2018

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Recommended Citation
Blake, William M., "LEWIS'S WOODPECKER NEST SUCCESS AND HABITAT SELECTION IN COTTONWOOD FLOODPLAIN VERSUS BURNED CONIFER FORESTS" (2018). *Graduate Student Theses, Dissertations, & Professional Papers*. 11191.
https://scholarworks.umt.edu/etd/11191

LEWIS'S WOODPECKER NEST SUCCESS AND HABITAT SELECTION IN COTTONWOOD FLOODPLAIN VERSUS BURNED CONIFER FORESTS

By

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Thesis

presented in partial fulfillment of the requirements
for the degree of

Master of Science
in Wildlife Biology

The University of Montana
Missoula, MT

April 2018

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Lewis’s Woodpecker Nest Success And Habitat Selection In Floodplain Versus Burned Habitats.

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ABSTRACT

Breeding habitat selection influences reproductive outcomes. Habitat selection may be adaptive and benefit populations, but it can also be maladaptive with negative consequences for populations. Understanding habitat selection and its influence on reproductive success, especially in species of concern, is critical for effective management. Lewis’s Woodpecker (*Melanerpes lewis*) is a Species of Concern that has experienced national population declines. We studied its abundance and reproductive success in two commonly selected breeding forest types (i.e., cottonwood floodplain and mixed-conifer burned), and nest-site characteristics (nest availability, food availability, and vegetation attributes) that have the potential to yield strong differences in abundance and reproductive success. We analyzed abundance estimates from valley-wide surveys, and computed nest success from 217 nests monitored in floodplain and burned forest. We found densities 2.5 to 5.5 times higher in floodplain than in burned forest, despite lower nest success in floodplain (73%) versus burned forest (86%). We found that Lewis’s chose to nest in tall trees, areas with low canopy cover, and in mature tree stands. Insect abundance did not explain differences in attrition or nest success across forest types, but phenology of insect availability and suitable tree density for nesting correlated with differences in abundances. Our research suggests management strategies aimed at conserving Lewis’s Woodpecker habitat need to focus on the retention of large diameter snags in both floodplain forest and mixed-conifer burned forest, as well as protecting recruitment of cottonwoods in the floodplain.

ACKNOWLEDGMENTS

As commonly found in many of life’s undertakings, my thesis work results from multiple collaborations with many individuals. Each contribution made by coworkers, collaborators, advisors, friends, and family members, was unequivocally important into shaping this final product. Acknowledging everyone who participated in the success of this project is an exercise bound to fail by nature, so I am sorry in advance if I forget to name anyone who helped me out, even in the smallest manner.

I would like to thank first my academic advisor, Tom Martin, for helping me with this endeavor. Tom had a huge influence on me, early on in my career. He hired me for my first wildlife job 12 years ago, gave me the opportunity to study birds all across the world, and has now seen me through my graduate degree. His guidance has helped mold me into a better field biologist and scientist. Tom has become a mentor, a friend, and will have a lasting impact on my future career.

Next I would like to thank Kate Stone. Kate kick started this project and believed in me through this entire process. Kate was instrumental in advising me has always been a fantastic supervisor. It has been a joy working together, starting several banding projects, and to study bird species that need conservation attention. I am lucky to call Kate a friend and will always look up to her. She is one of the kindest people I know, and one of the fiercest field workers I have had the pleasure to engage with.

I also want to thank my other committee members, Mark Hebblewhite and Bret Tobalske, for their comments and time they took to help me in developing this research. Mark and Bret are both remarkable human beings whom excel in many fields other than biology. Their knowledge and time dedicated to this project was invaluable.

I would like to thank Paul Guerinas and his family for their financial support during my recent career and graduate life. The Guerinas have become major contributors to conservation and research projects in western Montana. They have acquired and protected thousands of acres of land to preserve open country and wildlife through the creation of MPG Ranch. Without the generosity and love for conservation that the Guerinas family has shown this project would have never been possible, and for that I am forever grateful.

I extend my sincerest gratitude to Philip Ramsey who hired me prior to graduate school, and has continued to support me. Philip has provided me with countless options to better my career and my master's project.

There are many co-workers at MPG that I want to thank. I would like to acknowledge Gus Seward for risking his life and following me on perilous tree climbing adventures. Kerr Rasmussen and Debbie Leick who have shared their love for birds and provided unmeasurable support. Rebecca Durham who was instrumental in developing vegetation guidelines and volunteering many hours to my project. Joshua Lisbon, Beau Larkin, Sarah Norton, Ylva Lekberg, Cherin Spencer-Bower, Nick Francyck and Spencer Bradford helped in forging this project one way or another. Roni Patrick was instrumental in dealing with all new hires in the summer and making the administrative logistics as smooth as possible. Lorinda Bullington contributed helpful comments on written reports. Alan Ramsey helped me immensely develop all the nest video-monitoring strategies and he has unparalleled willingness to help me with investigating new technologies. I would like to thank Mike McTee, all the irrigation crews, Jeff Clarke, and ranch hand crews for all the groundwork they accomplished at MPG on a day-to-day basis. Finally, Mat

Seidensticker was instrumental in insect data and many field contributions for this project.

I am so honored and thankful to have joined the Martin lab. I enjoyed learning enormously from present and past lab members of the Martin lab, who helped me shape this project and provided invaluable criticism and sources of ideas for making my thesis better and stronger. Additionally all the staff at the Montana Wildlife Research Cooperative has always been welcoming and helpful to me. I thank everyone in the bird lab, especially Connor Armstrad , Skylar Sargent, Shelby Weigand, Susan Kieser, Cayla Daily, and others who watched countless hours of Lewis's nesting activities.

I also want to extend my acknowledgments to all the wildlife biology graduate students and professors at UM. I want to thank in particular: Will Janousek who helped me overcome many obstacles in developing the abundance models. Josh Nowak and Jessie Golding dedicated several hours of their time to help me in the initial process to developing and running the abundance models as well. I would like to thank all the professors for their paramount contributions to the wildlife biology program and to helping me become a better researcher.

I would like to thank all and every one of the crewmembers that helped collect data for this research. This group includes: Isaac VanDiest, Jennifer Hernandez, Aubrey Power, Macy Dugan, Richard Anderson, Franco Gigliotti, Sarah Straughan, Sarah Norton, Matt Seidensticker, Megan Figura, Sara Vick, Erika Swanson, Jake Holm, Clara Kober, Kenzie Prichard, Mary Ellyn Dupre, Erin Flynn, Jordan Meyer-Morey, Lauren Sullivan, and Rhianna Dilworth.

One of the most generous support for this project was indisputably that of many Bitterroot landowners who allowed us to monitor Lewis’s Woodpeckers on their land. Our fieldwork and data collection would never have been possible without the collaboration of several amazing people. I want to extend a special thank you to Tom Reed, Rick Armitage, Skalkaho Creek Ranch, Bart Morris, Sapphire Ranch, John Thomas, Debbie Thomas, Sula Peak Ranch, Craig Coates, Mike Richardson, CB Ranch, Molly Smith, Kyle Whyard, Triple Creek Ranch, Richard Beaudin, Mary Beaudin, and Bob Schroeder. Everyone was extremely generous and patient with us and I will always owe you my sincerest gratitude. Thank you for being the stewards of our lands.

I am extremely grateful on a personal level, to be surrounded by brilliant people, whose generosity, tolerance and open-mindedness cannot be rivaled. This group of friends has helped me through both difficult and great times in graduate school. Andy Boyce, Adam Mitchell, James Mouton, Sara Williams, Jessie Golding, Will Deacy, Caroline Deacy, Anne Shaeffer, Ryan Hegstad, Will Janousek, Riccardo Ton, Juan Oteyza, Karolina F. Calderon, and Diego F.B. Gómes thank you for everything.

My parents Dan and Vony, along with my siblings Laura and Thomas, and my entire family on both the French and American sides have always accepted me for who I am, and encouraged me to follow my dreams. I am forever thankful to all of them. My parents have always believed in me, despite knowing that my move across the Atlantic may entail seeing less of me. Finally, I would like to thank Maggie Riordan, the love of my life, for her wise advice and on-going support in every step I take. Maggie enabled me to find courage and confidence when I needed it the most.

TABLE OF CONTENTS

INTRODUCTION

Habitat selection refers to a hierarchical process of behaviors that results in organisms disproportionately using one habitat over others (MacArthur 1965, Rosenzweig 1981, Hutto 1987, Jones 2001, Morris 2003, Sergio et al. 2003). In particular, environmental attributes of habitats affect reproduction and survival (Fretwell 1972, Cody 1985). Understanding the habitat attributes that underlie habitat quality (i.e., environment's ability to provide conditions for individual and population persistence; Johnson 2007) and allow greatest reproductive success is important for managing populations, especially for species showing population declines. Abundance is often used as an indicator of habitat quality under the assumption that more individuals choose higher quality habitat. However, abundance can be a misleading indicator of habitat quality (Van Horne 1983, reviewed in Chalfoun and Schmidt 2012). Consequently, studying both abundance and reproductive success is important for assessing habitat quality.

Abundance may be an appropriate indicator of habitat quality when habitat selection is adaptive and more individuals choose the breeding habitat type with highest reproductive success among available habitats (Fretwell 1972, Martin 1998). Density-dependent effects from increased population density in the higher quality habitat may cause average reproductive success to equal levels in lower quality habitat with lower population density (Fretwell 1972). For example, bank vole (*Myodes glareolus*) females will lower their own reproductive success and share territories with their offspring when at high population density to maintain offspring survival (Mappes et al. 1995). The adaptive selection hypothesis (Martin 1998, Chalfoun and Schmidt 2012) predicts higher abundance or density in the habitat type with higher or equal reproductive success.

Alternatively, the mismatch hypothesis (Arlt and Pärt 2007, Chalfoun and Schmidt 2012) predicts disproportionate use of a habitat associated with low reproductive success (i.e., "Habitat Selection Mismatch Hypothesis"; Table 1a). Mismatched selection may occur in fast-changing environments or where cues have been decoupled from habitat quality, such as in human-modified landscapes (Weldon and Haddad 2005, Chalfoun and Martin 2007, Chalfoun and Schmidt 2012). Human modification of habitats is particularly important in current times because habitat loss and degradation is driving an increase in species extinction rates (Wilcox and Murphy 1985, Fahrig 2003). Negative population consequences can arise when more individuals choose habitats with low survival and reproductive success (i.e., ecological traps; Robinson et al. 1995, Fahrig 2003, Weldon and Haddad 2005, Martin 2014, Padilla and Rodewald 2015). Hence, understanding the relationship between habitat selection with respect to abundance and reproductive success is critical for proper habitat management.

Understanding the environmental features that influence habitat choice further facilitates management and is especially important for species in decline (Martin 1992a). Environmental features can include nesting or territory availability (Pöysä and Pöysä 2002, Saab et al. 2004), food availability (Smith et al. 2007), vegetative cover from predators (Martin 1992a), and other biotic and abiotic cues (Fretwell 1972, Martin 2001). Under the adaptive selection hypothesis, characteristics associated with preferred nest sites for instance, should convey highest reproductive success. In the case of nest-site mismatch, these nest choices will not convey higher reproductive outcomes (i.e., "Nest Site Selection Mismatch Hypothesis"; Table 1b). Determining if these choices lead to low reproductive success may help managers identify nest-site characteristics important to conserving species in decline.

Lewis's Woodpecker (*Melanerpes lewis*) is declining across North America (Sauer et al. 2014) and evidence for potential mismatch between habitat selection and reproductive success calls for testing the mismatch selection hypothesis (Table 1a). On one hand, abundance estimates for this species are derived from nationwide surveys (Sauer et al. 2014) but may not depict regional or landscape trends (Abele et al. 2004). On the other hand, reproductive success in Lewis's Woodpecker varies across habitat types and study systems but habitat attributes influencing reproductive success remain unclear (Vierling et al. 2013). Lewis's Woodpecker commonly nests in cottonwood floodplain and burned-conifer forests (Bock 1970, Linder 1994, Vierling 1997, Saab and Vierling 2001, Vierling et al. 2009, Zhu et al. 2012, Fylling 2013). Reproductive success may be lower in cottonwood floodplain than burned-conifer forest (Saab and Vierling 2001), despite Lewis's Woodpecker being historically associated with floodplain forests (Bock 1970, Vierling et al. 2013). Conifer forests that burned 10-15 years previously appear to have highest nest success (78-90%; Linder 1994, Saab and Vierling 2001, Gentry and Vierling 2007, Vierling et al. 2009). In contrast, Saab and Vierling (2001) found that cottonwood floodplain forest in Colorado appeared to have relatively low nest success. However, this floodplain study was limited to a highly disturbed forest with intensive grazing practices (Saab and Vierling 2001). If abundance is higher but reproductive success is lower in floodplain forest than burned, the cues used by Lewis's Woodpecker to identify high quality habitat may no longer be strongly linked to habitat quality (Saab and Vierling 2001). Additionally, if floodplain forest yields lower nest success, but is occupied at higher densities, then it may be negatively impacting populations. However, floodplain forest generally has higher primary productivity and associated food resources (Hansen et al. 2009) that may allow production of more young per nest and offset any reduction in nest success. As of 2018, comparisons of Lewis's Woodpecker nest success across cottonwood floodplain and conifer-burned forests with moderate or varying levels of anthropogenic disturbances are lacking. The potential for the mismatch selection hypothesis in Lewis's Woodpecker may contribute to this species decline, and identifying such mismatch is essential to its management.

