AN ABSTRACT OF THE THESIS OF

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Title: Resource Selection and Space Use of Western Long-eared Myotis (*Myotis evotis*) in a Western Juniper (*Juniperus occidentalis*) Woodland of Central Oregon.

Abstract approved:

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Dana M. Sanchez

Identifying habitat and spatial requirements of wildlife species across multiple spatial scales is a challenging, yet crucial component of wildlife management. Habitat use of bats is particularly difficult to study, and managing habitat to conserve bats is especially challenging because bats are highly vagile organisms that exploit several different types of habitat across many spatio-temporal scales. The status and distribution of bat populations is determined by the spatio-temporal pattern of quality roost sites and foraging areas across the landscape. However, knowledge of these limiting resources for bats and their distribution on the landscape is poorly known in western juniper (*Juniperus occidentalis* ssp. *occidentalis*) woodlands, even though at least 16 species of bat occur in these habitats across the western United States. Identifying habitat use by bats in western juniper woodlands is especially important due to recent landscape-scale efforts to remove juniper trees to improve habitat for greater sage-grouse (*Centrocercus urophasianus*), a species of major conservation concern in shrub-steppe habitats. Thus, the urgent challenge for land management agencies in western North America is to identify bat day

roost and foraging sites in order to develop management guidelines to conserve bats and their critical habitats.

The specific objective of this study was to identify habitat characteristics that are important to western long-eared myotis (*Myotis evotis*) during the reproductive season in western juniper woodland of central Oregon. I used radio telemetry to find day roost sites and investigate selection criteria for these sites by lactating female and male bats. I studied day roost site selection at three spatial scales: roost, plot, and home range. I found that females prefer to roost in rocks rather than in trees, whereas males did not display a preference towards either type of roost substrate. Bats that roosted in trees used primarily pre-settlement junipers (> 150 years old) with at least one cavity, and bats that roosted in rocks used primarily formations consisting on multiple boulders. More available roost sites within 17.8 m of a tree roost site (or within 5 m of a rock roost site) was associated with an increased likelihood that a particular tree or rock roost site was selected. Males selected rock roosts that had greater area of pre-settlement woodlands than shrub-steppe within a 1 km radius. These results suggest that roost site selection differs between lactating females and males and occurs at multiple spatial scales. Land management practices that retain pre-settlement trees during juniper removal treatments and protect areas with high densities of roost sites near water sources are likely to conserve or restore bat populations.

I also estimated home range size and the maximum foraging range of bats. Estimates of mean home range size were the largest ever reported for western long-eared myotis and among the largest for any *Myotis* species so far studied in North America. The mean 95% home range size for lactating females was 205.85 ha (SE = 47.94) and for males was 424.2 ha (SE = 187.2). The mean maximum foraging range for lactating females was 933 m (SE = 284.9) and males was 1522 m (SE = 532.8). Estimates of mean home range size and maximum foraging range did not

differ between lactating females and males; however, low statistical power likely precluded detecting a difference.

Lastly, I examined habitat selection at two spatial scales, (1) home range selection on the landscape scale and (2) foraging habitat selection within the home range. The probability of a location being selected by either lactating female or male bats decreased with increasing distance from day roost sites and water sources. Lactating females selected pre-settlement woodlands more than shrub-steppe habitat during foraging, but avoided areas with > 20% tree canopy cover more than areas with no canopy cover at the landscape scale. Males selected areas with 0.1% to 10% tree canopy cover more than areas with no canopy cover at the home range scale. To maintain foraging habitat for *M. evotis* in the study area, pre-settlement woodlands that are located near roost sites and water sources should be managed for variable tree densities.

Resource Selection and Space Use of Western Long-eared Myotis (*Myotis evotis*) in a Western Juniper (*Juniperus occidentalis*) Woodland of Central Oregon

by
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CONTRIBUTION OF AUTHORS

Dr. Dana M. Sanchez contributing to editing and writing chapters 1-4 and the study design of chapters 2-3. Dr. Daniel D. Roby and Dr. Ricardo Mata-Gonzalez contributed to editing chapters 1-4 and study design of chapter 2-3.

