Lea 2005). Live pine and riparian habitat have been transformed by dam and reservoir development, livestock grazing or
conversion of habitat to agriculture or urban use. In the Okanagan Valley, the center of Lewis’s Woodpecker range in British Columbia, live pine habitat has decreased by 57%, and riparian habitat occupies only a small fraction of its original area (up to 86% has been lost, Lea 2005). Fire regimes have also changed drastically since historic times. Low-intensity fires that once occurred frequently, promoting an open understory and regeneration of native vegetation, have been disrupted. Populations of non-native European Starlings, which expanded into British Columbia in the 1950s, could also contribute to population declines of Lewis’s Woodpeckers through aggressive competition for nesting sites (Campbell et al. 1990, Lewis et al. 2002).

Nest success and productivity of Lewis’s Woodpeckers vary among habitat types throughout their range. For instance, studies in burned habitat within Idaho and Wyoming found that Lewis’s Woodpeckers had relatively high nest success and productivity (Saab and Vierling 2001, Gentry and Vierling 2007) compared to Lewis’s Woodpeckers in burned habitat in British Columbia that had lower nest success and productivity (Zhu et al. 2012). One study of breeding performance in riparian habitat in Colorado found that Lewis’s Woodpeckers had far lower nest success and productivity than in riparian habitat in Montana (Saab and Vierling 2001, Fylling 2013). The mechanisms driving this variation are unclear. In this study we assess the reproductive success of Lewis’s Woodpeckers across three habitat types in British Columbia, Canada, and evaluate whether cavity availability, the abundance of nesting native and non-native competitors, predators, and foraging behaviors explain differences in breeding performance.

2.3. Methods

2.3.1. Study Area and Habitat Descriptions

Our study was located within the core of the Lewis’s Woodpecker’s Canadian range, the south Okanagan Valley and Boundary area of interior British Columbia. Within this larger area we monitored nests at 21 sites: ten in live pine, four in burned, and seven in riparian habitat. We defined a site as an area with one or more active Lewis’s Woodpecker nests separated by a distance of less than 1.5 km, the maximum distance we observed individuals traveling from the nest tree to forage. All sites had the
characteristically open tree canopy (~30% cover) and fairly dense understory (~60% cover) that Lewis’s Woodpeckers prefer, which creates ample space for flycatching and sufficient shrub cover for harboring insects for forage (Bock 1970).

The ten live pine sites were between 350 and 675 m in elevation. Tree composition included ponderosa pine exclusively, and the understory vegetation was mainly antelope-brush (*Purshia tridentate*) and sagebrush (*Artemisia tridentate*). The four burned sites were between 400 and 1100 m in elevation. Tree composition included Douglas fir (*Pseudotsuga menziesii*) and ponderosa pine where there had been a high-intensity burn 10-15 years ago. The most frequent understory shrubs were snowberry (*Symphoricarpos albus*), wax currant (*Ribes cereum*), and Oregon grape (*Mahonia aquifolium*). The seven riparian sites were between 500 and 600 m in elevation. These sites were composed of narrow strips (5 to 20 m wide) of habitat patches that paralleled the Kettle and Granby Rivers. Open areas containing agricultural, industrial or residential property often were adjacent to these riparian sites. Tree composition included primarily black cottonwood and secondarily, Douglas fir, although a few small stands of water birch (*Betula occidentalis*) and trembling aspen (*Populus tremuloides*) were present. Understory vegetation included Oregon grape, snowberry and saskatoon (*Amelanchier alnifolia*).

### 2.3.2. Field Methods

During 2013 and 2014, we located active Lewis’s Woodpecker nests by searching areas where previous nesting attempts had been documented by the Canadian Wildlife Service (unpublished). We followed a total of 96 nest attempts, all during the pre-laying nest renovation or egg-laying stages. In total, 74 nest trees were found, 22 of which were followed in both years. For riparian habitat, we followed a total of 42 nest attempts in 33 nest trees (21 attempts were monitored in each year) Eight nest trees were monitored in both years. In live pine habitat, we followed 35 nest attempts in 26 nest trees (19 nest attempts were monitored in 2013 and 16 in 2014). Nine nest trees in live pine habitat were monitored in both years. Finally, in burned habitat, we followed 19 nest attempts in 15 nest trees (eight nest attempts were monitored in 2013 and 11 in 2014). Four nest trees in burned habitat were monitored in both years. We visited nests at 2-5 day intervals, following Dudley and Saab’s guidelines for monitoring cavity-nesting birds (2003). We
were able to check contents of nests in cavities up to 16 m in height using wireless telescoping cameras, the TreeTop Peeper (Sandpiper Technologies, Maneca, California) and the Peeper Cam (IBWO.org David Luneau, Arkansas). For nests that we were able to access (n=55), we recorded the final clutch size after no additional eggs were laid between two visits. We also recorded the hatching success (the proportion of eggs that hatched), brood size seven days post-hatch, fledgling success (the proportion of young that fledged from the original brood size), and the productivity based on the number of nestlings last observed in the nest cavity before the expected date of fledging. For nests that we were unable to reach with equipment (n=41) we used parental behaviors to indicate the nesting stage. For example, an adult carrying food into the cavity showed that eggs had hatched and nestlings were present. We were unable to determine the clutch sizes or hatching success for these nests, but we determined the productivity by counting recently fledged young at or very near the nest cavity. We were able to access nests in live pine habitat more easily than nests in riparian and burned habitat (77% nests accessed in live pine, 47% in riparian, and 42% in burned). Therefore, productivity measures for nests that we were unable to access are a conservative measure and may slightly underrepresent the actual number of fledglings in the nests found at riparian and burned sites. When possible, we categorized the cause of nest failure into one of three categories: predation, abandonment/starvation and cavity/tree fell. When the nest failed between consecutive visits with no evidence of predation and parents were no longer seen at the nest for three consecutive visits, the nest was assumed to be abandoned/starved. Conversely if parents re-nest within three consecutive nest visits, then we assumed the nest failed due to predation.

To quantify the level of potential nest competition, we recorded nest locations of European Starlings, American Kestrels, Northern Flickers, and other Lewis’s Woodpeckers, within 50 m of each monitored Lewis’s Woodpecker nest using Garmin GPS devices. These four species occupy cavities of similar sizes (Martin et al. 2004; Sedgwick and Knopf 1990), and are considered competitors for the same cavities. Within the same area we also counted the number of surplus cavities, i.e. the number of cavities unused by any species but suitable for use by Lewis’s Woodpeckers. We considered a cavity to be suitable if it appeared fully excavated with an entrance size between 5 and 10 cm.
To assess the importance of predators to breeding performance of Lewis’s Woodpeckers, we conducted an audio and visual survey at each site for corvids between May and June in 2014. We recorded the number of American Crows (*Corvus brachyrhynchos*), Common Ravens, Black-billed Magpies (*Pica hudsonia*), Clark’s Nutcrackers (*Nucifraga columbiana*), and Steller’s Jays (*Cyanocitta stelleri*), all of which are known to prey on nestlings (Mulder 1978, Cain et al. 2003). Because surveys varied in length (between 20 and 90 minutes in duration) and corvids were not detected at 42% of sites, we classified sites as having relatively low or high corvid abundance using the residual values from a logistic regression of detection against survey duration. Low corvid density sites had negative residual values and high corvid density sites had positive residual values. We determined the presence of black bears (*Ursus americanus*) at each site based on detection of bear sign (sightings, prints, scat or recent claw marks on trees) at any point during the 2014 season.

To determine if differences in hatching success, nest success and productivity of Lewis’s Woodpeckers is linked to food availability, we quantified the provisioning rate and foraging area of pairs breeding in the three habitat types. We examined the variation in foraging behavior by quantifying the provisioning rate and foraging area of Lewis’s Woodpeckers at 29 nests. We surveyed 13 nests in 2013 (four in riparian habitat, six in live pine and three in burned) and 16 nests in 2014 (six in riparian habitat, six in live pine and four in burned) using one-hour focal observations. We surveyed 24 nests twice; once during the first 14 days of the nestling period and again between day 15 and 30 in order to capture a range of feeding behaviors when rearing young of varying age and brood size. The remaining five nests were only surveyed once because they failed prior to the second survey. Two observers were present for all surveys. One observer documented the number of feeding visits while the other mapped the maximum distance an individual foraged from the nest tree during each feeding trip using topographical maps. The mapping observer stood approximately 250 m from the nest and at a higher elevation (on a hill) to achieve a good view of the surrounding area. This particular method of mapping foraging observations was achievable because of the open habitats in which Lewis’s Woodpeckers generally forage, allowing the observer to have sight of the foraging bird during most of the survey (68% of the time on average). By documenting the amount of time during which observers had a visual of the bird we could show that observers were
able to follow the foraging birds in burned habitats for a slightly higher proportion of the survey than in the other habitat types (mean ± 95% CI, burned = 85 ± 5, riparian = 64 ± 12, live pine = 62 ± 16). Thus the measures for foraging behavior in burned habitat are the most accurate. We documented whether corvids were present at any point during the one-hour survey. We recorded the age of the nestlings, and after each foraging survey was complete, we confirmed the number of nestlings present. We used ArcMap (ESRI 2014 ArcGIS Desktop) to convert foraging locations to digital points and then calculated the area contained within these points.

2.3.3. Statistics

We compared the hatching success, nest success and productivity using Lewis’s Woodpecker nests for which we were able to collect data 2013 and 2014 across habitat types (hatching success n=55, nest success n=90, productivity n=34). We evaluated habitat-specific differences by comparing the means and 95% CI. We also determined how habitats differed in cavity abundance, density of nesting competitors, and surplus cavities. For nests where provisioning surveys were conducted (n=29), we assessed whether foraging area and feeding rate differed between habitat types. Finally, we assessed habitat-based differences in predator detections using the 2014 site-based survey data (n=19 sites).

We then examined how cavity availability, competitors and predators influenced habitat-specific variation in hatching success, nest success and productivity by evaluating the support for a series of generalized linear mixed effects models within three candidate model sets. Each candidate set had nine models (Table 2.1). We treated nest success and hatching success as binomial distributions, and productivity (fledgling number for successful nests) as poisson-distributed. We did not model nest survival using more complex models (Dinsmore et al. 2002) because nests were found and monitored from clutch initiation to eventual success or failure. Only nests monitored in 2014 (n=48) were included because predator surveys were only conducting during this year. We allowed intercepts to differ with each site by including site as a random factor for all models. Each candidate model set allowed breeding performance to vary depending on the number of heterospecific and conspecific competitors, cavity density, and surplus cavities (the
number of cavities minus the number of nesting competitors) and the presence or relative abundance of predators at a site. Predators were included as a composite predictor variable with two parameters. We also included two interaction models that allowed us to evaluate if cavity abundance was important at sites where bears and a high corvid abundance were detected. One interaction model included cavity abundance, predators, and the interaction between cavity abundance and the two predator types. The other interaction model included surplus cavities, predators, and the interaction between surplus cavities and predator type. We also included a habitat model and a null model to enable us to evaluate the relative support for mechanistic models in the candidate set. There was little variation in foraging behaviors between habitat types (see Table 2.3), so we excluded feeding rate and foraging area as predictor variables in these analyses.