The influence of nest-site characteristics on Lewis's Woodpecker reproductive success remains unclear particularly due to anthropogenic perturbations in prior studies (Vierling et al. 2013). Lewis's Woodpecker selects nesting in open canopy, with low density of small trees, and high density of large decaying trees near forest edges (Bock 1970, Linder 1994, Vierling 1997, Saab and Vierling 2001, Vierling et al. 2009, Zhu et al. 2012, Fylling 2013, Vierling et al. 2013). Mature stands in cottonwood floodplains provide edge habitat and open canopy important for foraging of flying insects (Bock 1970, Linder 1994, Vierling 1997, Saab and Vierling 2001, Vierling et al. 2009, Zhu et al. 2012, Fylling 2013). Both floodplain and burned forests offer high insect diversity and shrubs important for Lewis's Woodpecker foraging of fruits and insects (Saab and Vierling 2001, Vierling et al. 2013). However, anthropogenic disturbances can negatively impact foraging or nesting availability and negatively influence reproductive success (Vierling et al. 2013). Floodplain forest has been heavily impacted by urbanization, agriculture, logging, and river channelization (National Research Council 2002). Human impacts in the floodplain forest may be detrimental to Lewis's Woodpecker nest-site selection due to lower tree recruitment and lower availability of large-diameter snags for nesting (Vierling et al. 2013). In burned forests, Lewis's Woodpeckers select predominantly nests at low-elevation, high density of large mature snags, and prefer stands burned 4-17 years since fire (Abele et al. 2004, Gentry and Vierling 2007, Saab et al. 2009). Fire suppression and logging activities in burned forests may also reduce snag availability for nesting (Abele et al. 2004, Saab et al. 2009). Yet, comparisons across burned forests can be difficult due to differences in fire intensity, age since fire, elevation, and forest structure before fire (Saab et al. 2004, Saab et al. 2009). Anthropogenic disturbances in floodplain and burned forests may impact nest-site characteristics available to Lewis's Woodpecker (Saab and Vierling 2001, Abele et al. 2004, Saab et al. 2004, Saab et al. 2009, Vierling et al. 2013). Thus, Lewis's Woodpeckers may select for habitat characteristics that may equal or lower their reproductive success ("Nest-site Selection Mismatch Hypothesis"; Table 1b). This nest-site selection mismatch may contribute to overall population declines in either floodplain or burned forests, but careful comparisons of abundance and nest success among each habitat type are lacking due to the diversity of forest structures, ages, and human disturbances on the landscape.

Food availability may influence Lewis's Woodpecker habitat selection (i.e., "Food Availability Hypothesis"; Table 1c). Lewis's Woodpeckers primarily forage on flying insects during the nesting period (Bock 1970, Vierling et al. 2013). Phenological shifts in food availability rather than food abundance *per se,* could also contribute to a mismatch between habitat selection and reproductive success. Lewis's Woodpecker may attempt to time their nesting to match the peak of insect abundance when feeding their young (Bock 1970, Saab and Vierling 2001, Zhu et al. 2012). Furthermore, attrition and clutch size covary with food availability (Martin 1987). Lewis's Woodpecker may lay smaller clutch sizes in response to lower insect availability at the onset of the nesting season, thus we would expect to find smaller clutch sizes in the habitat type that has lower insect availability at the onset of the nesting season (i.e., "Clutch Size Hypothesis; Table 1d). Alternatively, if insect availability decreases throughout the season, Lewis's may experience greater loss (i.e., attrition) of young from starvation, and we would predict greater loss of young in the habitat type with great declines in insect availability (i.e., "Attrition Hypothesis"; Table 1e). Therefore, if either absolute levels or phenological impacts on insect availability were a limiting factor to nest success, we would expect high attrition and small clutch sizes with low insect availability.

Investigating abundance in relation to nest success and habitat characteristics selected for nesting (i.e., vegetation characteristics, food availability and timing of food resources) is therefore needed to understanding habitat features important to Lewis's Woodpecker. This study will provide detailed biological information on Lewis's Woodpecker nesting biology relevant to future management concerns in the face of declining populations. Additionally, calculating relative adult densities in each habitat will allow us to scale habitat selection differences between floodplain and burned forest. For instance, we will consider whether the density of trees and snags suitable (>23cm in diameter; Saab and Vierling 2001) to Lewis's Woodpeckers for nesting differs between floodplain and burned forest to correlate variation in Lewis's densities with snag densites (i.e., "Nesting Availability Hypothesis"; Table 1f). Lewis's choose larger diameter trees to locate their nest sites but may select against small diameter trees (Saab and Vierling

2001, Zhu et al. 2012). Therefore the availability of snag and tree densities across habitat types may explain why Lewis's are more abundant in one habitat type than others, despite limited influence of nest-site selection on nest success.

The Bitterroot Valley holds the highest density of known breeding Lewis's Woodpeckers in the state of Montana (eBird 2012, MASCR 2016). This valley has long provided local economic opportunities through farming and logging. However, the valley now faces residential development pressure, particularly in the valley bottoms. The ubiquitous nature of Lewis's Woodpecker nesting habitat in the Bitterroot Valley offers an exemplary study system to identify drivers of reproductive success across two commonly used habitat types at low to moderate risk of human perturbations.

We tested multiple hypotheses on the relationship and mechanisms between Lewis's Woodpecker density, nest success, and nest-site characteristics in floodplain versus burned forest. First, we tested for the habitat selection mismatch hypothesis (Table 1a). Finding further evidence for mismatch selection would highlight the importance into further research on adult survival rates and productivity to calculate whether mismatch selection is causing negative population growth (i.e. ecological trap) and participates in this species broad population declines. Furthermore, we investigated the nest-site selection mismatch hypothesis (Table 1b) to identify the mechanisms influencing nest success variation in both floodplain and burned forest. We tested whether food availability was an important habitat characteristic that explained differences in Lewis's density across forest types (Table 1c), and if it influenced variation in clutch size (Table 1d) or attrition (Table 1e). Prior studies assumed food availability was important for the timing and success in Lewis's Woodpecker nesting, yet these hypotheses remained untested (Bock 1970, Saab and Vierling 2001, Zhu et al. 2012, Vierling et al. 2013). Finally, we considered the nesting availability hypothesis (Table 1f). We measured the density of suitable nest trees between habitats, as a measure for nesting availability, to explain differences in Lewis's density across floodplain and burned forest. Our results suggest that mismatch selection may be general across this species of concern's breeding range, and point to implications for future research and management directives.

STUDY AREA

This study took place in the Bitterroot Valley (1000-2600 m in elevation) in southwestern Montana, USA (Figure 1) from 2015 to 2017. The valley runs approximately 160 km (95 miles) south to north along the Bitterroot River from the border of Idaho to the city of Missoula. The valley has experienced an increasing human population that radiates from the city of Missoula. Human population growth has caused significant loss of floodplain forest and reduction of low-severity forest fires (Hartwell et al. 2000, Theobald and Romme 2007). Despite a history of fire suppression on National Forest surrounding the Bitterroot Valley, fires of varying scales and severities occur annually, resulting in a patchwork of burned forests of various ages covering thousands of acres.

We compared the nesting habits of Lewis's Woodpecker in burned forests and in floodplain forests. The floodplain forest along the Bitterroot River is characterized by valley bottom or lower montane riparian woodlands and shrublands dominated by Black Cottonwood *(Populus balsamifera ssp. trichocarpa)*. The burned forest is considered as Rocky Mountain Ponderosa Pine (*Pinus ponderosa*) woodland and savanna (MF Guide 2016) in secondary regeneration stage since fire. This habitat is dominated by Ponderosa Pine and often occurs in warm, dry and exposed foothills mixed with grassland or shrubland openings, dominated by a graminoid understory. Burned sites also have regenerating riparian areas at the base of many foothills. Shrub species in these riparian areas included alder (*Alnus spp*.), red-osier dogwood (*Cornus stolonifera*), bunchberry (*Cornus canadensis*), willows (*Salix spp.*), thimbleberry (*Rubus parviflorum*), etc.

Aspect and slope vary greatly in burned forest compared to the flat floodplain forest. The Sapphire Mountains on the east side or the valley consists of low rolling mountains, while the Bitterroot Mountains to the west consists of steep terrain. Floodplain forests are relatively flat, with their limited topography related to historical changes in river channels and streambank erosion.

Nest-monitoring field sites were chosen to cover a wide spatial extent of the available nesting habitat found in the Bitterroot Valley but to compare similar conditions within each habitat type. All nest-monitoring field sites were separated by a minimum of 5 km (Figure 1). Floodplain sites were selected at least 1 km from any burned forest and occurred within the 100-year Bitterroot River floodplain. All burned sites were located at least 1 km from any floodplain, and were created by the Skalkaho fire of 2000. These burned sites represented forest burned 15-17 years prior to our study, which exceeds the generally known burned forest age preferred by Lewis's Woodpeckers (i.e., 5-18 years since fire; Abele et al. 2004, Saab et al. 2009, Vierling et al. 2013). Most sites that we studied burned at moderate or high severity. In 2015 we monitored 3 floodplain and 2 burned field sites. In 2016 we added two additional field sites in burned forest and one in floodplain forest. In 2017 we added one last floodplain field site, totaling nine field sites across habitat types in the last year of the study.

METHODS

Data Collection

Point counts. —We conducted point counts to investigate potential variation in abundance estimates of Lewis's Woodpeckers across floodplain and burned forests (i.e., mismatch hypothesis; Table 1a). In 2016 and 2017 we conducted point counts across the entire Bitterroot Valley to assess Lewis's Woodpecker adult abundance in floodplain and burned forests. We created two habitat layers for both burned and floodplain forests, and generated an equal number of random points in each habitat using ArcGIS (ESRI, Redlands, CA). We used a floodplain layer (USFS) within 1 km maximum distance from the Bitterroot River high-water mark. We used forest fires from 2000 to 2011 under 2300 m elevation to adequately represent 5-18 years old burned forests (USFS) that Lewis's Woodpeckers select for nesting (Abele et al. 2004). Within each habitat layer we selected 60 random points using a random number generator in ArcGIS (ESRI, Redlands, CA). Furthermore, we divided the floodplain in a northern portion from the towns of Missoula to Hamilton corresponding to an area of higher urban pressure and higher human activity, with a southern portion from Hamilton on south, corresponding to narrower valley bottoms with less anthropogenic disturbance.

We conducted point counts in early July at the middle of the nestling stage yet before peak fledging, corresponding with optimum adult activity feeding young (Vierling et al. 2013) to maximize detectability of adults. All point counts lasted 10 min. We recorded visual and auditory cues to confirm detection, and recorded time and distance to evaluate two types of detection probabilities: availability and perceptibility. Using time-removal methods, we set equal availability probability among our habitat types to represent the average detection probabilities linked to small scale (e.g., foraging) movements adult make during our counts, or whether Lewis's were available to be detected due to temporary emigration. Perceptibility probability was defined for each habitat type as the detection probability assessing count biases from our distance measurements (i.e., how likely are we to detect Lewis's Woodpeckers when present during our counts). We estimated distance using two types of rangefinders (Nikon ProStaff Rangefinder, and Bushnell The Truth Rangefinder). We limited visual detections to 500 m from point counts. We kept track of all woodpecker locations and movement to minimize the likelihood of double counting. Differentiating between adults and juveniles at a distance was difficult. Therefore, after July 10, when some nests in the floodplains had already fledged young; we decided to truncate floodplain observations of Lewis's of unknown age.

Nest searching and monitoring. —We monitored nests to investigate variation in nest success leading to the mismatch hypothesis (Table 1a) and factors influencing potential variation in success. Monitoring nests until each fledged young or failed, also provided information about clutch size variation for the clutch size hypothesis (Table 1d), and to monitor productivity and loss of young for the attrition hypothesis (Table 1e). We studied the nesting habits of Lewis's Woodpecker from 2015 to 2017 at multiple field sites in both floodplain and burned habitat types. We monitored core-breeding activity from May 1-15, when Lewis's Woodpeckers were arriving from spring migration, looking for mates, and establishing territories. We ended monitoring in August, once all known nesting activities were complete.

We searched for nests using behavioral and visual cues (e.g., calls, copulation events, adult going to cavity, etc.), and monitored cavities used in past years by Lewis's Woodpeckers. We monitored all nests two to three times per week for the entire nesting season until we determined the fate of each nest (i.e., failed or successful) using protocols adapted from Martin et al. (1997). We considered nests successful if they fledged at least one young from the nest (binary outcome: 0 or 1). For nests that we were able to access, we also recorded clutch size, brood size, and number of fledglings to assess attrition (i.e., percent of young lost in each nest between the number of eggs layed and the number of nestlings that fledge) and nest productivity. We used wifi-equipped miniature cameras with LED lights mounted to a telescopic fiberglass pole to observe nest contents, determine nesting stage, and count number of young (RTC Rick Wi-Fi Rigid Inspection Camera IOS/Android Compatible www.techtoolsupply.com; and IBWO's Wireless Inspection Camera www.ibwo.org).

We considered a nest active once it laid an egg or was found at a later nesting stage during incubation or nestling period. Additionally, we documented nesting activity at a subset of nests using video cameras (Sony HandyCam). Video cameras were set-up near the nest tree for 6-hr minimum per day to assess whether nests with unknown activity levels were active. These videos allowed us to determine whether nests too high to reach with our telescopic poles and peeper cameras were actually in incubation or nestling stage (e.g., adults bringing food to the nest corresponded to nestling stage).

Nest characteristics.— We collected data on nest tree and cavity features associated with each nest to assess factors influencing nest success. These nest-related covariates included nest height (m), nest orientation (degrees), nest tree species, tree health (live, partially dead, or dead), cavity code (newly excavated, expanded, old, or natural cavity), and cavity depth (cm).

Vegetation and habitat covariates. —We measured habitat characteristics to explore factors influencing nest-site selection (Table 1b) and nest success variation within each habitat type. After the breeding season in 2016 and 2017, we collected vegetation measurements by combining and modifying two schemes based on passerine nesting and woodpecker vegetation collection methods (Li and Martin 1991, Martin et al. 1997).

We used each nest tree as the center of an 11.3 m plot to collect various vegetative and habitat characteristics (Table 3). All “nest” plots were paired with two additional plots to measure available habitat characteristics not used for nesting. Random plots consisted in a close (20-120 m away), and far plot (120-250 m away) from the nest tree. These plots represented available nesting or foraging substrate at random distances, but systematic direction, from the nest. We selected a close plot because the nature of the floodplain and open nature of burned forests did not always provide available habitat beyond 120m. Far plots at 120-250m were originally chosen to represent daily foraging distances seen by Lewis’s to and from their nests (WMB observations). We generated a list of random distances in Excel. The “close plots” were chosen systematically down stream and parallel to the river or bottom of draw from the nest tree. The “far plots” were systematically located directly away from the river or bottom draw and perpendicularly away from the nest (Figure 2). We prioritized finding the closest dead or partially dead tree suitable to Lewis’s nesting (dbh >23 cm; Saab and Vierling 2001), containing at least one cavity with an entrance of at least >4 cm in diameter to establish the center of each random plot. However, if we did not find a suitable nest tree within 15 m of the designated Global Positioning System [GPS] location, we recorded all other vegetation measurements without nest-tree specific information and used this vegetation data in our analysis for available foraging habitat.