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CHAPTER 1: INTRODUCTION

Understanding the context of habitat use by wildlife species across multiple spatial scales is critical for wildlife conservation planning (Morrison et al. 2006). However, planning can be challenging because the relative influence of multiple processes and mechanisms at work in habitat selection might vary by scale (Wiens 1989). Thus, habitat requirements for a population cannot be described on a single spatial scale (Levin 1992). Landscapes are spatially heterogeneous, forming patches of habitat that vary in quality for a species. Configuration of habitat patches or pattern is one of many factors that influence species distribution (Wiens 1976, Turner 1989). The study of resource selection by wild animals is based on the premise that individuals select habitats that will maximize their fitness (Manly et al. 2002). Thus, habitat preference by individuals can be examined by comparing the characteristics of areas that individuals select to the characteristics of areas that are available to individuals, and the results can be extrapolated to the population if those individuals were selected at random from the population (Manly et al. 2002).

Bats are highly mobile organisms that exploit several different types of habitat during the reproductive season. As such, the stability of many populations of bats is determined by the spatial and temporal pattern and quality of resources across the landscape during the breeding season (Hayes 2003). Although identification of important resources for bats across multiple spatial scales is complex and challenging, a few consistent results are apparent. For example, the density and quality of roosts and their proximity to foraging areas and water sources are

important to many species of bats (Racey and Entwistle 2003, Barclay and Kurta 2007, Lacki et al. 2007, Duchamp et al. 2007).

During the reproductive season, bats spend the majority of time during a 24-hour period in day roosts, while the remaining hours are spent foraging and drinking water (Swift 1980, Barclay 1989). Day roosts provide sites for bats to rear pups, conserve energy, promote social interactions, and they provide protection from predators and adverse environmental conditions (Kunz and Lumsden 2003, Barclay and Kurta 2007). Foraging areas provide access to prey, and these areas are likely also selected for vegetation structure that maximizes foraging efficiency and access to water (Lacki et al. 2007). Even though the importance of roosts and foraging areas is well documented, the loss of these important resources is a constant threat to bat populations throughout the world (Racey and Entwistle 2003). Understanding the spatial relationship between bat resources and land use is fundamental for maintaining healthy populations of bats across the landscape (Hayes 2003). This task is made more difficult when species-specific roost site preferences are unknown within a given habitat and landscape type.

In the western United States, habitat use by bats in piñon (*Pinus monophylla*) and juniper (*Juniperus occidentalis* ssp. *occidentalis* and *J. osteosperma*) woodlands is not well known. Understanding habitat use of bats in piñon-juniper woodlands is important especially due to recent landscape scale efforts to remove trees to improve habitat quality for greater sage-grouse (*Centrocercus urophasianus*). Even though at least 16 species of bat occur in piñon-juniper woodlands across the western United States (Chung-MacCoubrey 1995, Chung-MacCoubrey 1996) our understanding of bat population distribution, ecology, behavior, and resource selection

is limited geographically to Colorado and New Mexico (Chung-MacCoubrey 1995, Chung-MacCoubrey 1996, Chung-MacCoubrey 1999, Chung-MacCoubrey et al. 2003, Chung-MacCoubrey 2005, O'Shea et al. 2011, Snider et al. 2013).