We used Akaike’s Information Criteria adjusted for small sample sizes (AICc) to calculate model weights for each model (Burnham and Anderson 2002). We chose the best models by using AICc model weights that quantify the strength of support for each model relative to the other included models. In the case that more than one model received strong support (<2 \( \Delta \text{AICc} \)), we conducted model-averaging to distinguish the relative importance of each parameter (Cade 2015). We used program R v3.1.3 (R Development Core Team, 2014) for all analyses, and called package ‘lme4’ to build generalized linear mixed effects models and package ‘MuMIn’ to calculate AICc and model-averages.

2.4. Results

2.4.1. Habitat Differences in Breeding Performance, Cavity and Competitor Density, Predators, and Foraging Behavior

Lewis’s Woodpeckers laid clutches containing, on average, 5.85 ± 1.7 SD eggs (range = 1-11, n=55 clutches). Clutch size was independent of habitat type. However, hatching success varied across habitats and, consequently, pairs nesting in riparian habitat had larger broods seven days post-hatch compared to those nesting in burned and live pine habitat. Over the two years of this study, Lewis’s Woodpeckers had higher nest success in riparian and live pine habitat than in burned habitat. Lewis’s Woodpeckers also produced more fledglings per successful nest in riparian habitat than in either of the other
habitats. Consequently, Lewis’s Woodpeckers nesting in riparian habitat had higher reproductive output per nesting attempt than pairs in both live pine and burned habitat (Table 2.2).

There was considerable variation in the number of suitable cavities, nest competitors, and surplus cavities within 50 m of nests in the three habitat types (Table 2.3). Cavities were most abundant in riparian habitat and least abundant in live pine habitat, where live trees may inhibit the excavation of cavities. The number of nesting Northern Flickers and American Kestrels did not differ across habitat types. However, European Starling nests were most abundant in riparian habitat and least abundant in live pine habitat. Taken together, there were more than two times the number of heterospecific competitors in riparian habitat than burned and live pine habitat. Conspecifics were also more abundant within a 50 m radius of monitored Lewis’s Woodpecker nests in riparian and burned habitat types when compared to the live pine habitat type that had no nesting Lewis’s Woodpeckers within 50 m of any nest (Table 2.3). Despite the greater number of competitors, there were many more surplus cavities in riparian habitat than in live pine habitat. (Table 2.3).

Predator surveys conducted in 2014 suggested there may be differences in the predator community across the three habitat types, although our ability to detect differences was low. Raw values of predator detections showed that sites in live pine were twice as likely to be classified as having a high density of corvids than sites in burned and riparian habitat. Similarly, we were twice as likely to detect bears at sites within burned and live pine habitat than at sites within riparian habitat (Table 2.3). We found that 36% (n=11) of nests that failed in burned habitat were depredated, 33% (n=9) of nests that failed in riparian were depredated, and 29% (n=7) of nests that failed in live pine habitat were depredated.

Lewis’s Woodpeckers foraged within an area of approximately 2.2 hectares when provisioning nestlings. Foraging area did not appear to vary with habitat type (Table 2.3), nor did foraging area increase with brood age or brood size. Lewis’s Woodpeckers foraged within a smaller area (mean ± 95% CI, 1.50 ± 0.59 ha) when corvids were present during provisioning surveys compared to survey periods without corvids (3.75 ± 1.94 ha). Pairs
provisioned, on average, 9.8 ± 6.9 SD times per hour. After controlling for brood size, there was little evidence that provisioning rate varied with habitat type (Table 2.3).

2.4.2. Factors Influencing Habitat-dependent Breeding Performance

The top model in the candidate set examining the influence of cavity availability, competitors, and predators on hatching success indicated that the proportion of eggs that hatch was lower in nests where both cavity density and surplus cavities were low (Table 2.4, Figure 2.1). Although the model including cavity density had slightly more support compared to the model including surplus cavities, their AICc weights were nearly identical (0.48 versus 0.42). Each model had over 10 times the support of the null and habitat models. The model-averaged parameter estimates did not help to distinguish between the models. The parameter estimates for both cavity density and surplus cavity effects both had parameter estimates and confidence intervals that did not span zero (estimate with 95% CI, cavity density = 0.07, 0.03-0.21; surplus cavities = 0.07, 0.04-0.25).

The top model in the candidate set examining how cavity availability, competitors, and predators influence nest success was the null model. The null model received similar support to the next best model, the habitat model (Table 2.5). Although there were several models that received strong support (<2 ΔAICc), all model-averaged parameter estimates had confidence intervals that bounded zero indicating that no variables in our analysis had a strong effect on nest success.

The top model in the candidate set examining how cavity availability, competitors, and predators influence the productivity of successful nests indicated that the number of fledglings produced was lower at nests where cavity density was low (Table 2.6, Figure 2.2). However, the model that included the surplus cavities term had similar support and both had 2.5 times the support of the null model and 6 times the support of the habitat model. The models allowing cavity density or surplus cavity effects to vary with presence of bears and high corvid abundance received negligible support. Together, the cavity density and surplus cavity models received 69% of the total model support. Model-averaging did not allow us to discriminate between the importance of cavity density and number of surplus cavities in influencing productivity of successful nests as model-
averaged parameter estimates for both variables were similar and both had 95% confidence intervals that did not bound zero (cavity density = 0.001-0.12, surplus cavities = 0.001-0.13).

2.5. Discussion

Lewis’s Woodpeckers are weak cavity-nesters, able to exploit tree cavities created by primary cavity-nesters in riparian, live pine and burned habitats within British Columbia, Canada. We found that nest success in riparian and live pine habitats was substantially higher than in burned habitat and that productivity of successful nests was highest in riparian habitat and lower in live pine and burned habitats. These results are consistent with previous studies on Lewis’s Woodpeckers in Montana and British Columbia (Fylling 2013, Zhu et al. 2012), but not consistent with studies on Lewis’s Woodpeckers in Colorado, South Dakota, and Idaho (Gentry and Vierling 2007, Saab and Vierling 2001) (see Appendix A.). Zhu et al.’s study included some of the same sites used in this study, but did not include any riparian habitat and the combined data from live pine and burned habitat. Nest success and productivity from Zhu et al.’s study was relatively low and comparable to the combined results from live pine and burned habitats from our study. Fylling (2013) found that nest success and productivity within riparian habitat in Montana was high and comparable to our results from riparian habitat in British Columbia. In contrast, Saab and Vierling (2001) found that Lewis’s Woodpeckers within riparian habitat in Colorado had much lower nest success and productivity (see Appendix A). This could be due to the higher grazing pressure within riparian habitats in Colorado, which has reduced the understory vegetation and likely reduced food availability for woodpecker nest provisioning. Alternatively, it is possible that cavity density may have been lower in Colorado compared to our sites in riparian habitat, although a measure of cavity availability was not conducted (Saab and Vierling 2001). Gentry and Vierling (2007) found that nests within burned habitat (17-20 years post-fire) in South Dakota had high nest success and productivity, while Saab and Vierling (2001) found that Lewis’s Woodpeckers in burned habitat (2-7 years post-fire) in Idaho had high nest success but moderate productivity (See Appendix A), both in contrast to our results where nest success and productivity in burned habitat (10-15 years post-fire) was low. Differences across regions in nest success and
productivity within burned sites cannot be explained by differences in fire history because both this study and Gentry and Vierling’s study took place within “older burns” (habitats burned at a high intensity between 10-20 years prior), and had opposing results. Black bears and avian predators such as Common Ravens and Steller's Jays were not present in the study areas in South Dakota (Gentry and Vierling 2007), which may account for the differences in breeding performance between Lewis’s Woodpeckers in South Dakota and those in our study. Predators only accounted for 33% of nest failures in this study. These regional differences in breeding performance mean that conservation planning for this species of concern may require recommendations that target the regionally important factors affecting productivity.

Competition for limited high quality cavities with European Starlings and native cavity-nesting birds has been argued to be a potential threat to Lewis’s Woodpecker populations (Kerpez and Smith 1990). European Starlings are an invasive species known to be particularly aggressive secondary cavity-nesters that can out-compete other cavity-nesting birds for nest sites (Kerpez and Smith 1990). Although we typically found multiple nests of heterospecific competitors near Lewis’s Woodpecker nests in this study, we found little evidence that competitors, including European Starlings, influenced habitat-based variation in breeding performance of Lewis’s Woodpeckers. Lewis’s Woodpeckers were able to reuse a high number of cavities in the second year of the study (63% of cavities compared to 37% and 47% found in two other studies from the United States (Saab et al. 2004, Linder and Anderson 1999)). In addition, the model that included the number of competitors surrounding each Lewis’s Woodpecker nest received negligible support in any of the three model sets investigating variation in habitat-specific breeding performance. Only 5% of 2013 Lewis’s Woodpecker cavities were used by European Starlings in 2014 (n=60), and we did not observe any nest takeovers within a breeding season. The latter two results differ from a study carried out in 2004 and 2005 in British Columbia in which 50% of Lewis’s Woodpecker nests were used by European Starlings in the second year and multiple nest takeovers by European Starlings during the breeding season (Zhu et al. 2012). Over the past 50 years, Breeding Bird Surveys conclude that there have been steady declines of European Starling populations in British Columbia (-3.7%/yr, Sauer et al. 2014). It may be that starling populations have reduced substantially across the 10-year period between Zhu et al.’s study and this study, and European Starling populations
may have declined sufficiently to no longer be a threat to Lewis’s Woodpeckers. Although we cannot conclude that there is an effect of nesting competitors (native or non-native) on Lewis’s Woodpecker breeding performance, we recommend that conservation measures include the retention of standing dead trees when possible because the loss of cavity trees may create more competition for nesting holes.

Predators of Lewis’s Woodpecker nests in British Columbia include black bears, corvids, mustelids such as the long-tailed weasel (*Mustela frontela*), and Douglas squirrels (*Tamiasciurus douglasii*) (Walters and Miller 2001, Paclik et al. 2009, Kozma 2011). Recent studies have demonstrated that indirect effects of perceived predation risk can cause changes in foraging behavior, vigilance, or habitat use of prey species, reducing their reproductive success (Clinchy et al. 2004, Sheriff et al. 2009, Lima 2009, Zanette et al. 2011). In this study, Lewis’s Woodpeckers remained closer to the nest when corvids were present, suggesting that they are sensitive to the presence of nest predators. Although we found little evidence that bears and corvids were responsible for the variation in breeding performance among habitat types, our predator abundance metrics were crude and the power to detect a difference was low. Thus, further work on the role of nest predators in habitat-based breeding performance is therefore warranted.