We measured variables known or thought to influence Lewis's Woodpecker nest-site selection from past studies and field observations. Within the 11.3 m vegetation plots, we recorded elevation (m), aspect (0-360 degrees), slope (%), average canopy cover (%), dominant canopy species, maximum and average shrub heights (m), branch touching nest tree (yes or no), nest tree height estimation (m), average canopy height (m), nest tree dbh (cm), nest tree species, heart rot (present or absent), nest tree burned class (unburned, trunk charred, branches lightly scorched, heavy scorch but alive, or totally burned or dead), nest tree condition (dead or alive), and live tree count per tree species and per diameter category (i.e., small = 8-23 cm, medium = 23-38 cm, large = 38-50 cm, and extra-large =>50 cm at dbh). We used these same live tree categories to count snags. Finally, we measured shrub cover class within the immediate 5 m from a used or available nest tree. All shrubs were identified to closest genus or species, and cover classes were categorized (1 = 0-1%, 2 = 2-5%, 3 = 6-25%, 4 = 26-50%, 5 = 51-75%, 6 = 76-95%, 7 = 96-100%).

Insect abundance. —We measured insect availability as part of our nest-site selection analyses (Table 1b), to ask whether Lewis's Woodpecker variation in density across habitat types correlated with food availability (Table 1c), and to assess the influence of insect availability on attrition and clutch size (Table 1d and 1e). We sampled aerial insects to assess temporal and geographical variation in arthropod communities within each habitat type because Lewis's Woodpecker primarily forage on aerial insects during the breeding season (Bock 1970, Vierling et al. 2013). We collected aerial insects at all field sites once in 2016, and 3 times in 2017. These sampling events corresponded to the relative peaks in incubation, nestling, and fledging periods. We made 3 250-m transects on all 9 field sites. Because many aerial insects are aquatic dependent for at least one developmental stage (i.e., egg, pupa, larva or adult), we used a sampling design that accounted for the distance from the nearest stream or drainage bottom. All bottom draws at burned sites were narrow and contained a small creek bed except for one site: Sula Peak Ranch. We determined the location of all three transects at each field site by systematically dividing the study areas in thirds. To place the first trap, we located the bottom of the draw in burned forest, or the edge to the Bitterroot River in floodplain forest. Each transect contained four insect sticky traps (Arbico Organics, Oro Valley, Arizona, USA) placed at increasing distance from the stream or bottom draw (Figure 3). The first sticky trap was placed above the stream or bottom draw. Then we walked directly away from the stream or draw and placed the second, third, and fourth traps, at 25 m, 100 m, and 250 m respectively away from the first sticky trap. We set-up all sticky traps 3-5 m high in the canopy (Figure 4) to dissociate from the forest boundary layer known to affect ground versus aerial insect communities (Kaimal and Finnigan 1994), and to represent the open canopy mimicking as best as possible the foraging habitat of Lewis's Woodpeckers.

We did not set up sticky traps if the weather forecast for the upcoming 72 hrs predicted more than a 50% chance of precipitation with more than 1 inch of total rain accumulation to maximize trap efficiency and reduce weather biases (i.e., colder weather and high wind days; Whitaker et al. 2000). We used sticky traps that had a blue side and yellow side because color of traps may attract different types of insects and choosing one single color may bias results. We left traps out at all sites for 3 days and counted and identified insects to taxonomic Order. Based on personal observations and prior research (Bock 1970), we assumed that foraging woodpeckers did not depend on extremely small insects such as *Culicoides* midges (<2 mm). Hence, we did not count trapped insects smaller than 2mm in length. All other insects were grouped by Order and counted.

Data Analysis

All analyses were conducted in RStudio (RStudio Team 2015) using the most current version update to R (R-3.3.3) core software (R Core Team 2017).

Population density. —We assessed population density from our abundance estimates to address our hypothesis about adaptive or mismatch habitat selection (Table 1a). We used our point count data to assess population densities in burned and floodplain forests. Perceptibility differences from distance biases may vary significantly across two habitat types due to differences in topography, forest structure, canopy enclosure, and bird behavior (Amundson et al. 2014, Kéry and Royle 2015). Hence, we used a hierarchical distance-sampling and time-removal N-mixture model in a Bayesian framework (Kellner 2017) to detect relative abundance in each habitat accounting for availability and perceptibility detection biases using time-removal and distance methods (Amundson et al. 2014, Kéry and Royle 2015). We integrated point count data into a multistate (i.e., four level) model and used Markov Chain Monte Carlo (MCMC) simulations to estimate northern floodplain abundance, southern floodplain abundance, burned forest abundance, and habitat associated perceptibility and availability probabilities. We set detection probability for availability, from the time-removal equations, as equal between habitats. We allowed detection probability for perceptibility to vary between habitats.

Nesting phenology. —We monitored the timing of important nesting stages to include nest phenology in our nest success calculations. We used hatch date for assessing variation in the timing of nest initiation. Choosing hatch date as the reference point in the nesting of Lewis's Woodpecker was biologically relevant because it marked the transition between incubation and nestling stages when adult activity and food requirements increase dramatically. We also had more accurate estimates for hatch date than laying or fledgling dates. All hatch dates were compared across years.

Nest success. —We calculated nest success and factors influencing nest success to test the mismatch habitat selection hypothesis (Table 1a) and to investigate causes for such variation. We used Shaffer's (2004) logistic exposure method to calculate daily nest survival rates (DSR). First, we analyzed nest success in one general model for both habitat types to compare the effects of year, field site (i.e., study plot), habitat, and date at hatching (DOY hatch date). We also used this approach between incubation stage (i.e., egg DSR) and nestling stage (i.e., nestling DSR), because survival estimates can vary with nesting phenology. Secondly, we investigated the influence of habitat characteristics on nest success (Table 1b) in two separate analyses for each habitat type, to assess the influence of nest-site characteristics on the variation in Lewis's nest success.

For each of these analyses, we explored possible interactions between categorical and continuous covariates measured from the habitat characteristics using prior knowledge and personal observations. We included any significant ($P < 0.05$)

interactions into the full models. The full model represented all hypothesized covariates that may influence nest success. For both the general, and separate habitat analyses, we conducted a “backward” stepwise Akaike’s Information Criterion [AIC] selection on this full model, using the stepAIC function in package “MASS” (Venables and Ripley 2002). We selected the model with the lowest AIC value, as the top model to predict nest success. To determine if site-level insect availability influenced nest success estimates, we calculated the mean number of insect per Order, captured per trap at each field site. We were then able to include these estimates in nest success models and use insect counts per site as a covariate influencing nest success.

Nest-site selection. —We conducted two separate analyses for floodplain and burned forest to identify which factors within each habitat type were associated with choice in nest sites. We also included the mean number of insect counts per site as a covariate to our nest-site selection models. Due to multicollinearity issues (Appendix A), we removed maximum shrub height, canopy height, dbh, and extra-large diameter trees, from the full model in floodplain forest. In burned forest, we found multicollinearity between several covariates (Appendix B), and removed from the full model maximum shrub height, dbh, and total snag counts.

We used a Generalized Linear Model (GLM) approach with a binomial logistic regression link function to model Lewis’s Woodpecker nest site use versus availability. We compared used plots from available vegetation plots in a resource selection function (RSF; Manly et al. 2002). The dependent variable was the “used or available” covariate (binary outcome: 1 or 0). Then, to assess all potential combinations of covariates we built a full model for both floodplain and for burned forest. We again proceeded with variable selection using the stepAIC function (Venables and Ripley 2002). For each habitat type, we chose the model with the lowest AIC value as the top model of nest-site selection. Finally, we compared the number of trees and snags suitable for Lewis's Woodpecker nesting (i.e., tree or snag dbh >23 cm) at both: used nest, and random available plots among floodplain and burned forest to estimate the importance of large diameter trees in Lewis's Woodpecker nest-site selection (Table 1f). We compared tree and snag densities by conducting studentized t-tests between habitats to assess if tree and snag density was associated with nest-site selection across habitat type.

Nest success versus nest-site selection. —To determine whether factors associated with nest-site selection influenced nest success (Table 1b) we combined the variables in both top models for nest-site selection in floodplain and burned forest and analyzed nest success with this combination of covariates.

Attrition and clutch size. —To assess nestling attrition in relation to insect availability (Table 1e) we calculated attrition as the percentage of nestlings that survived by dividing the number of fledged young per successful nest (i.e., nests that fledged at least one young) by the number of eggs initially laid in that nest. We assumed attrition to be normally distributed across our study area. We conducted a studentized t-test between floodplain and burned forest to evaluate the difference in attrition between habitat types. We also analyzed whether clutch size varied with timing of nesting as a function of insect availability (Table 1d) in a separate GLM analysis. We ran one model with clutch size as the dependent variable by using covariates previously shown to affect nest success.

Insect availability. —We assessed the influence of insect availability on nest-site selection (Table 1b), on Lewis's Woodpecker differences across habitats (Table 1c), to measure food influence on clutch size and attrition (Table 1d-e), and to investigate causes for variation in insect availability between sites. We calculated mean number of insects caught per trap at each field site and included this estimate in our nest-site selection analyses. Secondly, we conducted a separate GLM analysis to investigate which factors influence insect availability between floodplain and burned forest. We used the following covariates: insect Order, sampling date, distance from water (i.e., categories: 1-4), habitat type, and site. We also included any interaction between covariates that was significant.

RESULTS

Abundance Estimates

Mean abundance was highest in the southern floodplain, and 2.5 to 5.5 times greater in floodplain compared with burned forest (Figure 5). Availability probability (i.e., Lewis's availability to be counted during our counts) across our entire study area was 71.8 ± 7.2%. Perceptibility probability (i.e., detection probability for Lewis's present within our counts) was significantly different between floodplain and burned habitat types. Not surprisingly, perceptibility was highest (41.0 ± 6.5%) in burned forest where visibility is often better due to more open vegetation, whereas both southern and northern floodplain forests had lower associated perceptibilities (19.3 ± 2.6%; 15.7 ± 1.5%, respectively) (Figure 6).

Nest Success Across Habitat Type

We monitored a total of 150 nests in floodplain, and 108 in burned forest over the course of three seasons (Table 2) and were able to determine the fate of 217 nests. In floodplain forest, predation accounted for 17 of 33 nest failures, with an additional 8 unknowns that were likely predation, versus 11 of 16 failures and 4 unknowns in the burned. Mean hatch date differed between habitat types (t = -3.876, *P* < 0.001). With a mean hatch date of June 18th (SD = 7.4 days) in floodplain forest, versus June 22 (SD = 6.0 days) in burned forest. These hatch dates reflect an earlier start in floodplain forest, with the earliest nest initiated on May 31, versus June 10 in burned forest.

The best-supported model for nest success included habitat type, hatch date and nesting stage (Table 4; Figure 7). Floodplain forest had lower (*P* = 0.013) overall nest success (i.e., 73.3%, CI = 68.3-77.6%) than burned forest (86.2%, CI = 81.6-89.7%). Nest success declined later in the summer in both habitat types (Table 4; Figure 7); nest success in the nestling stage (floodplain: 79.0%, CI = 74.9-82.5%, vs. burned: 91.6%, CI = 88.5-93.7%) was consistently higher (β = 0.061; *P* < 0.001) than in the incubation stage (floodplain: 65.7%, CI = 60.6-70.3%, vs. burned: 85.5%, CI = 81.6-88.6%).

Habitat Influences on Nest Success

In floodplain forest, the top model for nest success included: heart rot, dead or alive nest tree, nest entrance orientation, hatch day, nest height, canopy cover, and heart rot*nest height interaction (Table 5a). However, only hatch day (negative influence on nest success with increasing hatch date) and the interaction of heart rot with nest height were significant (Table 5a). This interaction indicated that in the absence of heart rot (i.e., tree fungal disease), nest height did not influence nest success, but when heart rot was present nest success declined with increasing nest height (Figure 8). Our data suggests that most nests that failed in trees with heart rot were depredated.

In burned forest, all nests but 4 were found in trees with the highest burn class (4 = totally burned), so we were not able to include burn class as a covariate. Our top model included a significant influence of average shrub height and a marginal effect of nest height (Table 5b). The next two models were within 2 ΔAIC and included the addition of branches touching the nest tree and elevation (Table 5b), but the addition of these covariates had no significant effect on nest success.

Insect Availability

Overall insect counts did not differ between habitats (t = -0.094, *P* = 0.925). However, Diptera (i.e., flies: t = 2.464, *P* = 0.014), Ephemeroptera (i.e., mayflies: t = 2.789, *P* = 0.008), and Thrichoptera (i.e., caddisflies: t = 2.880, *P* = 0.008) were more abundant, and Coleoptera (i.e., beetles: t = -2.278, *P* = 0.025) were less abundant in floodplain than in burned habitat (Figure 9).

The top model predicting insect availability included: site, julian date, distance from water, Order of insect, and two interactions. The interaction of distance*site reflected a consistent effect of distance*habitat among sites. This interaction showed that burned sites had significantly more insects than floodplain sites at the stream edge (Figure 10a). However, insects decreased with increasing distance from water in the burned forest, while staying relatively stable in the floodplain forest such that insect abundance was greater in floodplain than burned with increasing distance from water (Table 6a).

The interaction of date*site again reflected a consistent effect of date*habitat whereby field sites in floodplain forest showed a significant increase in insects over the summer and a decreased over the summer in burned sites (Figure 10b). By August 1st floodplain sites had significantly higher insect availability than burned sites (Table 6b).

Attrition Levels And Clutch Size

Despite differences in insect abundance between habitats (Figure 9), clutch size did not differ between habitats (t = 1.539, $P = 0.128$). Clutch size did not follow temporal patterns of insect availability in each habitat and instead decreased over the season in both habitat types ($\beta = -0.092$, SE = 0.013, $P < 0.001$). We found 10% higher (t = -2.240, $P = 0.028$) attrition in floodplain forest than in burned forest.