To better understand habitat use of bats in piñon-juniper woodlands, I used radio telemetry to examine roost site selection, space use, and habitat selection by lactating female and male western long-eared myotis (*M. evotis*) in a western juniper woodland of central Oregon. Western long-eared myotis is a common species of bat that occurs in several different habitats throughout the western United States and Canada (Manning and Jones 1989, Rabe et al. 1998, Chung-MacCoubrey 2005, Rancourt et al. 2005, Arnett and Hayes 2009, Nixon et al. 2009, O'Shea et al. 2011, Snider et al. 2013). Similarly, this species exhibits flexible roosting behavior that is highly variable across spatio-temporal scales and uses a wide variety of substrates as roosts (Manning and Jones 1989, Vonhof and Barclay 1997, Rabe et al. 1998, Chung-MacCoubrey 2003, Rancourt et al. 2005, Arnett and Hayes 2009, O'Shea et al. 2011, Snider et al. 2013). Less is known about habitat selection and space use, but foraging areas appear to be closer to water sources than random areas (Waldien and Hayes 2001).

In Chapter 2, I examine roost site selection at three spatial scales: roost, plot, and home range. At the roost scale, I identified the type (substrate) of roosts used by individual bats. Additionally, I characterized features of roosts that are known to be important for western long-eared myotis and other species of bats (Waldien et al. 2000, Rancourt et al. 2005, Barclay and Kurta 2007, Arnett and Hayes 2009, Snider et al. 2013). At the plot level, I counted the number of (1) available tree roost sites, (2) pre-settlement juniper trees (> 150 years old), and (3) post-

settlement juniper trees (< 150 years old) within 17.8 m of tree roost sites, and the number of rock crevices within 5 m of rock roost sites. This analysis was conducted to determine whether characteristics within close proximity of a roost site influences roost site selection. At the home range level, I calculated the area (ha) of pre-settlement woodlands within a 1-km radius of roost sites using Geographic Information Systems (GIS). Analysis at this scale was intended to determine whether bats are selecting roost sites in areas of pre-settlement woodlands over those in shrub-steppe habitat.

In Chapter 3, I estimated home range size and the maximum foraging range of male and lactating female bats. These results will identify space use requirements of bats during the reproductive season and can be used to define boundaries where important resources could be protected to conserve populations of bats. Furthermore, I examined habitat and spatial requirements of western long-eared myotis at two spatial scales, (1) the second order selection or home range selection on the landscape and (2) the third order selection or resource selection within the home range. I developed hierarchical models for lactating females and males to examine the relationship between habitat selection and spatial scale. This will identify resources that are important to bats at both the home range and landscape scales.

In Chapter 4, I summarize my findings for roost site selection, space use, and habitat selection of *Myotis evotis*. Furthermore, I discuss the scope of inference of this study and provide comments on future studies involving resource selection of bats in juniper woodlands.

CHAPTER 2: ROOST SITE SELECTION OF WESTERN LONG-EARED MYOTIS (*MYOTIS EVOTIS*) IN A WESTERN JUNIPER WOODLAND OF CENTRAL OREGON

Abstract

Several bat species occur in piñon (*Pinus monophylla*) and juniper (*Juniperus occidentalis* ssp. *occidentalis* and *J. osteosperma*) woodlands across the western United States, yet factors influencing roost site selection in these habitats are poorly known. Piñon-juniper woodlands have expanded beyond their historical geographic range of variation in the western United States over the last 150 years, since European settlement. Many former stands of widely-spaced old-growth juniper (pre-settlement trees) are now crowded with younger trees (post-settlement trees). Currently, federal and state land management agencies and private landowners are removing juniper trees to restore shrub-steppe habitat for greater sage-grouse (*Centrocercus urophasianus*) across its geographic range, with little understanding of the effects on roost site availability and roost site selection by bats. I used radio telemetry to examine roost site selection of western long-eared myotis at three spatial scales (roost, plot, and home range scales). Lactating females selected rock crevices as roosts more frequently than tree cavities, while frequency of roost use by males was more evenly distributed between tree roosts and rock roosts. The majority of tree roosts were in pre-settlement trees that had at least one cavity. The odds that a tree was selected as a roost site increased with the number of available tree roosts within 17.8 m of the roost site. Preference by lactating females for rock roost sites increased with the number of available rock roosts within 5 m of the roost site and decreased with distance from water. Preference by males for rock roost decreased if the roost was a single rock compared to an

aggregate of rocks, increased with the number of available roosts within 5 m of the roost site, decreased with distance from water, and increased with area of pre-settlement juniper woodland within 1 km of the roost site. These results provide support for protecting several types of roosts in juniper woodlands to conserve existing populations of western long-eared myotis. In particular, pre-settlement juniper trees and rock formations should be protected near water sources.