Shortages of nest cavities are well-documented to limit populations of some secondary and weak cavity-nesting birds (Newton 1994, 1998, Aitken and Martin 2012). In this study, the cavity density immediately surrounding a nest as well as the number of surplus nesting cavities were the most important factors to influence hatching success, and ultimately the productivity of Lewis’s Woodpeckers. Acquiring a high quality cavity can be important at all nesting stages. The ability for eggs to hatch relies mainly on temperature stability within the nest tree that allows for proper embryo development within the eggs (Webb 1987). Therefore, it is possible that pairs nesting in riparian and burned habitats that had high hatching success may have had the opportunity, through sufficient cavity availability, to choose a cavity that properly insulated their clutches. Alternatively, it may be that hatching success was high for Lewis’s Woodpecker clutches within habitats where it was less important for pairs to be vigilant for predators, thus allowing pairs to incubate clutches consistently. The ability of pairs to produce at least one young is likely due to a release from predation pressure, considering predation is the highest cause of
nest failure in birds (Martin 1993). Both live pine and riparian habitat had high nest success (~80%), and a slightly lower proportion of nests that failed did so due to predation (29% and 14%, respectively) versus burned habitat (33%). In riparian and live pine habitat, predators may have been either less likely to locate active nests because of more dense vegetation concealing the nest (riparian habitat), or because nests are generally more spatially distant (live pine habitat) versus clumped. Producing many fledglings is likely linked to food availability and/or the parents’ abilities to feed the young. It is possible that Lewis’s Woodpeckers nesting in riparian habitat type close to agricultural areas where pairs produced the greatest number of fledglings per successful nest had access to more nutritious prey (pers. observ.).

In this study, we investigated some factors that could be responsible for habitat-based breeding performance of Lewis’s Woodpeckers in British Columbia. However, there are other plausible mechanisms that we were unable to explore. For example, variation in food quality across habitat types may affect productivity, but was not measured. Lewis’s Woodpeckers, like other woodpeckers in the genus *Melanerpes*, are opportunistic foragers, but feed nestlings a diet of mainly insects, (Koenig et al. 2008) which have a high nutritional content (Eeva et al. 2010). Although pairs were provisioning at similar rates in our study, it is possible that pairs were feeding more nutritious food to nestlings in the riparian habitat. This may have allowed for them to support larger broods, thus producing more fledglings. A second alternative explanation is that habitats differ in the amount of exposure that nests have to predators. For example, it is possible that sites 10-19 years post-burn (like ours) present increased foraging opportunities for nest predators, which then, in turn, may use burned sites more frequently. If burned sites are targeted foraging areas of nest predators, then nests in burned habitat may have a greater chance of being depredated. Nests appeared to experience predation in similar proportion across habitats, but a slightly greater proportion of nests that failed in burned habitat failed due to predation (36%) than nests in riparian (33%) and live pine (29%) habitat. We encourage further research into variation in food quality and differences in nest exposure to predators as potential drivers of habitat-based breeding performance in Lewis’s Woodpeckers.
2.5.1. Conclusion

Here we show that riparian habitat may provide critical habitat for Lewis’s Woodpeckers in British Columbia because nest success and productivity of Lewis’s Woodpeckers is highest in these habitats. Although non-native European Starlings were suspected to play a role in the decline of Lewis’s Woodpecker populations, our data suggest they do not influence breeding performance differences among habitats in British Columbia. Our results instead suggest that the low hatching success in live pine habitat and low productivity in both live pine and burned habitat may be due to limitation of nesting cavities. We suggest that other factors such as the quality of food provisioned or variation in nest exposure to predators should be examined in more detail. We highlight that since our results differ from those in some other regions, conclusions regarding critical habitat for species at risk should not be based solely on breeding performance data from one region.

2.6. References


2.7. Figures

Figure 2.1. Relationship between a) cavity density and b) surplus cavities and hatching success (the proportion of eggs in a clutch that hatched) of Lewis’s Woodpeckers in British Columbia, Canada in 2013 and 2014.
Figure 2.2. Relationship between a) cavity density and b) surplus cavities and fledging success (the number of fledglings produced per successful nest) of Lewis's Woodpeckers in British Columbia, Canada in 2013 and 2014.
### 2.8. Tables

**Table 2.1.** Summary of candidate model sets examining how habitat, cavity density, competitors and predators influences the breeding performance of Lewis’s Woodpeckers in British Columbia, Canada.

<table>
<thead>
<tr>
<th>Model Name</th>
<th>Model</th>
<th>Justification</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null</td>
<td>Null</td>
<td></td>
</tr>
<tr>
<td>Habitat</td>
<td>Habitat</td>
<td>Breeding performance of Lewis’s Woodpeckers can vary across habitat types (Saab and Vierling 2001).</td>
</tr>
<tr>
<td>Cavity Density</td>
<td>Cavity Density</td>
<td>Cavities are a limited resource (Newton 1994). Fewer cavities may mean less choice in a nesting cavity, possibly forcing Lewis’s Woodpeckers to use low quality cavities.</td>
</tr>
<tr>
<td>Competitors</td>
<td>Competitors</td>
<td>Heterospecific competitors may have negative direct (cavity usurpation) and indirect (reduction of cavity availability) effects on Lewis’s Woodpecker breeding performance.</td>
</tr>
<tr>
<td>Lewis’s woodpeckers</td>
<td>Lewis’s woodpeckers</td>
<td>Benefits of group living may include locating high quality foraging areas through social learning or group nest defense against predators (Morand-Ferrond 2011).</td>
</tr>
<tr>
<td>Surplus Cavities</td>
<td>Surplus Cavities</td>
<td>Cavities are a limited resource (Newton 1994). Lewis’s Woodpeckers may be forced to use low quality cavities when experiencing high competition.</td>
</tr>
<tr>
<td>Predator</td>
<td>Bear + Corvid</td>
<td>Predators can effect breeding performance through direct (Kozma 2011, Purcell and Verner 1999) or indirect (perceived) (Zanette et al. 2011) predation.</td>
</tr>
<tr>
<td>Predator effects interact with Cavity Density</td>
<td>Density + Bear + Corvid + Density:Bear + Density:Corvid</td>
<td>In areas with low cavity availability, Lewis’s Woodpeckers may be forced to use low quality cavities. In the presence of predators, they may experience lowered reproductive success.</td>
</tr>
<tr>
<td>Predator effects interact with Surplus Cavities</td>
<td>Surplus + Bear + Corvid + Surplus:Bear + Surplus:Corvid</td>
<td>In the face of competition, Lewis’s Woodpeckers may be forced to use low quality cavities. In the presence of predators, they may experience lowered reproductive success.</td>
</tr>
</tbody>
</table>
Table 2.2. Habitat-specific breeding performance (mean ± 95% CI) of Lewis’s Woodpeckers in British Columbia, Canada.

<table>
<thead>
<tr>
<th></th>
<th>Riparian</th>
<th>Live Pine</th>
<th>Burned</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clutch Size</td>
<td>6.30 ± 0.78 (n=20)</td>
<td>5.52 ± 0.56 (n=27)</td>
<td>5.88 ± 1.35 (n=8)</td>
</tr>
<tr>
<td>Hatching Success</td>
<td>0.80 ± 0.07 (n=18)</td>
<td>0.59 ± 0.09 (n=26)</td>
<td>0.77 ± 0.19 (n=7)</td>
</tr>
<tr>
<td>Brood Size</td>
<td>5.11 ± 0.69 (n=18)</td>
<td>3.35 ± 0.65 (n=26)</td>
<td>4.71 ± 1.80 (n=7)</td>
</tr>
<tr>
<td>Nest Success</td>
<td>0.79 ± 0.13 (n=42)</td>
<td>0.80 ± 0.12 (n=35)</td>
<td>0.42 ± 0.23 (n=19)</td>
</tr>
<tr>
<td>Productivity per Successful Nest</td>
<td>2.61 ± 0.45 (n=33)</td>
<td>1.86 ± 0.31 (n=28)</td>
<td>1.88 ± 0.59 (n=8)</td>
</tr>
<tr>
<td>Productivity per Attempted Nest</td>
<td>2.05 ± 0.49 (n=42)</td>
<td>1.49 ± 0.35 (n=35)</td>
<td>0.79 ± 0.49 (n=19)</td>
</tr>
</tbody>
</table>
Table 2.3. Variation (mean ± 95% CI) in cavity abundance, competitors, surplus cavities, foraging behaviors and proportion of sites with a high corvid abundance and presence of bears across three habitat types in British Columbia, Canada.

<table>
<thead>
<tr>
<th></th>
<th>Riparian</th>
<th>Live Pine</th>
<th>Burned</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Cavities</td>
<td>9.28 ± 1.63 (n=40)</td>
<td>3.63 ± 1.02 (n=35)</td>
<td>7.05 ± 2.12 (n=19)</td>
</tr>
<tr>
<td>Heterospecific Competitors</td>
<td>1.24 ± 0.37 (n=42)</td>
<td>0.51 ± 0.22 (n=35)</td>
<td>0.84 ± 0.51 (n=19)</td>
</tr>
<tr>
<td>Lewis’s Woodpeckers</td>
<td>0.71 ± 0.25 (n=42)</td>
<td>0 (n=35)</td>
<td>0.58 ± 0.37 (n=19)</td>
</tr>
<tr>
<td>European starlings</td>
<td>0.93 ± 0.35 (n=42)</td>
<td>0.31 ± 0.18 (n=35)</td>
<td>0.63 ± 0.51 (n=19)</td>
</tr>
<tr>
<td>Surplus Cavities</td>
<td>6.42 ± 1.69 (n=40)</td>
<td>2.11 ± 0.98 (n=35)</td>
<td>4.74 ± 1.92 (n=19)</td>
</tr>
<tr>
<td>Feeding Rate Residuals</td>
<td>1.92 ± 3.47 (n=20)</td>
<td>-1.92 ± 2.65 (n=21)</td>
<td>0.59 ± 4.25 (n=12)</td>
</tr>
<tr>
<td>Foraging Area (ha)</td>
<td>2.20 ± 1.04 (n=20)</td>
<td>2.57 ± 0.98 (n=21)</td>
<td>1.96 ± 1.02 (n=12)</td>
</tr>
<tr>
<td>Proportion of sites with high corvid abundance</td>
<td>0.20 ± 0.39 (n=5)</td>
<td>0.50 ± 0.33 (n=10)</td>
<td>0.25 ± 0.49 (n=4)</td>
</tr>
<tr>
<td>Proportion sites with bears present</td>
<td>0.20 ± 0.39 (n=5)</td>
<td>0.50 ± 0.33 (n=10)</td>
<td>0.50 ± 0.57 (n=4)</td>
</tr>
</tbody>
</table>
Table 2.4  Summary of candidate model set examining the influence of habitat, cavity density, predators, and competitors on the Hatching Success (the proportion of eggs that hatch) of Lewis’s Woodpeckers in British Columbia, Canada. We used Akaike’s Information Criterion for small sample sizes (AICc). We described model fit by the number of parameters (K), difference in Akaike’s Information Criterion (ΔAICc) and weight of evidence (wi), the likelihood of each model relative to all other models in the candidate set.