Nest-Site Selection

Lewis's Woodpeckers in floodplain forest primarily chose nest sites that differed from available sites in nest tree height, reduced canopy cover, and marginally for extra-large snags, and large trees (Table 7a). In burned forest our top model (AIC= 123.30) indicated Lewis's Woodpecker preferred to nest in taller trees, avoided smaller snags, and marginally preferred medium snags (Table 7b). Extra-large snags in the next model (AIC=124.09), elevation in the third model (AIC=124.67), or average shrub height included in the fourth model (AIC=124.90), were not significant additions in burned forest.

Lewis's Woodpecker nest trees differed between floodplain and burned forest (t = 2.475, $P = 0.015$). Lewis's chose on average, extra-large cottonwood trees averaging 73.0 ± 19.1 cm in diam (CI = 36-145 cm) in floodplain forest, versus dbh of 66.2 ± 17.2 cm in ponderosa snags in burned (CI = 36-102 cm).

Habitat Differences

Tree and snag density of dbh >23cm suitable to Lewis's Woodpecker differed ($P < 0.001$) between floodplain (132 ± 100 stems/hectare) and burned (60 ± 43 stems/hectare) forests (Figure 11).

DISCUSSION

Adaptive habitat selection theory predicts greater or equal density in the habitat that provides higher fitness compared to other available habitats (Fretwell 1972). However, many recent studies have found evidence for mismatched habitat selection, in which a species found at higher density in one habitat has lower reproductive success than in other habitats it occupies (reviewed in Chalfoun and Schmidt 2012). This pattern was also observed in Lewis's Woodpecker in cottonwood floodplain forest in Colorado compared to burned forest in Idaho (Saab and Vierling 2001), where nest success was lower in floodplain forest than burned forest. Yet, the lack of precise abundance estimates have so far limited a clear testing of the habitat selection mismatch hypothesis for Lewis's Woodpeckers (Table 1a), and there has not been additional testing of this pattern in other parts of this species range. Hence, the influence of habitat selection on Lewis's Woodpecker reproductive success remains unknown, limiting applicable management recommendations.

We found 2.5 to 5 times higher Lewis's Woodpecker densities in floodplain forest than burned forest, but lower nest success in cottonwood floodplain forest than in burned conifer forest, supporting the mismatch selection hypothesis (Table 1a). Anthropogenic pressure may explain density differences between the southern portion and the northern portions of our study. In the northern floodplains human density and urbanization is much higher than in the southern part. Increased residential development encroaches on floodplain forest and there is higher control of river flow regimes that disrupts cyclical flooding of valley bottoms and limits recruitment of cottonwoods. The lower nest success found in floodplain than in burned forest may reflect anthropogenic disturbances in these habitats as well. Floodplain systems are commonly subjected to grazing, as was our system, and to the conversion of adjacent habitats to agriculture or pasture systems (National Research Council 2002, Tockner and Stanford 2002). Differences in reproductive success among floodplain forest may reflect different grazing and farming pressures (Abele et al. 2004). A prior study in cottonwood floodplain forest included more intensive agricultural systems (i.e., heavy grazing and pesticide use, Saab and Vierling 2001) than at our site. Reproductive success was substantially lower in this heavily perturbed floodplain system (46%, Saab and Vierling 2001) than in our Bitterroot floodplains (73%). Presumably, nest success is even higher in pristine floodplain forest, although studies of demography in such conditions are needed. Given that pristine floodplain systems would have been the standard conditions over evolutionary time, then high reproductive success in such conditions would make their preference evolutionarily adaptive. Habitat cues that were adaptive over evolutionary time can cause high densities and low reproductive success when these cues are embedded in anthropogenically disturbed habitat in current time (Martin 1992b). Such effects could explain the higher densities of Lewis’s Woodpecker on floodplain forest despite low nest success, although studies across floodplain forests with differing levels of anthropogenic disturbance are needed to understand their impacts on nest success of Lewis's Woodpeckers.

Understanding the habitat cues that influence habitat preference and nest success are needed (i.e., nest-site selection hypothesis; Table 1b). In both habitat types, Lewis’s Woodpeckers chose tall nest trees, open habitat (i.e., selection against dense canopy cover or small snags), and an added presence of larger trees and snags near the nest sites (also Vierling et al. 2013). In both habitats, Lewis’s Woodpecker nested in trees or snags

>55 cm in dbh 75% of the time. We found Lewis's Woodpecker to nest in larger trees and snags in floodplain than in burned forests, which correlates with the increased availability of extra-large diameter stems in floodplain forest. This increased density of habitat cues (i.e., large snags and trees) can explain why Lewis's Woodpeckers are more abundant in floodplain forest (Table 1f).

Nest success may benefit indirectly from greater tree and snag density, due to increased cover and choice of optimal cavities for nesting. Wider cottonwood corridors along the floodplains of the Bitterroot River, compared to fragmented and degraded floodplain forest in intensive farmland landscapes (e.g., Saab and Vierling 2001), may provide enhanced nesting availability and protection from predators. Predation was the leading cause for nest failure in both floodplain and burned forest, similar to prior studies (Vierling et al. 2013). We found limited evidence to suggest that nest-site selection in both floodplain and burned forest influenced nest success. In our system, predation occurred during the transition period from incubation to hatching of eggs (WMB personal obs.). Nest success was lower earlier in the nesting stage (i.e., incubation vs. nestling stage; Figure 7), compared to prior studies (Saab and Vierling 2001, Zhu et al. 2012). Early nest failure may have allowed time for Lewis's Woodpeckers to initiate a second nest but we found minimal evidence of renesting (9 of 217 nests) similar to other studies (Saab and Vierling, 2001, Newlon and Saab 2011, Zhu et al. 2012).

Across our study system, temporal patterns in insect availability more closely matched offspring demand in floodplain than in burned forest. Insect availability during Lewis's Woodpecker nestling and fledgling periods peaked in late summer and were greater in floodplain than burned habitat (Figure 10b). Insect availability abundance also did not explain differences in Lewis’s Woodpecker densities (Table 1c), clutch size (Table 1d), or attrition (Table 1e). First, woodpecker abundances result from habitat selection after returning from migration, which occurs in May when insects were more abundant in burned than floodplain (Figure 10b) and opposite to woodpecker densities. Second, clutch size did not differ between habitats despite large differences in insect abundance between habitats at the beginning of nesting. Finally, the increased insect abundance in floodplain forest during the nestling period might predict reduced attrition of young, but attrition was higher in floodplain forest. Thus, food abundance did not seem to explain habitat selection or reproductive success.

Several environmental stresses may influence the differences in nest success between our two habitats. Nest competition with other secondary cavity-nesters may prevent Lewis’s Woodpeckers from selecting optimal cavities in floodplain forest (Zhu et al. 2012). For instance, European Starling (*Sturnus vulgaris*) is an invasive species from Europe and is found ubiquitously throughout the floodplain forest, but rarely in burned forest (WMB and KRS obs.). Starlings are fierce secondary cavity-nest-competitors, and are known to compete with Lewis’s Woodpeckers (Vierling 1997), and other woodpeckers (Ingold 1994). Starlings can initiate nesting several weeks prior to Lewis’s Woodpeckers arrival to the breeding grounds (Ingold 1994). Hence, burned forest may allow Lewis’s Woodpeckers to colonize areas of low density with minimal competition.

Lewis's Woodpeckers have shown regional-wide, and long-term declines in their population sizes (Sauer et al. 2014), causing them to be designated a species of national management concern in the U.S. (Abele et al. 2004), and Canada (Zhu et al. 2012). The greater abundance in floodplain forest with lower reproductive success may contribute to this population problem. Yet, the extent to which the preference for floodplain forest contributes to the population problem depends on general rates of reproductive success in floodplain forest. Our estimates of nest success in floodplain (73.0%) were not as low as found in other floodplain (i.e., 46.0%; Saab and Vierling 2001) and other habitat types (Zhu et al. 2012). This difference can yield critical differences in population trends. Lewis's Woodpecker produced an average 2.19 ± 1.67 fledglings (n = 67) per successful nest in our floodplain forest. Fledgling and adult survival have not been estimated for Lewis's Woodpecker. However, fledgling survival of a congener (*M. carolinus*) for the first 3 weeks after fledging was found to be 0.92 (Cox and Kesler 2012), which is typical of species with long nestling periods (Martin 2014, Martin et al. 2018). Adult survival was estimated for two congeneric species: Red-bellied Woodpecker (*M. carolinus*), and Red-headed Woodpecker (*M. erythrocephalus*) at 0.62 and 0.68 (Ingold 1989, Karr et al. 1990). If we assume that Lewis's has a similar adult survival rate as its congeners, or an average of 0.65, and juvenile survival is 2/3 of adult survival given high fledgling survival, then nest success of 0.73, and production of 2.19 fledglings per successful nest could yield a stable or slightly increasing population ($\lambda = 1.00$, calculated as: adult survival + nest success*fledgling productivity). On the other hand, the nest success of 0.46 found by Saab and Vierling (2001) would lead to a declining population given the same assumptions ($\lambda = 0.82$). Also, while populations in Montana may be currently stable, our estimates of nest success suggest that they are on the edge of turning negative ($\lambda = 1.00$) if nest success declines any further in this floodplain forest. Thus, anthropogenic disturbance of preferred floodplain forests may contribute substantially to population declines of this species.

MANAGEMENT IMPLICATIONS

Our research suggests Lewis's Woodpecker density is higher in floodplain forest despite anthropogenic pressures associated with this habitat. Provided that cottonwood floodplain forests are in global threat and anthropogenic activities are increasing in this system, we advocate for fencing cottonwood patches. Fencing especially in areas of high grazing practices with heavy damage to young cottonwoods, or in areas where there is low seedling survival and recruitment, will enhance cottonwood stand persistence. To this date, no or limited urban laws restrict development in floodplain or riparian buffer zones, hence residential development is increasing in floodplain forest.

Our results suggest burned forests provided limited snag availability to nesting Lewis's Woodpeckers despite higher reproductive success and no apparent difference in insect availability. Burned-forest monitored for Lewis's Woodpecker nest success in our study was 15-17 years-of-age since fire. Most studies point out that Lewis's Woodpeckers prefer burned forests 4-11 years since fire. Our results suggest that moderate intensity fires remain important to Lewis's Woodpecker nesting beyond this 4-11 years since fire (Abele et al. 2004, Saab et al. 2009). In addition, the importance of snag retention to Lewis's Woodpecker nest-site selection is known to increase with burned age (Saab et al. 2009). Post-fire logging had limited effect on Lewis's Woodpecker nest-site selection in burned forest at 1-4 years since fire, but salvage logging negatively impacted Lewis's Woodpeckers in older burns from 4-11 years since fire (Saab et al. 2009). Hence, burned forests of older age (in our study: 15-17 years since fire) may be more important than previously documented, and delineate importance of implementing salvage logging recommendations. The ubiquity of salvage logging throughout the Bitterroot National Forest and private lands, and the increased age of post-fire habitat monitored in our study may explain the lack for Lewis's Woodpecker nest availability in our study area.

Ultimately, human perturbation to the landscape infringes on natural habitat important to woodpecker foraging and nesting. In both floodplain and burned forests, the importance of large diameter trees and snags is multifold for this species and communities of cavity nesters and excavators. To this date, we found no forestry guidelines implementing snag retentions for the nesting of Lewis's Woodpeckers. Most recommendations focus on the year immediately after a fire to control for erosion, benefit highest economical revenue from logging 'green trees' and in rare instance to preserve nesting habitat of the Black-backed Woodpecker (*Picoides arcticus*). Several local initiatives do however exist within The Department for Natural Resources, which commonly retains one or two large-diameter trees per acres of logging and can implement stricter thinning projects (e.g., DNRC Huntley Butter Timber Sale 2018). However, we found no statewide agency guidelines for increasing woodpecker habitat in timber sales or salvage programs. Yet wildlife habitat remains of lowest priority for timber sales on public land. The logging industry generally associates wild fires with a loss in economic value on the stands of timber. Public land snag retention programs, especially for large diameter snags at low elevation ideal to Lewis's Woodpecker nesting, do not exist and timber sales for salvage logging of burned forest provide a delicate balance between public opinion, local financial revenue and wildlife habitat.

We recommend managing post-fire burned forests and floodplain corridors to enhance retention of large trees and snags (i.e., dbh >55 cm) to enhance Lewis's

Woodpecker nest availability for long-term population persistence (>15-18 years). Retention of large-diameter snags does not inhibit all options for salvage-logging operations. Salvage logging of large-diameter snags in the first year after fire can exert an additive effect on snag limitation for Lewis's Woodpeckers (Saab et al 2009) and most cavity nesters (Hutto and Gallo 2006). Salvage logging however, especially in dense forest patches can increase openness of habitat and may be beneficial in the first 1-4 years since fire to Lewis's Woodpeckers if large-diameter snags are preserved (Abele et al. 2004, Saab et al. 2009).

However, the occurrence of fire on the landscape more than post-fire management is important to many species including Lewis's Woodpeckers (Hutto and Gallo 2006). Fire suppression or managing for no fire, likely would have negative consequences for Lewis's Woodpeckers since floodplain forest is at higher risk of anthropogenic disturbances and conducive to lower reproductive success of Lewis's Woodpeckers than in burned forest. Additionally, the amount of acres of potential Lewis's Woodpecker habitat in burned forest far exceeds the extent of floodplain habitat across the species range. Management of national forests to include wildfires as a recurrent natural disturbance on the landscape is likely to impact Lewis's Woodpecker nesting availability and future population projections far more than the acts of individual private landowners along the floodplain forest. Managing for wildfires is crucial to Lewis's Woodpecker persistence on the landscape if mismatch habitat selection is a general pattern across the species range.

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TABLES

Table 1. Summary table for our main study hypotheses comparing density, nest success and nest-site characteristics in Lewis's Woodpecker in floodplain versus burned forest.

	Hypothesis	**Study Predictions**
a)	Habitat Selection Mismatch	The habitat associated with the highest Lewis's Woodpecker density (or relative abundance) will have lowest reproductive success.
b)	Nest-site Selection Mismatch	Habitat characteristics selected for nest-site selection will not covary with reproductive success.
c)	Food availability	The habitat associated with highest insect availability will have highest Lewis's Woodpecker density.
d)	Clutch size	The habitat with earlier peak in insect availability will be associated to larger clutch sizes.
e)	Attrition	The habitat with lower insect availability will be associated with greater attrition rates.
f)	Nesting Availability	The habitat with highest density of available trees and snags suitable for nesting will be associated with higher Lewis's Woodpecker density.

Table 2. List of field sites and number of monitored Lewis's Woodpecker nests per year.

Habitat Type	Site	Active Nests			
		2015	2016	2017	Total
Floodplain Forest					150
	Kelly Island	-	8	5	
	Sapphire Ranch	8	17	12	
	MPG Ranch	15	12	8	
	Lee Metcalf NWR	20	17	8	
	CBR Ranch	-	-	20	
Burned Forest					108
	Skalkaho Creek Ranch	12	9	10	
	North Rye Creek	-	5	10	
	Sula Peak Ranch	-	13	10	
	Laird Creek	16	12	11	
	Total	71	93	94	

Table 3. Vegetation characteristics recorded during vegetation surveys at the end of the breeding season.

Plot Level	**Covariate**	**Method**
Nest Tree	Longitude and longitude	GPS unit reading
	Elevation	From GPS unit or from lat/long
	Canopy cover *(above nest tree)*	Using 4 densiometer readings
	Branches touching nest tree	Yes/no
	Nest tree dbh	Using a dbh tape
	Nest tree height (m)	Using a clinometer
	Average canopy height *(above nest tree)*	Using a clinometer
	Burn Class	0=unburned, 1=trunk charred, 2=branches lightly scorched, 3=heavy scorch, alive 4=totally burned, dead
	Nest tree dead or alive	Dead=0, alive=1
	Heart rot presence	Yes/no
5m Plot	Average shrub height (m)	Using measuring tape: 0= none, 1= 0-0.5m, 2= 0.6-1m, 3= 1.1-3m, 4= >3m
	Maximum shrub height (m)	Same as average shrub height (above).
	Shrub cover listed for each shrub species	Classes 1: 0-1%, 2: 2-5%, 3: 6-25%, 4: 26-50%, 5: 51-75%, 6: 76-95%, 7: 96-100%
11.3m Plot	Live tree count by species and size categories	Using dbh tape: small: 8-23 cm; medium: 23-38 cm; large: 38-50 cm; extra-large: >50 cm.
	Snag count by species and size categories	Using dbh tape: small: 8-23 cm; medium: 23-38 cm; large: 38-50 cm; extra-large: >50 cm.
	Dominant canopy species	
	Ecosystem class	
	Additional ecosystem class	
	Slope *(of general area)*	Using a compass
	Aspect *(of general area)*	Using a clinometer

Table 4. Top model in the analysis of Lewis’s Woodpecker nest success in the Bitterroot Valley between floodplain and burned habitat.

	Estimate	Standard Error	Z value	P value	
(Intercept)	10.40	3.210	3.239	0.0012	**
Burned habitat	1.20	0.304	3.932	$8.44\ e^{-5}$	***
Hatch day	-0.04	0.019	-2.120	0.0340	*
Nestling stage	1.23	0.260	4.742	$2.11e^{-6}$	***

Table 5. Top models for our Lewis's Woodpecker nest success analyses describing the influence of environmental factors on nest success in a) floodplain and b) burned forests.

a) Floodplain forest

	Estimate	Standard Error	Z value	P value	
(Intercept)	14.40	5.348	2.693	0.00709	**
Heart rot	2.97	2.066	1.439	0.15007	
Dead or alive	-0.45	0.534	-0.842	0.39954	
Nest orientation	0.01	0.002	0.930	0.35239	
Hatch day	-0.06	0.031	-1.986	0.04701	*
Nest height	0.01	0.056	0.152	0.87903	
Canopy cover	0.02	0.010	1.605	0.10859	
Heart rot* nest height	-0.27	0.131	-2.042	0.04113	*

b) Burned forest

(Intercept)	6.41	1.063	6.028	$1.66e^{-9}$	***
Nest height	-0.11	0.064	-1.703	0.0885	.
Average shrub height	0.80	0.387	2.072	0.0383	*

Table 6. Model summaries for the two significant interactions of habitat characteristics influencing insect availability across floodplain and burned forest, by a) habitat and distance, and b) habitat and date.

a) Interaction of habitat and distance on insect availability

	Estimate	Standard Error	Z value	P value	
Distance 2	-1.17	0.828	-1.409	0.159141	
Distance 3	-0.02	0.835	-0.026	0.979305	
Distance 4	0.40	0.823	0.484	0.628518	
Burned Habitat	3.07	0.837	3.672	0.000256	***
Distance2*burned	-3.17	1.261	-2.517	0.012016	*
Distance3*burned	-5.12	1.338	-3.827	0.000139	***
Distance4*burned	-4.98	1.340	-3.715	0.000216	***

b) Interaction of habitat and date on insect availability

Date 7/7/17	1.88	0.732	2.574	0.01022	*
Date 8/1/17	1.71	0.776	2.210	0.02738	*
Burned Habitat	2.20	0.928	2.374	0.01780	*
7/7/17*burned	-1.54	1.188	-1.295	0.19566	
8/1/17*burned	-3.91	1.261	-3.104	0.00197	**

Table 7. Lewis’s Woodpecker nest-site selection top resource selection function models in: a) floodplain forest and b) burned forest.

a) Floodplain forest

	Estimate	Standard Error	Z value	P value	
Canopy cover	-0.03	0.010	-2.958	0.00310	**
Nest tree height	0.10	0.033	3.067	0.00216	**
Large trees	0.23	0.138	1.690	0.09107	.
Extra-large snags	0.42	0.230	1.822	0.06853	.

b) Burned forest

Nest tree height	0.13	0.035	3.706	0.00021	***
Small snags	-0.53	0.201	-2.630	0.00854	**
Medium snags	0.42	0.227	1.846	0.06493	.

FIGURES

Figure 1. Bitterroot Valley Lewis’s Woodpecker study area with floodplain nest monitoring field sites (🔵) and burned field sites (🟡).

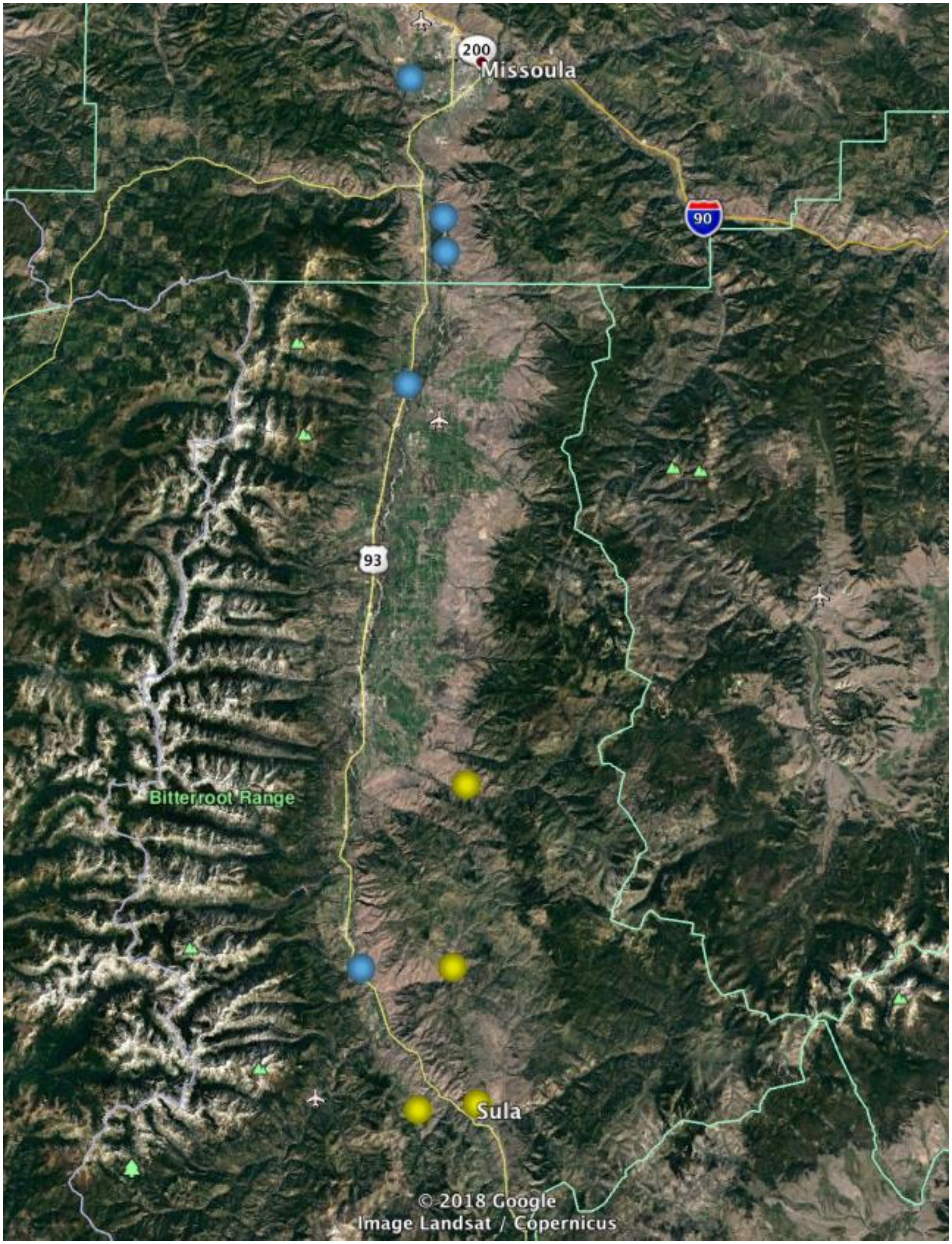


Figure 2. Systematic “use-available” vegetation sampling design, for each Lewis’s Woodpecker nest. The “nest plot” centered around the nest tree consists in two circles including an inner 5m radius circle for immediate shrub cover, and an 11.3m radius circle for all other vegetation characteristics. Two random plots associated with the nest, are represented here, as two other available snags. One available plot chosen within 20-120m from nest tree named “close plot” found parallel and downstream from river or creek flow. One other available plot chosen within 120-250m from nest tree, named “far plot” in the opposite direction from the from the stream’s location. Each of these two snags will also contain 5m and 11.3 m radius plots.

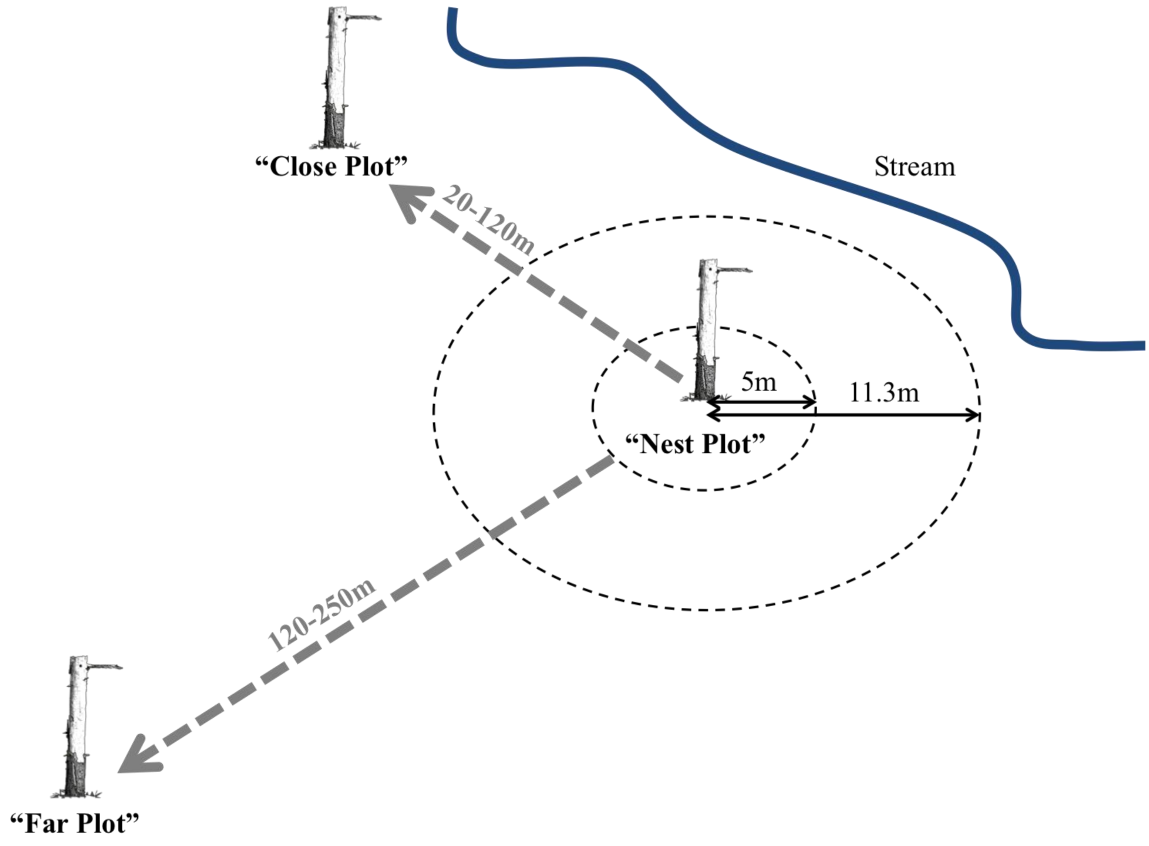


Figure 3. Systematic insect transect sampling design. All Lewis's Woodpecker nest monitoring field sites were divided in three general areas from the river or main bottom drainage, and we established 3 transects within. Each transect started above the creek or river, and projected in the direction furthest from the stream bed. On each transect four sticky traps were deployed on previously set trap lines. The first trap was set-up above the stream, and the remaining three traps at 25m, 100m and 250m away.