<table>
<thead>
<tr>
<th>Hatching Success (n=25)</th>
<th>K</th>
<th>ΔAIC</th>
<th>wi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cavity Density</td>
<td>3</td>
<td>0.00</td>
<td>0.48</td>
</tr>
<tr>
<td>Surplus Cavities</td>
<td>3</td>
<td>0.29</td>
<td>0.42</td>
</tr>
<tr>
<td>Habitat</td>
<td>4</td>
<td>5.09</td>
<td>0.04</td>
</tr>
<tr>
<td>Null</td>
<td>2</td>
<td>6.42</td>
<td>0.02</td>
</tr>
<tr>
<td>Lewis’s Woodpeckers</td>
<td>3</td>
<td>6.42</td>
<td>0.02</td>
</tr>
<tr>
<td>Bear + Corvid</td>
<td>4</td>
<td>7.16</td>
<td>0.01</td>
</tr>
<tr>
<td>Heterospecific Competitors</td>
<td>3</td>
<td>8.34</td>
<td>0.01</td>
</tr>
<tr>
<td>Surplus * Bear + Surplus * Corvid</td>
<td>7</td>
<td>10.56</td>
<td>0.00</td>
</tr>
<tr>
<td>Cavity Density * Bear + Cavity Density * Corvid</td>
<td>7</td>
<td>10.65</td>
<td>0.00</td>
</tr>
</tbody>
</table>
**Table 2.5.** Summary of candidate model set examining the influence of habitat, cavity density, predators, and competitors on the Nest Success (≥1 fledgling) of Lewis’s Woodpeckers in British Columbia, Canada. We used Akaike’s Information Criterion for small sample sizes (AICc). We described model fit by the number of parameters (K), difference in Akaike’s Information Criterion (ΔAICc) and weight of evidence (Wi), the likelihood of each model relative to all other models in the candidate set.

<table>
<thead>
<tr>
<th>Nest Success (n=48)</th>
<th>K</th>
<th>ΔAICc</th>
<th>Wi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null</td>
<td>2</td>
<td>0.00</td>
<td>0.24</td>
</tr>
<tr>
<td>Habitat</td>
<td>4</td>
<td>0.20</td>
<td>0.21</td>
</tr>
<tr>
<td>Heterospecific Competitors</td>
<td>3</td>
<td>0.97</td>
<td>0.14</td>
</tr>
<tr>
<td>Surplus Cavities</td>
<td>3</td>
<td>1.75</td>
<td>0.10</td>
</tr>
<tr>
<td>Cavity Density</td>
<td>3</td>
<td>1.93</td>
<td>0.09</td>
</tr>
<tr>
<td>Lewis’s Woodpeckers</td>
<td>3</td>
<td>1.96</td>
<td>0.09</td>
</tr>
<tr>
<td>Cavity Density * Bear + Cavity Density * Corvid</td>
<td>7</td>
<td>2.17</td>
<td>0.08</td>
</tr>
<tr>
<td>Bear + Corvid</td>
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<td>3.77</td>
<td>0.04</td>
</tr>
<tr>
<td>Surplus * Bear + Surplus * Corvid</td>
<td>7</td>
<td>5.32</td>
<td>0.02</td>
</tr>
</tbody>
</table>
Table 2.6. Summary of candidate model set examining the influence of habitat, cavity density, predators, and competitors on the Productivity of Lewis’s Woodpeckers in British Columbia, Canada. We considered productivity to be the number of fledglings from each nest that was able to produce ≥1 fledgling. We used Akaike’s Information Criterion for small sample sizes (AICc). We described model fit by the number of parameters (K), difference in Akaike’s Information Criterion (ΔAICc) and weight of evidence (wi), the likelihood of each model relative to all other models in the candidate set.

<table>
<thead>
<tr>
<th>Productivity of Successful Nests (n=34)</th>
<th>K</th>
<th>ΔAICc</th>
<th>Wi</th>
</tr>
</thead>
<tbody>
<tr>
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<td>0.36</td>
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<td>Surplus Cavities</td>
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</tr>
<tr>
<td>Null</td>
<td>2</td>
<td>1.85</td>
<td>0.14</td>
</tr>
<tr>
<td>Lewis’s Woodpeckers</td>
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<td>3.88</td>
<td>0.05</td>
</tr>
<tr>
<td>Heterospecific Competitors</td>
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<td>0.05</td>
</tr>
<tr>
<td>Habitat</td>
<td>4</td>
<td>4.05</td>
<td>0.05</td>
</tr>
<tr>
<td>Bear + Corvid</td>
<td>4</td>
<td>5.65</td>
<td>0.02</td>
</tr>
<tr>
<td>Surplus * Bear + Surplus * Corvid</td>
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<td>10.45</td>
<td>0.00</td>
</tr>
<tr>
<td>Cavity Density * Bear + Cavity Density * Corvid</td>
<td>7</td>
<td>10.74</td>
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</tr>
</tbody>
</table>
Chapter 3.

Nest Tree Persistence and Cavity Dynamics

3.1. Abstract

Tree cavities may persist for over a decade, making them usable by cavity-nesting species for many years. Nest trees may be less likely to persist in years of severe weather, in regions affected by large-scale insect infestations, or in particular habitat types that contain tree species that decay more quickly. Because animals tend to make decisions on returning to the same breeding location based on previous years’ success, cavity-nesting birds may reuse nest trees less frequently from one year to the next in regions or habitat types that support fewer successful nests. Lewis’s Woodpeckers (Melanerpes lewis), listed as Threatened in Canada, are weak excavators that rely on pre-existing cavities for nesting. We studied nest tree persistence and reuse by Lewis’s Woodpeckers within six regions of British Columbia, and also described reuse patterns in the context of the local cavity nesting community. We found that nest tree persistence was generally high (98.6% persisted each year, n=2158 tree-years). However, persistence was lowest in the final two years of the study and was lower in the Boundary region than in other regions. When trees persisted Lewis’s Woodpeckers reused 62.4% of nest trees (n=349 tree-years), and reused 58% of cavities (n=34 cavities monitored in 2013 and 2014). The reuse rates for secondary and weak-cavity nesting species in this study are similar to what has been found in other studies. The fact that nest tree persistence may be declining in the same region that is also very productive in terms of breeding success (riparian habitat type) indicates that there may be a need to protect riparian habitat there to ensure healthy Lewis’s Woodpecker populations in British Columbia.

3.2. Introduction

Tree cavities, often found in old, decayed trees, are a critical resource used by many animals for nesting and roosting throughout the year (Newton 1994, Martin and Eadie 1999). In some forests, trees can remain standing for 25 years after death, allowing
cavities to be reused for decades (Yamasaki and Leak 2006). For this reason, the maintenance of standing dead trees, also called ‘wildlife trees’ is incorporated into many forest management plans. In temperate North America, the majority of tree cavities are created by primary excavators (mainly woodpeckers). Cavities are then used by members of a complex web of cavity-users, including those that cannot or rarely excavate for themselves, called secondary and weak cavity-nesters. (Martin and Eadie 1999, Aitken et al. 2002).

Cavities in North American forests tend to persist for 7-15 years depending on forest management activities and the extent of tree decay (Edworthy and Martin 2013), and can be reused many times throughout their ‘lifespan’ (Sedgwick 1997, Martin and Eadie 1999, Aitken et al. 2002). The extent to which cavities are reused is extremely variable. In British Columbia, primary cavity-nesting species rarely reused (6.9%) cavities made the previous year, whereas weak excavators reused 11.4% of cavities and secondary cavity-nesters reused 30% of cavities (Aitken et al. 2002). Reusing existing cavities may have negative consequences, such as a higher risk of exposure to ectoparasites or harmful bacteria that survive in old substrate (Short 1979, Gonzalez-Braojos et al. 2012). However, cavity excavation is an energetically costly task that can take weeks to complete (Short 1979). Cavity reuse may therefore be adaptive if the lower energetic costs and time saved allow individuals to advance their laying date and increase the length of the breeding season (Wiebe et al. 2007).

The density of cavities and the likelihood that cavities are reused can depend on the rate of cavity creation, the extent to which cavities persist, and the tendencies of cavity-nesting animals to reuse cavities. The creation of cavities can be influenced by wildfire prevalence, insect or fungus infestations, and the abundance of primary cavity-nesting species (Koch et al. 2008, Robles and Martin 2014). For example, in Tasmania Australia, fire influenced cavity production in dry forests, while insect abundance was related to cavity production in the wet forests because insects facilitate cavity excavation (Koch et al. 2008). Factors that may decrease cavity persistence include forest harvest, weather disturbances, and insect outbreaks. Edworthy and Martin (2013) found that median cavity longevity was lower in harvested forests because the remaining trees are susceptible to wind throw. In addition, broad-scale infestations of the mountain pine beetle
(Dendroctonus ponderosae) may cause substantial treefall several years post-infestation (Lewis and Hartley 2006), or encourage salvage logging of beetle-killed trees in impacted areas (Saab et al. 2011, Lindenmayer et al. 2012), both of which may reduce the abundance of wildlife trees on the landscape (Ritchie 2008).

The rates at which cavities are reused can be associated with the costs of reuse, which may vary with the prevalence of ectoparasites and the availability of holes. Further, many bird species are known to make reuse decisions based on previous experience. Several studies have shown that birds that had a successful nesting attempt tend to reuse nest sites more frequently (Gavin and Bollinger 1988, Ingold 1991, Hoover 2003). Factors that increase nesting success such as low predation risk or high food abundance, may therefore impact nest tree reuse differently across years and may cause variation in reuse across regions.

Lewis’s Woodpeckers (Melanerpes lewis) are weak excavators, whose populations are declining throughout their range (-2.7%/yr between 1966 and 2010, Sauer et al. 2014). Population declines are attributed to loss of habitat and competition with other cavity-nesting birds like the American Kestrel (Falco sparverius), Northern Flicker (Colaptes auratus), and the invasive European Starling (Sturnus vulgaris) (Campbell et al. 1990, Lewis et al. 2002). In Canada, Lewis’s Woodpeckers are found in six regions of the south-central and southern British Columbia: the Cariboo-Chilcotin, Thompson-Nicola, Okanagan-Similkameen, Boundary, West Kootenay, and East Kootenay (Environment and Climate Change Canada 2016) (see Figure 3.1). Lewis’s Woodpeckers breed in previously excavated cavities in large deciduous or coniferous trees within riparian black cottonwood (Populus trichocarpa) forests, live ponderosa pine (Pinus ponderosa) forests, and burned coniferous forests (Bock 1970, Linder and Anderson 1998, Zhu et al. 2012). Management of Lewis’s Woodpeckers requires knowledge of factors that may influence the persistence of nest trees, a critical resource (Environment and Climate Change Canada 2016). In addition, it is important for managers to understand community interactions within the nest web that may alter the reuse of wildlife trees by Lewis’s Woodpeckers.
In this study we explored how the probability of nest tree persistence and reuse of these trees by Lewis’s Woodpeckers varied with tree species, habitat type and geographic region. We predicted that the probability of nest tree persistence would be lower in deciduous tree species (such as black cottonwood, trembling aspen (Populus tremuloides) and water birch (Betula occidentalis)) versus coniferous tree species (such as Douglas fir (Pseudotsuga menziesii), ponderosa pine, and western larch (Larix occidentalis)) because deciduous trees decay at a faster rate and are relatively shorter-lived (Wildlife/Danger Tree Assessor’s Guide 2012). However, the probability of nest tree persistence could currently be lower in pine trees since these species are susceptible to pine bark beetle (Miller and Keen 1960). We predicted that the probability of nest tree persistence could be lower in the Thompson-Nicola and Boundary region because the former has been severely impacted by pine bark beetle and the latter is more urban and proximity to urban areas may cause more nest trees to be removed for safety and aesthetics reasons (Environment and Climate Change Canada 2016). Finally, we predicted that riparian habitat may have a lower probability of nest tree persistence overall because riparian systems experience periodic flooding events that may cause increased wildlife tree loss, and riparian habitat in British Columbia is commonly located near urban environments. Lewis’s Woodpeckers frequently reuse nest trees and cavities (Linder and Anderson 1998, Saab et al. 2004). If Lewis’s Woodpeckers are more likely to reuse nests where they reproduce successfully, we would predict that nest tree reuse would be higher in riparian trees within riparian habitat (see Chapter 2). However, nest tree reuse could be lower in riparian habitat because there are a greater number of cavities in this habitat (Chapter 2). Cavity-nesting competitors, particularly European Starlings, are more abundant in the Boundary region (see Chapter 2), and elevated levels of nest-site competition could lead to lower nest tree and cavity reuse in this region. We evaluated these predictions using an 11 year nest tree monitoring dataset from BC. We also compare patterns of nest tree persistence and reuse at the large scale with more detailed information on the cavity dynamics of Lewis’s Woodpecker collected at a local scale in two regions over two years.
3.3. Methods

3.3.1. Field Methods

The Canadian Wildlife Service has monitored nest trees used by Lewis’s Woodpeckers within six regions of British Columbia, Canada (Cariboo-Chilcotin, Thompson-Nicola, Okanagan-Similkameen, Boundary, West Kootenay, and East Kootenay) over a 17-year period (1997-2014). Nest trees were located by Canadian Wildlife Service staff and volunteers who searched within habitat considered suitable for Lewis’s Woodpeckers and in areas that local biologists suggested were used by Lewis’s Woodpeckers. Nest trees were also added to the dataset when reports of breeding Lewis’s Woodpeckers were received from landowners. Observers visited nest trees to determine if they were still standing and assess whether they were being used by Lewis’s Woodpeckers. Nest tree visits were scheduled to occur between June 15 and July 15 each year in order to incorporate the period of time that nests have the highest detection probability (due to nestling begging calls and frequent nest visits by parent Lewis’s Woodpeckers). A nest tree was considered active if an adult was observed to carry food into a cavity, carry a fecal sac out of a cavity, or if nestlings were observed or heard inside a cavity. Observers recorded whether the cavity was in a tree or a telephone pole, recorded the tree species, and collected GPS coordinates at the nest tree. In subsequent years, a subset of nest trees were re-visited to determine if they were still present, and if they were still being used by Lewis’s Woodpeckers. A nest tree was considered to be reused if there was evidence of an active nest cavity or observers documented recently fledged young near the nest tree. Observers spent ~20 minutes searching 100 m around each nest tree for active nests not previously documented, and any new nests that were found during these visits were recorded.

We used data collected between 2003 and 2014 for analyses, as data prior to 2003 were sparse. We excluded data from nest sites in telephone poles because they comprised only 1.6% of all observations. We extracted data from trees used in multiple years to assess whether a nest tree present in year t was present in year t+1. We included data where trees were visited in year t+1 and/or known to be present in year t+x. The dataset we used in analyses included 2,158 pairs of observations. If trees persisted we
assessed whether trees that were used by Lewis's Woodpeckers in year t were also used by Lewis's Woodpeckers in year t+1. The dataset that we used in this analysis included 349 pairs of observations.

We also examined the probability of nest tree persistence and cavity reuse in detail by monitoring the reuse of nest trees between regions at the local scale. Nest trees were located in four sites in the Boundary region and six sites in the Okanagan-Similkameen region. We located 36 nests in the Boundary region and 32 in the Okanagan-Similkameen region in 2013 between May 1 and June 15, searching areas where previous nesting attempts had been documented by the Canadian Wildlife Service (unpublished). We considered a cavity to be active by observing nesting behaviour as previously described, and where possible determined whether the cavity contained eggs or nestlings using wireless telescoping cameras (the TreeTop Peeper (Sandpiper Technologies, Maneca, California) and the Peeper Cam (IBWO.org David Luneau, Arkansas)). We subsequently located all cavities within 100-m of every Lewis’s Woodpecker nest tree location used by three other species: European Starlings, Northern Flickers, and American Kestrels. We marked the nest trees of each species with a digital point using a GPS device and a metal tag. To identify whether a specific cavity in a nest tree was reused we recorded the height, direction and shape of the cavity opening. We monitored Lewis’s Woodpecker nests over the course of the breeding season (May-July, 2013 see Chapter 2) and revisited each nest tree the following year to check for re-occupancy (May 10-June 15, 2014). During the 2013 breeding season we documented nest activity, such as egg laying, incubating and nesting provisioning, during the course of weekly visits to each nest tree, to determine whether the nests were successful in producing at least one fledgling. We documented cases where nest trees and cavities used by Lewis’s Woodpeckers or their competitors were lost because of tree fall, or we found evidence of cavity destruction by bears. In 2014 we revisited all of the nest trees that we had found in 2013 and recorded whether the tree was still standing, the cavity remained intact, and the cavity was occupied. We determined cavity occupancy using previously described behavioral indications of nesting activity at the cavity. If the cavity was no longer there or usable, we characterized the apparent cause of loss into one of four categories: 1) the entire tree had fallen, 2) the portion of the tree housing the cavity had fallen, 3) there was evidence of destruction by a bear, or 4) the
cavity entrance was enlarged beyond ~10cm diameter, the size we considered useable by Lewis’s Woodpeckers, with no evidence of tampering by predators.

3.3.2. Statistical Methods

We used a generalized linear model with a binomial distribution and a logit link function to examine the influence of year, habitat type (riparian, live pine and burned), region (Thompson-Nicola, Okanagan-Similkameen, Boundary/West Kootenay, and East Kootenay), and tree species/group (Douglas fir, ponderosa pine, western larch, and a group of riparian species) on the probability of nest tree persistence and reuse from one year to the next. We combined data from black cottonwood, water birch and trembling aspen trees (called ‘riparian group’), because we had insufficient data to analyze the persistence and reuse of water birch and trembling aspen separately. We also combined nests found in the West Kootenay and the adjacent Boundary region because of the small number of nests located in West Kootenay. In both analyses we created a candidate model set that included models with all combinations of the four main effects. In the analysis examining the probability of persistence of nest trees from one year to the next, we also included interactions between year and habitat type, year and tree species, and habitat type and tree species. Although decay class may likely influence nest tree persistence (Edworthy et al. 2012), we did not include this factor in our analysis because data collection of decay class was inconsistent in this dataset and because of the difficulty in comparing decay class categories between deciduous and coniferous species. This candidate set, therefore, included 20 models. The smaller dataset examining reuse of nest trees by Lewis’s Woodpeckers precluded the inclusion of models that included interaction terms. Consequently, this candidate set included 13 models. Although nest trees were revisited multiple times and active nests could be monitored in more than one two-year period we did not include tree identity as a random term because there was no evidence that this improved the statistical models. We assessed whether to include random terms by comparing a complex model with and without tree identity as a random term (tree identity as random effect AICc=320, no random effect AICc=318).

We used an information theoretic approach to assess the relative support for the models included in the two candidate sets examining how tree species, habitat type,
region, and year affected the probability of nest tree persistence and reuse. We used Akaike’s Information Criterion adjusted for small sample sizes (AICc) to calculate model weights for each model (Burnham and Anderson 2002). We chose the best models by using AICc model weights that quantify the strength of support for each model relative to the other included models. We used program R v3.1.3 (R Development Core Team 2014) for all analyses.

3.4. Results

3.4.1. Broad-scale Nest Tree Persistence and Reuse

Over the 11 year period (2003-2014), the overall probability that trees used by Lewis’s Woodpeckers persisted from one year to the next averaged 98.6%. The top model in the candidate-set examining factors influencing the probability of nest tree persistence indicated that persistence varied across years and among regions. This model (Year + Region) had 2 times the support of the next best model that included only year, and more than 40 times the support of the Null model. Year was included in all of the well-supported models (<4 ΔAIC) and had a parameter likelihood estimate of 1.0 (Table 3.1). The probability of nest tree persistence appeared to decline from the early 2000’s to 2014, and was markedly lower in 2013 and 2014 than earlier in the study (Figure 3.2). Region was included in two of the well supported models and had a parameter likelihood estimate of 0.48. Nest tree persistence appeared to be lower in the Boundary region than in the East Kootenay, Okanagan-Similkameen or Thompson-Nicola regions (Figure 3.3). After controlling for year effects, the probability that a nest tree persistence from one year to the next was slightly lower in the Boundary region (mean with 95% CI; 0.915, 0.853-0.952) compared to the East Kootenay (0.977, 0.961-0.986) and the Okanagan-Similkameen regions (0.947, 0.904-0.972). Model estimates for the Thomson-Nicola region were low but had a high degree of uncertainty (0.857, 0.552-0.967). Habitat Type and Tree Species were each included in only one of the well supported models and had low parameter likelihood estimates (0.26 and 0.21).