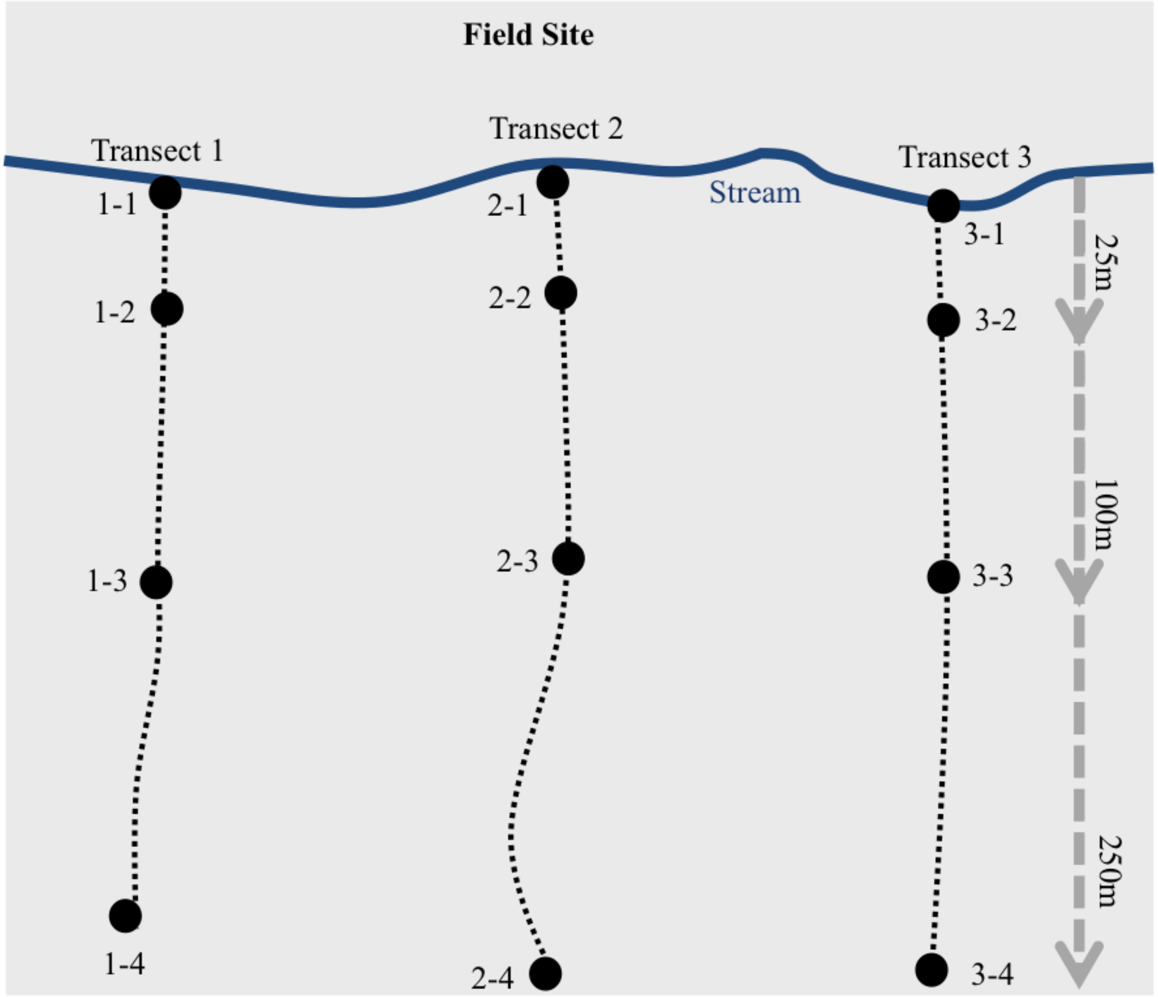


Figure 4. Trap line design for sampling insect availability using sticky traps. Zoomed-in sticky trap picture below is an example of sticky trap “KEL 1-1-17”, which is the trap on Transect 1 above the river at Kelly Island field site. This schematic shows the line set-up going over prominent branch 3-5 m above ground. All trap lines are flagged with orange flagging at base of tree in order to relocate lines with ease in subsequent visits.

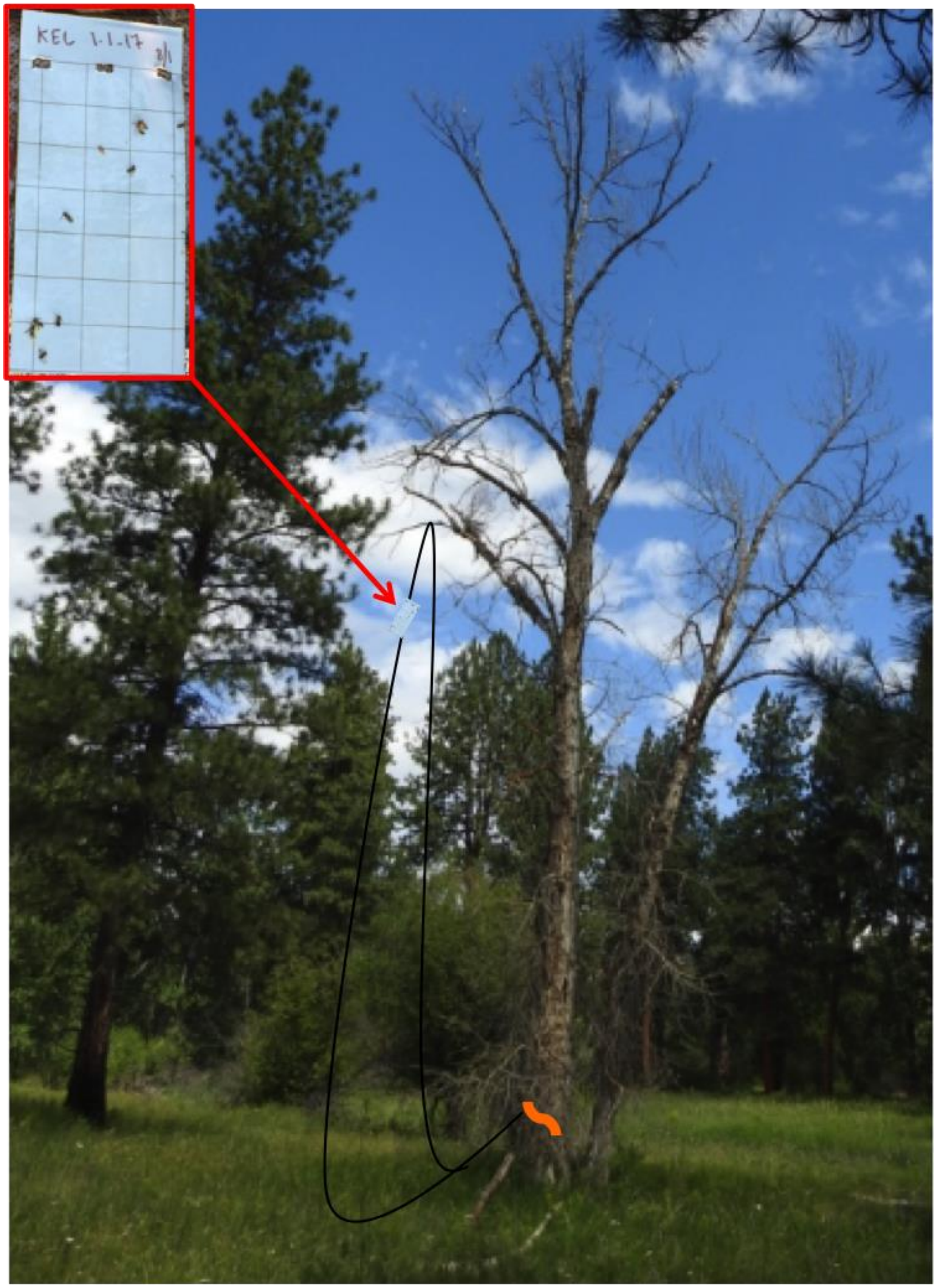


Figure 5. Mean Lewis's Woodpecker abundance estimates per habitat type, calculated per point count.

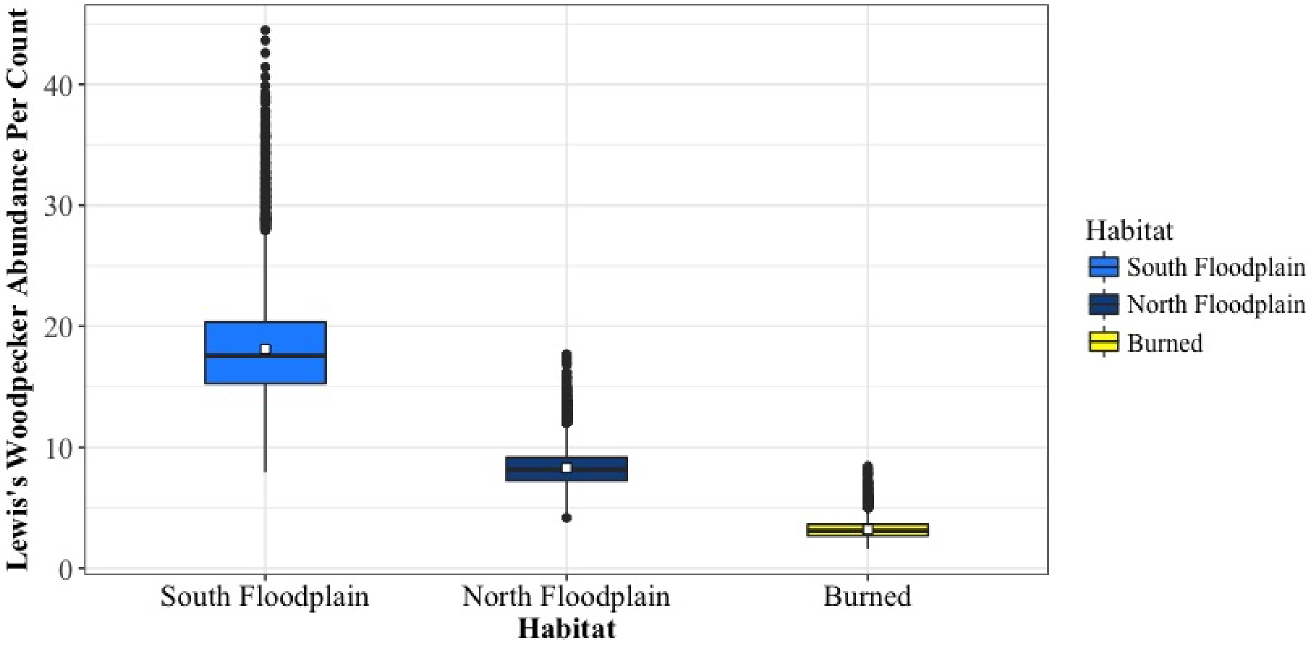


Figure 6. Mean perceptibility probabilities to detect Lewis’s Woodpeckers per habitat type, calculated via our Lewis’s Woodpecker abundance analysis.

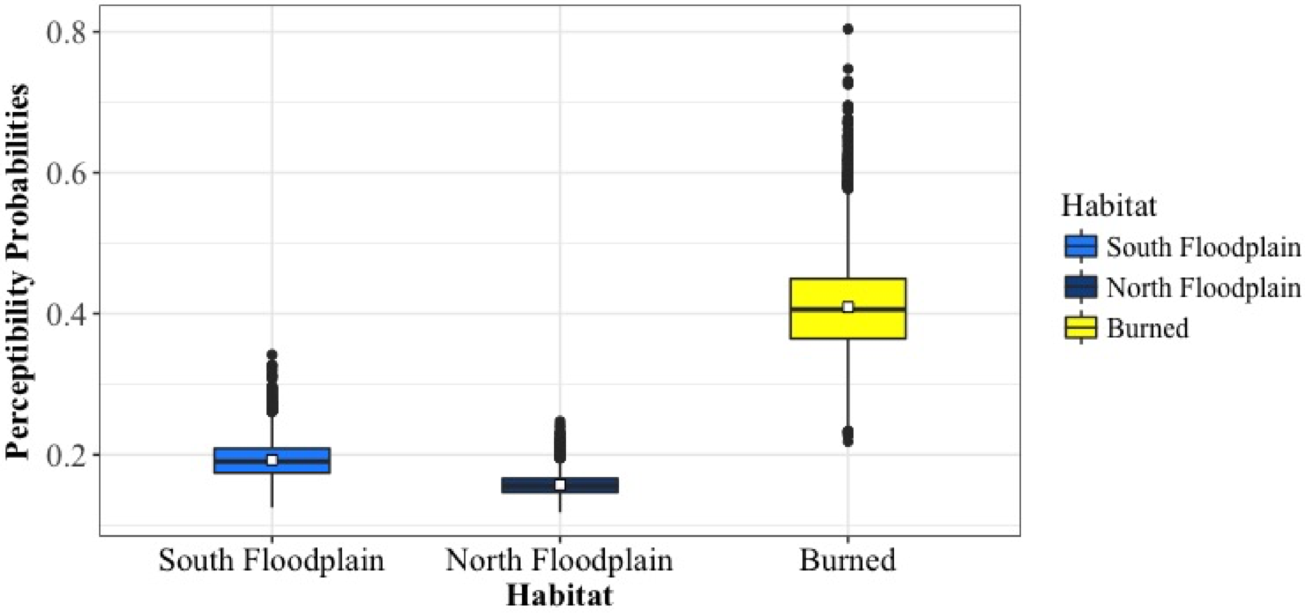


Figure 7. Predicted Lewis's Woodpecker nest success per nest stage, and number of nests in each habitat type with increasing hatch date. Regression lines represent the predicted nest success for either incubation or nestling stages for each corresponding hatch date. For instance, we found one nest in the floodplain that hatched on May 31 (i.e., day=151), from which we plotted the predicted nest success for the associated incubation stage and nestling stage. The histograms represent the number of nests found per hatch date.