The overall probability that a nest tree used by Lewis’s Woodpeckers in one year was reused the next was 0.624. The top model in the candidate-set examining nest tree
reuse also indicated that reuse varied across years and among regions. This model had 2.3 times the support of the next best model that included only tree species, and had over 50 times the support of the null model (Table 3.2). The year parameter was included in 4 of the 5 well-supported models and had a parameter likelihood estimate of 0.91. The probability of nest tree reuse varied considerably across years, but in contrast to the analysis of nest tree persistence, temporal patterns in reuse did not show a decline over the 11 years of the study (Figure 3.4). Region was included in 3 of the 4 well-supported models and had a parameter likelihood estimate 0.68. The probability that Lewis’s Woodpeckers reuse trees in the Boundary and East Kootenay region was lower (0.504 and 0.500, respectively) than the probability of reuse in the Okanagan-Similkameen and Thompson-Nicola regions (0.689 and 0.786, respectively) (Figure 3.5). Tree species and habitat type parameters both had lower parameter likelihood estimates (0.14 and 0.13, respectively).

3.4.2. Local Scale Nest Tree and Cavity Persistence, Reuse and Reasons for Loss

In 2013, we located 68 nest trees used by Lewis’s Woodpeckers. Six of these trees were also used by European Starlings while two others were also used by Northern Flickers. An additional 33 nest trees within 100 m of each Lewis’s Woodpecker nest were used by potential nest competitors (European Starlings (n=19), Northern Flickers (n=9), and American Kestrels (n=5)). The majority of nest trees located in 2013 were still present in 2014 (Lewis’s Woodpecker nest trees, 94.1%; all nest trees, 96%).

Overall, 57.8% of the Lewis’s Woodpecker nest trees that were still standing in 2014 (n=64) were reused by Lewis’s Woodpeckers. In contrast to the analysis of the large scale dataset, Lewis’s Woodpeckers did not reuse the trees differently between the two regions (Boundary, 60.0%; Okanagan-Similkameen, 56.7%; $\chi^2=0.0$, df=1, p=1.0).

In 2013, we found 70 cavities used by Lewis’s Woodpeckers. Of these 70 cavities, four were lost during the 2013 season (two due to the tree falling, one due to the cavity falling, and one cavity entrance was sufficiently enlarged by nestlings and was no longer suitable). Five more were lost before the start of the 2014 breeding season (one lost due to the tree falling, three lost due to the cavity falling, and one destroyed by a bear). Finally,
an additional two cavities were lost during the 2014 breeding season (one due to the tree falling, and one due to the cavity falling). In total, 11 Lewis’s Woodpecker cavities were lost (15.8%). We found 44 additional cavities used by potential competitors (European Starlings (n=28), Northern Flickers (n=11) and American Kestrels (n=5)) in the areas surrounding active Lewis’s Woodpecker nests. Three Northern Flicker cavities were destroyed by bears in 2014. In contrast, none of the cavities occupied by American Kestrels or European Starlings in 2013 were lost.

Out of the 114 cavities used by the four cavity-nesting species in 2013, 100 cavities remained in 2014, and 71 were used by one of the four cavity-nesting species. Reuse of cavities appeared to vary by cavity-nesting species. Lewis’s Woodpeckers and European Starlings were more likely to reuse a cavity than Northern Flickers and American Kestrels (Table 3.3). Lewis’s Woodpeckers reused 62.7% of the 59 cavities that remained intact in 2014. Although not statistically significant, cavities where Lewis’s Woodpeckers bred successfully in 2013 were more likely to be reused by Lewis’s Woodpeckers in 2014 than cavities where Lewis’s Woodpeckers were unsuccessful in 2013 (successful: reuse=62%, n=29 nests, unsuccessful: reuse=33% n=9 nests, $X^2=0.27$, df=1, p=0.60). Of those cavities that were not used by Lewis’s Woodpeckers (n=22), half were used by potential nest competitors. Northern Flicker cavities that were not used by Northern Flickers in 2014 were more likely to be used by other species of the nest web, whereas American Kestrels and European Starling cavities that were not reused by the same species were rarely occupied by other species in the nest web (Table 3.3).

### 3.5. Discussion

#### 3.5.1. Nest Tree Persistence

Nest trees are a critical resource for the Lewis’s Woodpecker, a weak cavity-nesting species. We found that the probability of Lewis’s Woodpecker nest tree persistence across British Columbia was high overall (0.986), but appeared to decline in the last two years of the study (2012-2014). Declines in the probability of nest tree persistence cannot be explained by recent urban development because human population of the region has increased steadily over the time period of the study. The declines could
also not be explained by extreme weather conditions, as there were no extreme weather events in 2013 or 2014. Persistence may have declined in the final two years of the study because there is a lack of suitable cavities in younger trees and the nest trees used by Lewis’s Woodpeckers are aging and have higher mortality. Continued monitoring of nest trees over time will be crucial to determine if the pattern of declining persistence continues in the future.

We found evidence for regional, rather than habitat or tree species differences in the probability of nest tree persistence. Nest trees in the Boundary region are predominantly found in urban-modified areas. We therefore expected nest trees in the Boundary region to have a lower probability of persistence if urbanization increased the number of nest trees that were felled for safety or aesthetic reasons. Lewis’s Woodpecker nest trees in the Boundary region were slightly less likely to persist than nest trees found in the Okanagan-Similkameen and East Kootenay regions. However, urbanization effects are unlikely to be due to the removal of trees for safety or aesthetics as very few nest trees were felled (4 nest trees) during the course of the study. We also expected that nest trees in the Thompson-Nicola region would have a lower probability of persistence because of the large-scale pine bark beetle infestations in this region. After controlling for year effects, mean nest tree persistence in the Thompson-Nicola region was relatively low. However, the confidence intervals around this estimate were large and overlapped with estimates of nest tree persistence in other regions. The high degree of uncertainty is likely a consequence of the smaller sample size in the Thompson-Nicola region; only 6.2% of all paired observations were located in the Thompson-Nicola and only 4 trees were monitored in the final 2 years of the study. Additional data are therefore required to determine if pine bark beetles are having a detectable effect on nest tree persistence. Nevertheless, the presence of regional rather than habitat or tree species effects on nest tree persistence is somewhat surprising. Nest trees in the Boundary region consist predominantly of black cottonwood trees within riparian habitat. Regional differences may therefore be due to both differences resulting from being in greater proximity to urban areas and differences in the distribution of habitats and tree species across regions.
3.5.2. **Nest Tree Reuse**

Lewis’s Woodpeckers, a weak cavity-nester, are expected to reuse nest trees and nest cavities (Bock 1970), and at a higher rate than primary cavity-nesters (Sedgwick 1997, Aitken et al. 2002, Saab et al. 2004). We found, unsurprisingly, that nest tree reuse was high and that cavity reuse by Lewis’s Woodpeckers was greater than those of a stronger excavator, the Northern Flicker. We also found that nest tree reuse was greater in the Thompson-Nicola and Okanagan-Similkameen than the Boundary and East Kootenay region. Both the Boundary and East Kootenay regions contain higher proportions of riparian habitat than Thompson-Nicola and Okanagan-Similkameen, and riparian habitats have a higher density of nesting heterospecific competitors relative to the other habitat types (Chapter 2). Differences in nest tree reuse between regions could therefore be a consequence of variation in heterospecific competition for nest cavities. Alternatively, it is possible that Lewis’s Woodpecker populations are declining more rapidly in the Boundary and East Kootenay, leading to lower reuse of nest trees from one year to the next in these regions.

Population declines of the Lewis’s Woodpecker have been attributed in part to competition with European Starlings for suitable nest cavities (Environment and Climate Change Canada 2016, Campbell et al. 1990, Lewis et al. 2002). Previous work in the Okanagan-Similkameen region of British Columbia indicated that European Starlings usurped multiple cavities during the breeding seasons of 2004 and 2005 in British Columbia, suggesting that starlings may be negatively impacting breeding Lewis’s Woodpeckers (Zhu et al. 2012). In contrast, we found little evidence that European Starlings negatively impact the ability for Lewis’s Woodpeckers to secure a nesting cavity. European starlings rarely occupied nest cavities used by Lewis’s Woodpeckers in the previous year. In fact, cavities used by Lewis’s Woodpeckers were lost more to native species than to the invasive European Starling in the following year. Additionally, we did not observe any nest takeovers by European Starlings during the two breeding seasons. (Table 3.3). An event that we witnessed may suggest in actuality that Lewis’s Woodpeckers are formidable competitors. In 2013, an active Lewis’s Woodpecker nest tree at a burned site fell after a storm event, and three Lewis’s Woodpecker pairs subsequently ejected two starling pairs that were nesting in the immediate surroundings.
from their cavities. One of these Lewis’s Woodpecker pairs was able to re-nest successfully. Although some species of cavity-nesting birds appear to be susceptible to usurpation by European Starlings (Red-bellied Woodpecker Ingold 1989, Gila Woodpecker Kerpez and Smith 1990), some studies have suggested that European Starlings may not negatively impact Lewis’s Woodpeckers during the breeding season (Vierling 1998) and may not be responsible for population declines (Koenig 2003).

3.5.3. Conclusions

Lewis’s Woodpeckers face a diversity of threats to their persistence, such as urban and agricultural encroachment, dam development, and western pine beetle (Dendroctonus brevicomis) infestations that have degraded suitable nesting habitat across British Columbia over the past half century (Environment and Climate Change Canada 2016). Habitat availability for Lewis’s woodpeckers may reduce even more in the future by continued declines in persistence of suitable nest trees, caused by falling of beetle-killed trees in the Thompson-Nicola region or increased occurrence of severe weather induced by climate change. As a weak cavity-nesting species, cavity availability may be critical to the stability of Lewis’s Woodpecker populations (Newton 1994). Our previous work indicated that cavity availability may currently limit populations of Lewis’s Woodpeckers (see Chapter 2). In addition, the apparent lower persistence of nest trees in the Boundary region may be cause for concern. The majority of Lewis’s Woodpecker nests in the Boundary region are found in riparian forest, which is a severely degraded habitat type in western North America. Interruptions to the natural flooding cycle in the past half century, caused by urban encroachment along rivers and dam development may be limiting regeneration of trees in riparian forests (Lea 2005). If a sufficient number of wildlife trees are not replaced through regeneration, then these forests may have far fewer wildlife trees in the future. In British Columbia, productivity of Lewis’s Woodpeckers in riparian forests is two times higher than coniferous forests (see Chapter 2). Therefore understanding the reasons for the decline in wildlife tree persistence in riparian forests, as well as addressing potential regeneration issues, may be important for the population trajectory of this species at risk. Further study of possible effects of extreme weather events causing substantial tree falling in riparian habitat or effects of pine beetle on treefall in the Thompson-Nicola may help managers devote conservation efforts where they are
most needed. It is imperative that monitoring is continued to determine whether the pattern of increased loss of nest trees will continue in future years. Additionally, continued research on nest tree reuse as well as interactions between species in this nest web would help to clarify if the lower reuse that we observed in the Boundary and East Kootenay regions is due to surplus suitable cavities that allow birds choice in other quality cavities, whether a high abundance of other cavity-nesting birds in these regions are preventing Lewis's Woodpeckers from reusing cavities at a higher frequency, or whether there are more severe population declines of Lewis's Woodpeckers in the Boundary and East Kootenay regions that are preventing reuse.