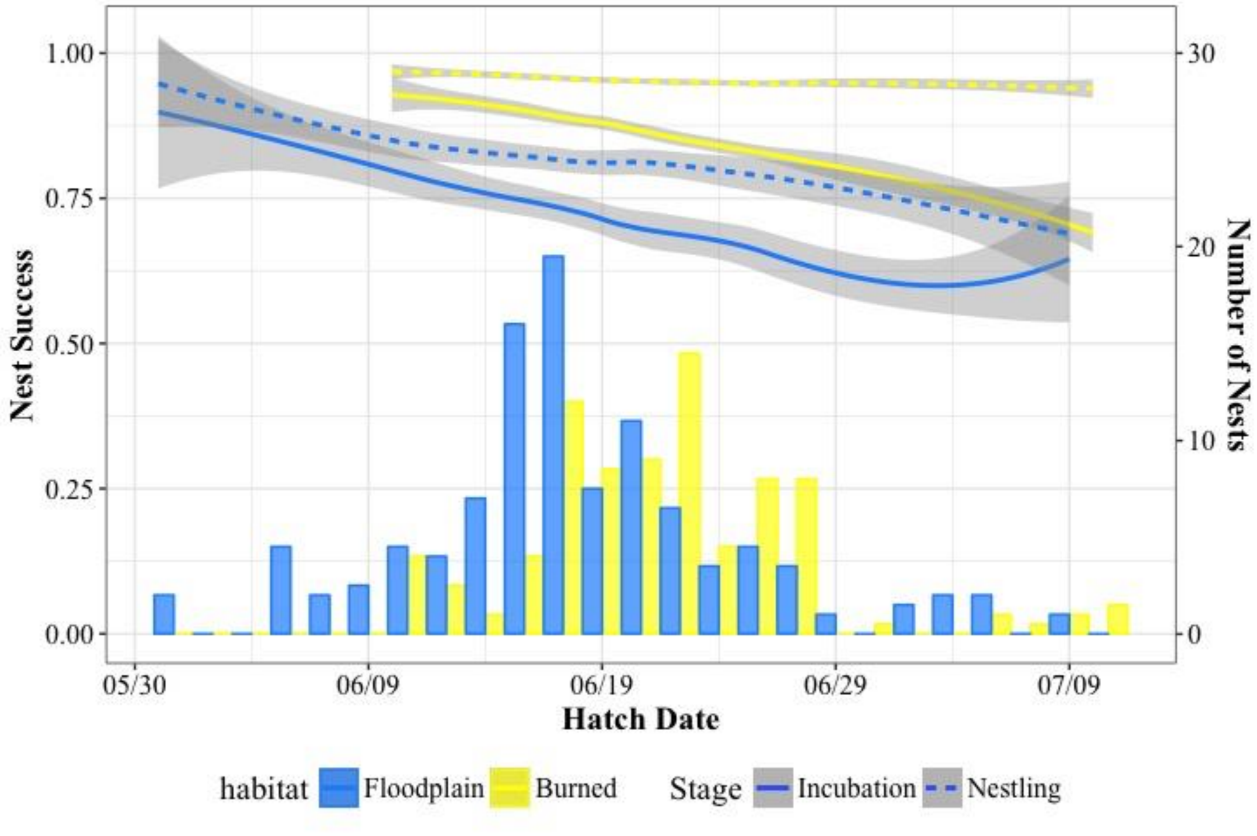


Figure 8. Predicted Lewis's Woodpecker nest success in floodplain forest after accounting for the significant interaction of nest height with heart rot.

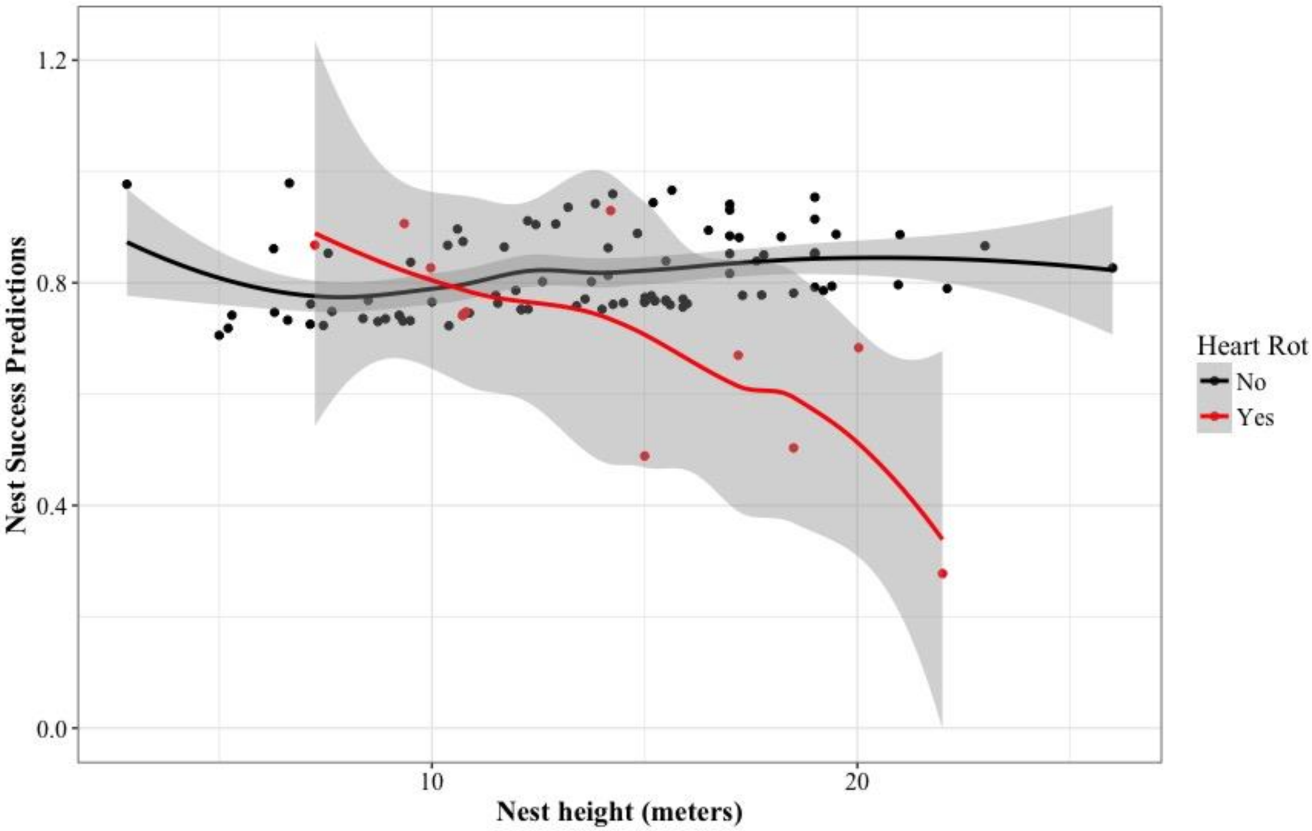


Figure 9. Insect availability by Order between floodplain and burned forest. Stars (i.e., *) on the x-axis in front of any insect name, indicate insect Orders where we found abundance differences between the two habitats.

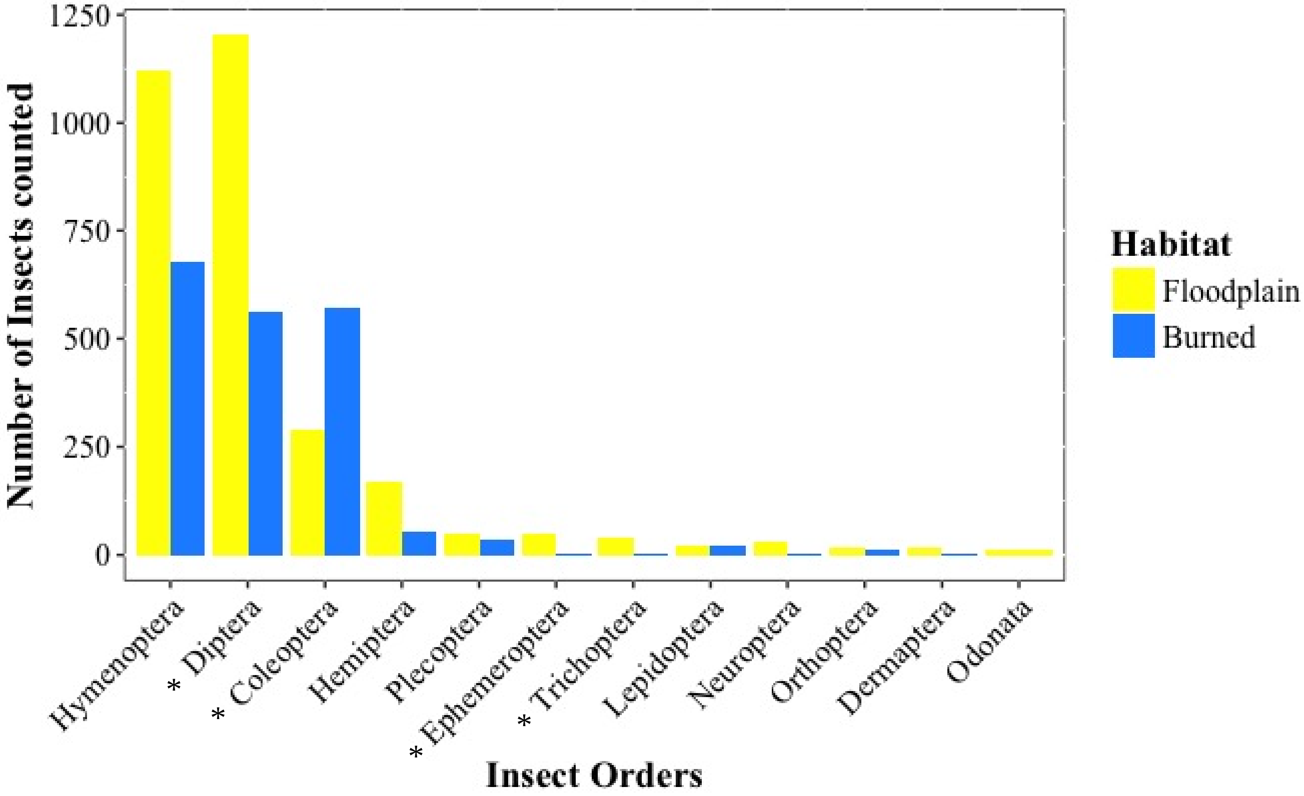
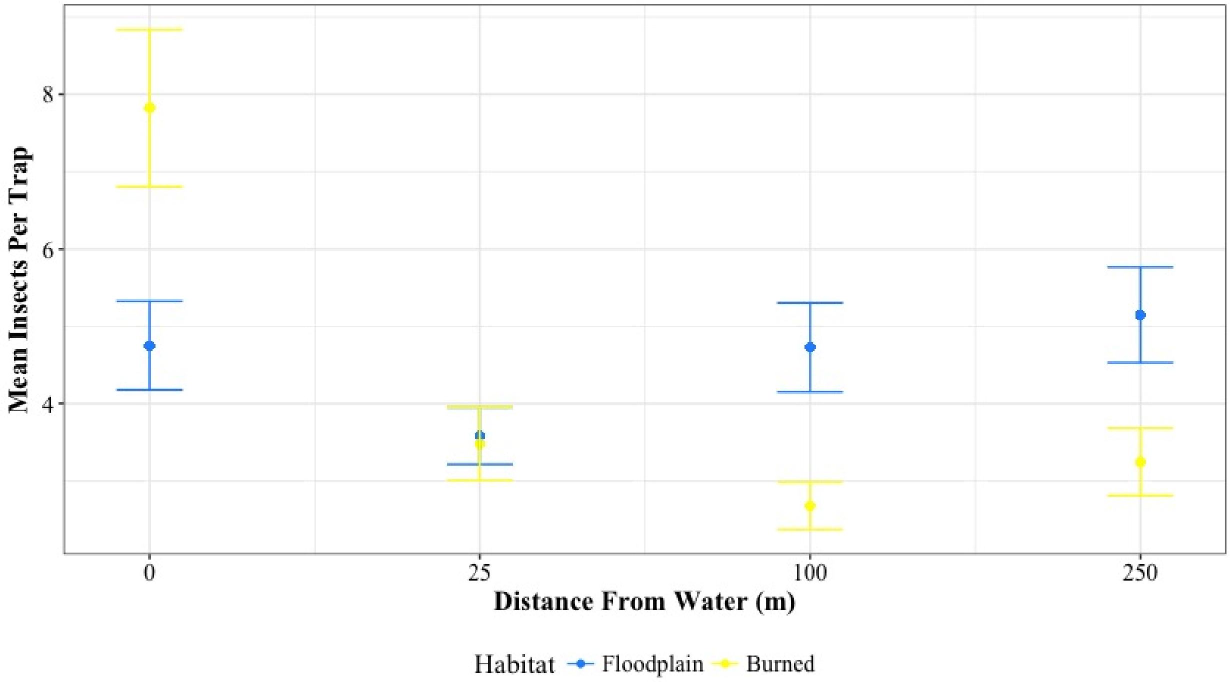


Figure 10. Interaction of a) habitat type and distance to water and b) interaction of habitat and date as influences on insect availability.

a) Interaction of habitat type and distance.



b) Interaction of habitat and date with incubation and nestling periods.