3.6. References
3.7. Figures

Figure 3.1. The six regions that Lewis’s Woodpeckers currently occupy in British Columbia.
Figure 3.2. Variation in the probability of Lewis’s Woodpecker nest tree persistence across 11 years (2004-2014) in British Columbia, Canada.
Figure 3.3. Variation in the probability of Lewis’s Woodpecker nest tree persistence across four broad regions in British Columbia, Canada.
Figure 3.4. Variation in the probability of Lewis’s Woodpecker nest tree reuse from one year to the next in British Columbia, Canada from 2004-2014.
Figure 3.5. Variation in the probability of Lewis’s Woodpecker nest tree reuse from one year to the next across four regions in British Columbia, Canada.
3.8. Tables

Table 3.1. Model summaries for nest tree persistence in British Columbia. We used Akaike’s Information Criterion for small sample sizes (AICc). We described model fit by the number of parameters (K), difference in Akaike’s Information Criterion (ΔAICc) and weight (wi), the likelihood of each model relative to all other models in the candidate set.

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Table 3.2. Complete model summaries for sequential nest tree reuse by Lewis’s Woodpeckers in British Columbia. We used Akaike’s Information Criterion for small sample sizes (AICc). We described model fit by the number of parameters (K), difference in Akaike’s Information Criterion (ΔAICc) and weight (wi), the likelihood of each model relative to all other models in the candidate set.

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Table 3.3. Variation in the reuse of cavities by five species of cavity-nesting birds (no. [%]) in British Columbia in from 2013 to 2014. LEWO=Lewis’s Woodpecker, AMKE=American Kestrel, EUST=European Starling, NOFL=Northern Flicker, WESO=Western Screech-Owl

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<th>EUST</th>
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Chapter 4.

General Conclusions

In this thesis I examined the breeding performance of Lewis’s Woodpeckers across three habitat types used in British Columbia and studied the influence of cavity density, predators, competition and foraging behaviors on their habitat-based variation in breeding (Chapter 2). I also examined the temporal and spatial patterns in the probability of nest tree persistence and reuse of cavities in the nest web in order to provide knowledge of future habitat conditions and considerations for the management of Lewis’s Woodpecker populations in Canada (Chapter 3).

I demonstrated in Chapter 2 that the breeding performance of Lewis’s Woodpeckers in British Columbia varied with habitat type. Lewis’s Woodpeckers nesting in riparian habitat had higher nest success and were able to produce more fledglings from each successful nest than in both live pine and burned habitats. Overall reproductive output for nests in riparian habitat is 1.4 times that of live pine habitat, and 6.8 times that of nests in burned habitat, a result that was consistent across the two years of the study. The nesting success and productivity of successful nests in live pine and burned habitat in this study (67% nest success, 1.9 fledglings/successful nest) are consistent with earlier work conducted in these habitats in British Columbia (52% nest success, 1.8 fledglings/successful nest, Zhu et al. 2012). The high breeding performance that I found in riparian habitat (79% nest success, 2.6 fledglings/successful nest) is also consistent with a study of Lewis’s Woodpeckers nesting within riparian habitat in Montana (89% nest success, 3.1 fledglings/successful nest, Fylling 2013). However, breeding performance results that we found within burned habitat (42% nest success, 1.8 fledglings/successful nest) are different from a study of nests in burned habitat in Idaho (78% nest success, 1.8 fledglings/successful nest, Saab and Vierling 2001) and South Dakota (90% nest success, 3.4 fledglings/successful nest, Gentry and Vierling 2007). This highlights the importance of regionally-specific data on reproductive performance for developing recovery strategies for Lewis’s Woodpeckers.
An important application of the demographic data from this study would be to determine whether populations in riparian, live pine and burned habitats are ‘source’ populations (i.e. populations able to produce enough young to offset adult mortality) or ‘sink’ populations (i.e. populations dependent on immigration to maintain a stable population size). Determining the source-sink status across habitat types would give managers more knowledge about the ability for the growth of the Lewis’s Woodpecker populations in Canada. The source-sink status could be calculated using the habitat-based demographic data from this study combined with data on adult and juvenile survivorship of Lewis’s Woodpeckers. However, there is currently no information on the adult and juvenile survivorship of Lewis’s Woodpeckers.

Vierling and Saab (2001) calculated population growth rates for Lewis’s Woodpeckers in burned forests in Idaho and riparian forests of Colorado using estimates of adult and juvenile survival derived from other *Melanerpes* woodpeckers (Acorn Woodpeckers: Stacey and Taper 1992, Koenig and Mumme 1987, Red-bellied Woodpeckers: Karr et al. 1990, Martin 1995, Red-headed Woodpeckers: Martin 1995). Using these estimates, Vierling and Saab (2001) showed that burned habitats were likely a source and riparian habitats were likely a sink. Applying the same approach to each of our habitat types in British Columbia using the habitat-based reproductive results from this study and the survival estimates in Table 4.1, we find that populations of Lewis’s Woodpeckers in riparian habitat are likely to be source populations. Eight of the nine combinations of adult and juvenile survival estimates for *Melanerpes* woodpeckers produce estimates of lambda (\( \lambda \)) that are greater than one (\( \lambda = 0.95-1.33 \), Table 4.2). Populations in live pine habitat may be either source or sink populations; six of nine combinations of adult and juvenile survival estimates produce estimates of lambda that are greater than one (\( \lambda = 0.85-1.17 \), Table 4.2). In contrast, we find that populations of Lewis’s Woodpeckers in burned habitat are likely to be sink populations (\( \lambda = 0.73-0.98 \), Table 4.2). I estimate that lambda is less than one even when using the highest estimates of juvenile and adult survival documented for other *Melanerpes* woodpeckers.

Habitat-specific breeding performance of Lewis’s Woodpeckers appeared to be driven by differences in cavity density. Riparian habitat had 2.6 times the number of cavities within 50 m of each nest site than live pine habitat and 1.3 times the number of
cavities than burned habitat. After controlling for differences in the number of nesting competitors that make some cavities unavailable to Lewis’s Woodpeckers, riparian habitat had 1.4 times the number of surplus cavities than burned habitat and 3 times the number of surplus cavities than live pine habitat. Cavity availability can be an important factor in some cavity-nesting species. Correlational studies show a relationship between cavity or snag density and nest density (Raphael and White 1984, Zarnowitz and Manuwal 1985, Carey 1995). Experimental studies show that increases in cavity density can lead to an increase in the number of breeding pairs (Brawn and Balda 1998, Cornelius 2008, Aitken and Martin 2012). For instance, the addition of nest boxes led to an increased breeding density of Mountain Chickadees (*Poecile gambeli*) and red squirrels (*Tamiasciurus hudsonicus*) in the central interior of British Columbia, suggesting that high quality cavities were limiting (Aitken and Martin 2012). Greater cavity availability may increase the likelihood that Lewis’s Woodpeckers are able to occupy a high quality nest cavity. Cavity quality is known to influence the reproductive success of cavity-nesting birds because cavities of the proper size, shape, or orientation can deter predators and lessen the impact of weather events (Li and Martin 1991, Goodenough et al 2008, Zhu et al. 2012, Isaac et al. 2008, Rico and Sandoval 2014). For instance, Zhu et al. (2012) found that cavity shape was a cavity characteristic that predicted whether nests were successful for Lewis’s Woodpeckers in British Columbia.

I anticipated that cavity density and hence quality may be more important when risks of predation are higher. However, I found no evidence that the role of cavity quality was dependent on the presence of bears or of the relative abundance of corvids at our sites, or that the presence of predators alone was influencing breeding performance. I only collected data on two members of the predator community and my assessment of predation risk was relatively crude. Other studies have cited squirrels as a potential or even major predator of cavity-nests (Purcell et al. 1999, Fisher and Wiebe 2005), and while squirrels did occur in each habitat type, based on anecdotal observations they appeared to be much more abundant in riparian habitat where Lewis’s Woodpeckers had both high nest success and produced the highest number of fledglings per successful nest. Therefore, it is unlikely that squirrels explained the observed differences in breeding performance. Other predators, such as long-tailed weasels and pine marten (*Martes martes*) are also known to depredate cavity nests (Fisher and Wiebe 2005, Walters and
Miller 2001, Purcell et al. 1999). If present at our sites, weasels and martens would likely occur in live pine and burned habitat types where there is currently less urban interface overall (Ordeñana et al. 2010). I did find that Lewis’s Woodpeckers reduced the area in which they foraged while provisioning, and they slightly decreased the provisioning rate in the presence of corvids. Behavioral changes due to perceived predation are understood to have negative consequences on every stage in nesting birds (Zanette et al. 2011). This indicates that there may be effects of predators on breeding performance that were unable to detect under our current methods, therefore further work on the interaction between cavity availability and predators may be warranted. However, because only 33% of nests failed due to predation in this study, it is possible that predators play a less important role in this system.

Nest trees and nest cavities are a critical resource for cavity-nesting species that may persist for many years (Yamasaki and Leak 2006, Edworthy et al. 2012). In Chapter 3 of this thesis I showed that Lewis’s woodpecker nest trees monitored by Canadian Wildlife Service over the entire Canadian breeding range as well as nest trees monitored at a local level over two years had a high probability of surviving from one year the next (98.6% probability persistence over entire range, 94% persisted locally). Cavities used by Lewis’s Woodpeckers within these nest trees also had fairly high persistence (84% persistence). The broad-scale data conducted over 11 years suggests that nest trees were less likely to persist in the later years of the study (2012-2013 and 2013-2014). This is a concern, and so continued monitoring of nest trees is required to determine if the lower likelihood of year-to-year persistence observed during the final periods of this study actually represent a continuing downward trend.

Lewis’s Woodpeckers, like many other weak and secondary cavity-nesting species had a high rate of nest tree and cavity reuse (62.4% reuse of nest trees in long-term dataset, 63.7% reuse of tree cavities in local dataset). I expected that European Starlings would replace many cavities used by Lewis’s Woodpeckers in the previous year since European Starlings are an aggressive secondary cavity-nester and suspected to have an impact on the declining populations of Lewis’s Woodpeckers in British Columbia (Zhu et al. 2012, Environment and Climate Change Canada 2016). However, I found little evidence that Lewis’s Woodpeckers lost cavities to other cavity-nesting species from one year to
the next. When cavities were used by a competitor in year 2 of the study (18% of the cavities), they were more likely to be occupied by a native competitor (Northern Flicker) than by an invasive one (European Starling). This result along with the lack of evidence that European Starlings influence breeding performance of Lewis’s Woodpeckers (Chapter 2) indicates that they may not be an important driver of the population declines of Lewis’s Woodpeckers in Canada. Research in other regions also found little evidence that European Starlings are negatively impacting Lewis’s Woodpecker reproductive success (Vierling 1998, Koenig 2003). On the other hand, it is also possible that population declines of European Starlings that have occurred across British Columbia since 1970 (Government of Canada 2014) may explain why I did not detect an effect of European Starlings on breeding Lewis’s Woodpeckers. Additional management actions such as European Starling eradication programs may not be necessary at this time.

Nest trees in the Boundary region were slightly less likely to persist than nest trees in the East Kootenay and Okanagan-Similkameen regions. Although we found no evidence for direct effects of urban encroachment by the cutting of wildlife trees for safety or aesthetics, indirect effects of urbanization could be impacting wildlife trees in the Boundary region, where suitable Lewis’s Woodpecker habitat is located in close proximity to urban areas. I expected nests within the Thompson-Nicola region to have the lowest persistence if the pine bark beetles were impacting Lewis’s Woodpecker nest tree persistence. Although I did find that the Thompson-Nicola had lower persistence when controlling for year effects, there was a high degree of uncertainty in this estimate due to the small sample size, so this result should be treated cautiously. Further work is warranted to assess detectable impacts of pine bark beetle in the Thompson-Nicola region, given the widespread recent outbreak. There was little evidence that nest tree persistence differed among tree species, and it is possible that this could be due to pine bark beetle effects on coniferous trees combined with the generally faster rate of tree decay of deciduous tree species.

The Boundary region, which had relatively low nest tree persistence and nest tree reuse compared to the other regions in British Columbia, had the highest proportion of riparian habitat. Lower nest tree persistence and reuse in this region may be of concern because, as I found in Chapter 2, riparian habitats are the most productive of the three
that Lewis’s Woodpeckers occupy in British Columbia. In order to improve our understanding of the mechanism behind the increased loss of nest trees during the later years of the study in the Boundary region, research on regional weather patterns and flooding events, as well as focused studies on both the direct cutting of nest trees surrounding urban areas as well as indirect effects of urban areas on nest tree loss are warranted.

4.1. Management Implications

The main objective of the federal Recovery Strategy for the Lewis’s Woodpecker is to maintain or increase the regional populations and the distribution of Lewis’s Woodpeckers within Canada (Environment and Climate Change Canada 2016). This thesis has important implications for the management and recovery of Lewis’s Woodpecker populations in the three habitat types that they occupy in British Columbia. I found that Lewis’s Woodpecker nests in riparian habitat have high nest success and productivity, nests in live pine habitat have high nest success and moderate productivity, and nests in burned habitat have low nest success and moderate productivity (Chapter 2). These data combined with survival estimates from other Melanerpes woodpeckers suggest that in Canada, riparian habitats act as a source whereas burned habitats may act as a sink. Since riparian habitat is the most productive habitat for Lewis’s Woodpeckers in British Columbia (Chapter 2), it is important to manage and maintain the populations breeding there, and where possible, increase the amount of riparian forest. I found in Chapter 3 that the probability of Lewis’s Woodpecker nest tree persistence from one year to the next declined over the 11 year period, particularly in 2012-2013 and 2013-2014. The probability of nest trees persisting from one year to the next was also relatively low in the Boundary region of British Columbia. Riparian habitat, which is best represented within the Boundary region, occurs adjacent to human development more often than the other two habitat types. Riparian systems are known to be one of the most degraded habitats in western North America, and may be declining due to lack of regeneration (Ohmart 1994, Lea 2005). Given the importance of riparian habitat for Lewis’s Woodpeckers in British Columbia and the potential increased loss of nest trees in the last two years of this study, it would be prudent to ensure cavity availability for the future by identifying areas where
tree regeneration may be lacking and encouraging the regeneration of cottonwood trees in riparian habitat. Knowledge of regeneration of stands in addition to nest tree persistence data would help predict future suitable habitat for the Lewis’s Woodpecker in Canada. On the other hand, management efforts may also be needed in live ponderosa pine habitats. There is far more live pine habitat (3,518 km²) within Lewis’s Woodpecker breeding range in Canada than there is burned (766 km²) or riparian habitat (458 km²) (Gyug 2013). Because nests in live pine habitat had high nest success and were moderately productive in addition to the largest area in British Columbia, total output of Lewis’s Woodpecker fledglings is highest in live pine habitat compared to riparian and burned habitat types. Therefore, focusing management efforts on increasing cavity density and thus increasing the availability of choice in quality nest sites could be important in live pine habitat. The community in Bend, Oregon, U.S.A. successfully placed 25 cavity nest boxes in burned pine landscape in 2003, and by 2008 18 of 25 were used by breeding Lewis’s Woodpeckers (Kook and Moodie 2008), so the use of cavity nest boxes to increase the density of breeding Lewis’s Woodpeckers may be a worthwhile endeavor. Another method for increasing cavity density is inoculating live trees with fungus or girdling trees to encourage the creation of wildlife trees. The Canadian Wildlife Service has already begun inoculating trees in the East Kootenay region for the purpose of creating nest trees, and have since documented woodpecker use of these trees (Environment and Climate Change Canada 2016). These activities to increase cavity abundance, particularly in live pine habitats, should continue in the future. Burned habitat will likely become more available as fires become more frequent due to climate change, but considering the results of this study, managers should not lose sight of the conservation requirements of the other two habitat types.

### 4.2. References


Raphael, M., White, M., 1984. Use of snags by cavity-nesting birds in the Sierra Nevada (California, USA). Wildlife Monographs, Number 86. The Wildlife Society Bethesda, Maryland, USA.


Table 4.1. Survival estimates for *Melanerpes* Woodpeckers

<table>
<thead>
<tr>
<th>Species</th>
<th>Juvenile Survivorship</th>
<th>References</th>
<th>Adult Survivorship</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acorn Woodpecker</td>
<td>0.35, 0.57</td>
<td>Stacey and Taper 1992, Koenig and Mumme 1987</td>
<td>0.59, 0.75</td>
<td>Stacey and Taper 1992, Koenig and Mumme 1987</td>
</tr>
<tr>
<td>Red-bellied Woodpecker</td>
<td></td>
<td></td>
<td>0.68</td>
<td>Karr et al. 1990</td>
</tr>
<tr>
<td>Red-headed Woodpecker</td>
<td></td>
<td></td>
<td>0.62</td>
<td>Martin 1995</td>
</tr>
</tbody>
</table>
Table 4.2 Estimates of population growth (lambda) for Lewis’s Woodpeckers in a) Riparian b) Live Pine and c) Burned habitat types in British Columbia, Canada. Lambda is estimated using all combinations of juvenile survival and adult survival estimates from Table 4.1.

a)

<table>
<thead>
<tr>
<th>Riparian</th>
<th>Low Adult Survivorship</th>
<th>Mean Adult Survivorship</th>
<th>High Adult Survivorship</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low Juvenile Survivorship</td>
<td>0.95</td>
<td>1.02</td>
<td>1.11</td>
</tr>
<tr>
<td>Mean Juvenile Survivorship</td>
<td>1.06</td>
<td>1.13</td>
<td>1.22</td>
</tr>
<tr>
<td>High Juvenile Survivorship</td>
<td>1.17</td>
<td>1.24</td>
<td>1.33</td>
</tr>
</tbody>
</table>

b)

<table>
<thead>
<tr>
<th>Live Pine</th>
<th>Low Adult Survivorship</th>
<th>Mean Adult Survivorship</th>
<th>High Adult Survivorship</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low Juvenile Survivorship</td>
<td>0.85075</td>
<td>0.92</td>
<td>1.01</td>
</tr>
<tr>
<td>Mean Juvenile Survivorship</td>
<td>0.9327</td>
<td>1.00</td>
<td>1.09</td>
</tr>
<tr>
<td>High Juvenile Survivorship</td>
<td>1.01465</td>
<td>1.08</td>
<td>1.17</td>
</tr>
</tbody>
</table>

c)

<table>
<thead>
<tr>
<th>Burned</th>
<th>Low Adult Survivorship</th>
<th>Mean Adult Survivorship</th>
<th>High Adult Survivorship</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low Juvenile Survivorship</td>
<td>0.73</td>
<td>0.80</td>
<td>0.89</td>
</tr>
<tr>
<td>Mean Juvenile Survivorship</td>
<td>0.77</td>
<td>0.84</td>
<td>0.93</td>
</tr>
<tr>
<td>High Juvenile Survivorship</td>
<td>0.82</td>
<td>0.89</td>
<td>0.98</td>
</tr>
</tbody>
</table>
Appendix A.

Regional variation in Nest Success (the production of ≥1 fledgling) and Productivity per successful nest (number of fledglings) in Burned, Riparian and Live Pine Habitat Types

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>Location</th>
<th>Year</th>
<th>Nest Success</th>
<th>Productivity</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Burn</td>
<td>British Columbia</td>
<td>2015</td>
<td>42% (n=19)</td>
<td>1.80 (n=8)</td>
<td>This study</td>
</tr>
<tr>
<td>Burn</td>
<td>South Dakota</td>
<td>2007</td>
<td>90% (n=55)</td>
<td>3.42 (n=50)</td>
<td>Gentry and Vierling 2007</td>
</tr>
<tr>
<td>Burn</td>
<td>Idaho</td>
<td>2001</td>
<td>78% (n=283)</td>
<td>1.78 (n=221)</td>
<td>Saab and Vierling 2001</td>
</tr>
<tr>
<td>Riparian</td>
<td>British Columbia</td>
<td>2015</td>
<td>79% (n=42)</td>
<td>2.60 (n=33)</td>
<td>This study</td>
</tr>
<tr>
<td>Riparian</td>
<td>Montana</td>
<td>2013</td>
<td>89% (n=18)</td>
<td>3.06 (n=16)</td>
<td>Fylling 2013</td>
</tr>
<tr>
<td>Riparian</td>
<td>Colorado</td>
<td>2001</td>
<td>46% (n=65)</td>
<td>1.70 (n=30)</td>
<td>Saab and Vierling 2001</td>
</tr>
<tr>
<td>Live Pine</td>
<td>British Columbia</td>
<td>2015</td>
<td>80% (n=36)</td>
<td>1.86 (n=29)</td>
<td>This study</td>
</tr>
</tbody>
</table>