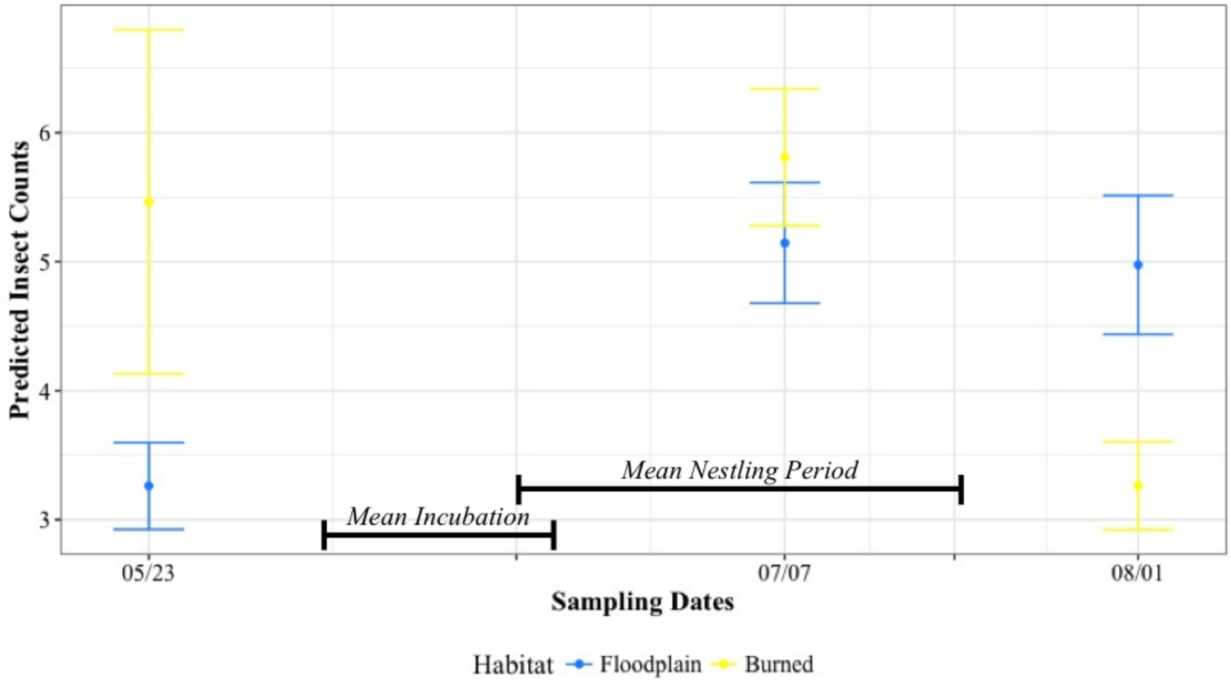
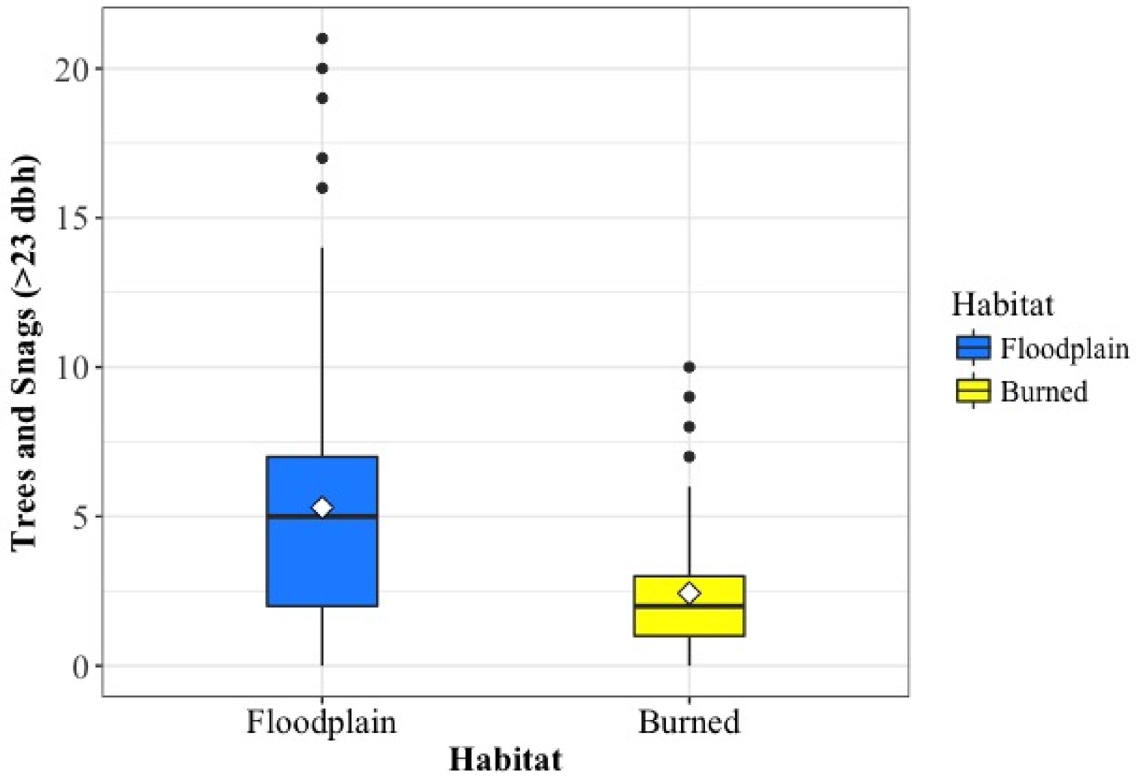
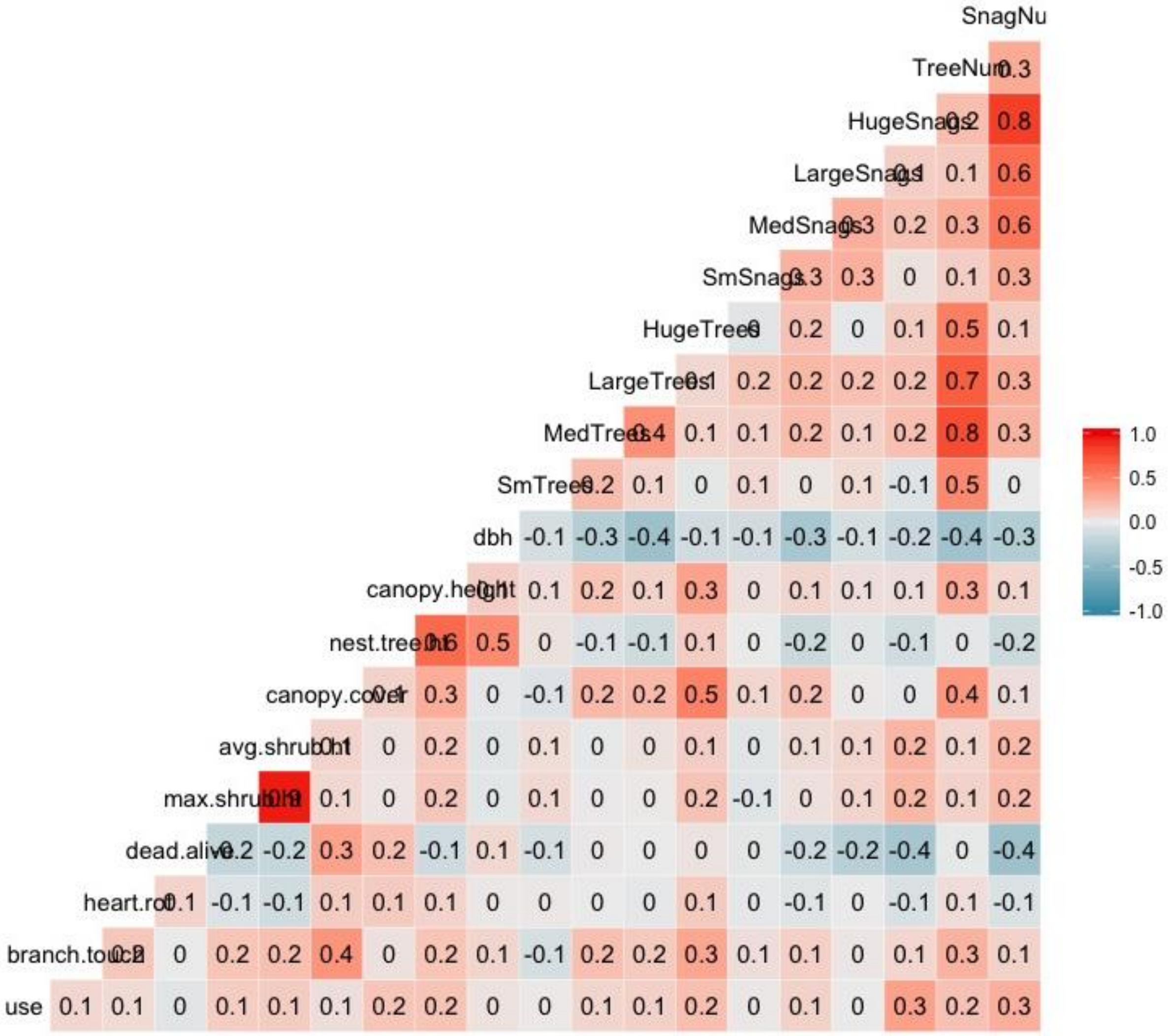


Figure 11. Comparison of mean trees and snag counts (i.e., stems/plot) with dbh>23cm suitable to Lewis's Woodpecker nesting, between floodplain and burned forest. Each plot was 11.3m radius plots, so y-axis corresponds to stem density per 401m^2 (i.e., Area= radius*radius*pi).



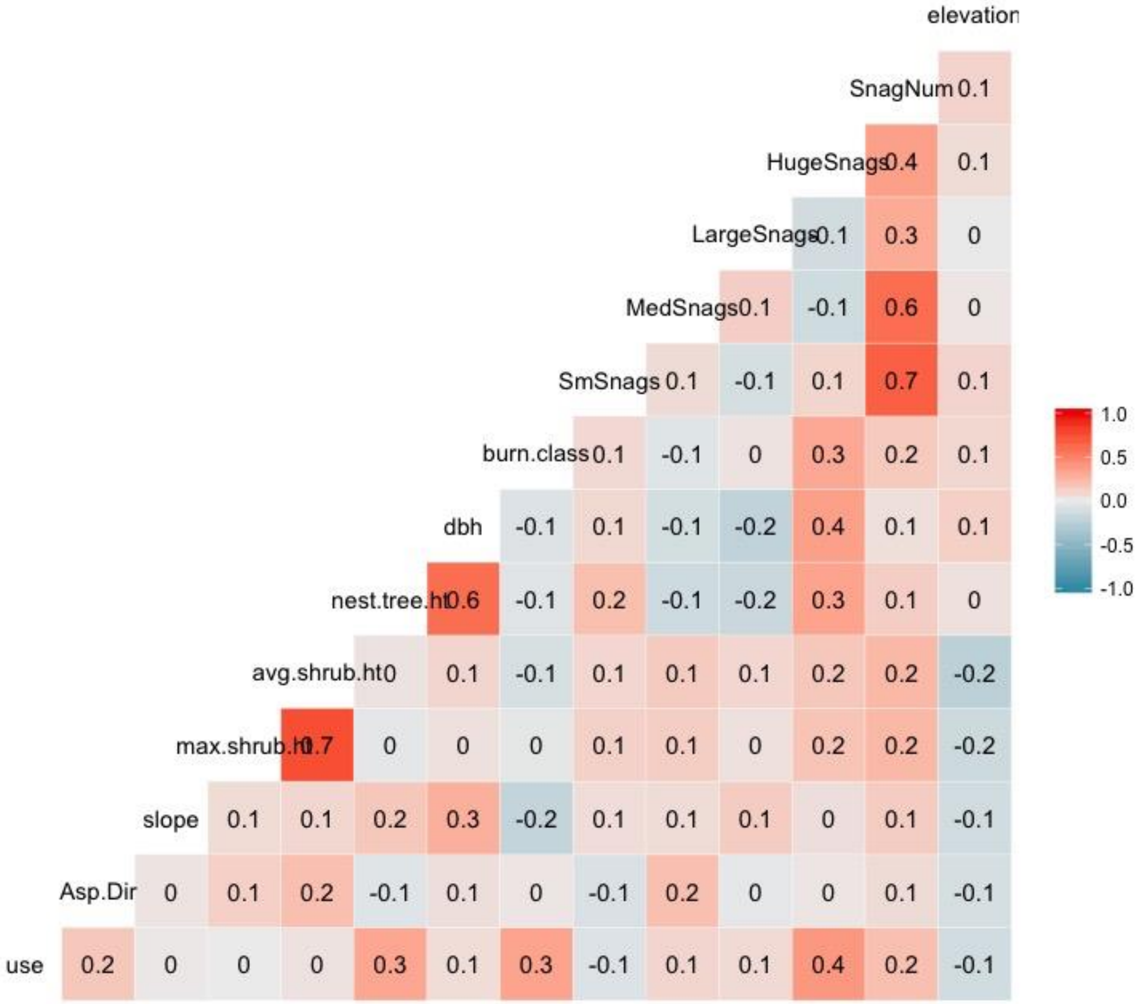
APPENDIX A. COLLINEARITY OF FLOODPLAIN FOREST COVARIATES

Matrix of standard error of coefficients for all continuous covariates originally considered for the nest-site selection analysis in floodplain forest. Multi-collinearity was resolved through AIC comparisons when $R^2>0.6$ (dark red or blue colors).



APPENDIX B. COLLINEARITY OF BURNED FOREST COVARIATES

Matrix of standard error of coefficients for all continuous covariates originally considered for the nest-site selection analysis in burned forest. Multicollinearity was resolved through AIC comparisons when R^2>0.6 (dark red or blue colors).



	Asp.Dir	slope	max.shrub.ht	avg.shrub.ht	nest.tree.ht	dbh	burn.class	SmSnags	MedSnags	LargeSnags	HugeSnags	SnagNum	elevation
elevation													
SnagNum													0.1
HugeSnags												0.4	0.1
LargeSnags											-0.1	0.3	0
MedSnags										0.1	-0.1	0.6	0
SmSnags									0.1	-0.1	0.1	0.7	0.1
burn.class								0.1	-0.1	0	0.3	0.2	0.1
dbh							-0.1	0.1	-0.1	-0.2	0.4	0.1	0.1
nest.tree.ht						0.6	-0.1	0.2	-0.1	-0.2	0.3	0.1	0
avg.shrub.ht					0	0.1	-0.1	0.1	0.1	0.1	0.2	0.2	-0.2
max.shrub.ht				0.7	0	0	0	0.1	0.1	0	0.2	0.2	-0.2
slope			0.1	0.1	0.2	0.3	-0.2	0.1	0.1	0.1	0	0.1	-0.1
Asp.Dir		0	0.1	0.2	-0.1	0.1	0	-0.1	0.2	0	0	0.1	-0.1
use	0.2	0	0	0	0.3	0.1	0.3	-0.1	0.1	0.1	0.4	0.2	-0.1