Introduction

Loss of roosting habitat is a constant threat to bat populations throughout the world (Racey and Entwistle 2003). The challenge remains for land management agencies in North America to identify important roosting areas in order to develop management guidelines to conserve bats and their associated habitats. Regionally, biologists and land managers must have an understanding of bat species distribution, habitat associations, seasonal habitat requirements, and interactions with land use practices to make informed decisions regarding bat conservation and management (Ball 2002).

There are at least 16 species of bat that occur in piñon (*Pinus monophylla*) and juniper (*Juniperus occidentalis* ssp. *occidentalis* and *J. osteosperma*) woodlands across the western United States (Chung-MacCoubrey 1995, Chung-MacCoubrey 1996). However, roost site selection by bats in piñon-juniper woodlands is not well understood. Previous research on bats in piñon-juniper woodlands is limited geographically to Colorado and New Mexico. These studies have examined bat species composition and distribution (Chung-MacCoubrey 1995, Chung-MacCoubrey 1996, Chung-MacCoubrey et al. 2003, Chung-MacCoubrey 2005), roost site

fidelity (Chung-MacCoubrey 2003), and roost site selection (Chung-MacCoubrey 1996, Chung-MacCoubrey 1999, Snider et al. 2013).

Expansion of piñon-juniper woodlands post-European settlement has created significant changes in vegetation communities across much of the western U.S. over the last 150 years (Burkhardt and Tisdale 1969, Young and Evans 1981, Miller and Tausch 2001, Miller et al. 2005, 2008, Johnson and Miller 2006). The most dramatic shifts have occurred in the Great Basin, where woodlands (tree canopy cover > 10%) and savannas (tree canopy cover < 10%) have increased from < 3 million ha to > 30 million ha since the 1870s (Miller and Tausch 2001). In Oregon, western juniper woodland has increased from 600,000 ha to 2.6 million ha during the last 85 years (Rowland et al. 2008). Multiple, potentially interacting mechanisms, such as fire exclusion, reduced fuels due to livestock grazing, changes in air temperature and moisture regimes, and increased CO_2 levels, have been associated with juniper expansion into shrub-steppe communities post-European settlement (Romme et al. 2009).

Prior to post-settlement expansion, western juniper woodlands were mostly limited to small patches that were less susceptible to wildfire due to a sparse understory vegetation community that allowed these pre-settlement woodlands (> 150 years old) to persist (Burkhardt and Tisdale 1969, Young and Evans 1981, Miller and Rose 1999). An exception to this landscape configuration is in central Oregon, where pre-settlement woodlands and savannas form relatively large stands (> 100 km², Waichler et al. 2001). Pre-settlement woodlands and savannas are now undergoing tree infill, but the mechanisms for this transition are less understood than the factors influencing tree expansion into shrub-steppe communities (Romme et al. 2009).

The impacts to wildlife populations from juniper tree infill and expansion of juniper woodlands are still unclear for most species, but some species are likely to decline while others will benefit from this transition (Reinkensmeyer et al. 2007). For example, tree expansion into shrub-steppe communities degrades this habitat (Miller et al. 2000) and can even cause habitat loss, displacing wildlife species that depend on these mostly treeless landscapes to fulfill their life cycle requirements (i.e., sagebrush obligate species, Baruch-Mordo et al. 2013). In an attempt to restore greater sage-grouse (*Centrocercus urophasianus*) habitat across the species' range, the Bureau of Land Management (BLM) and the Natural Resources Conservation Service (NRCS) have recently intensified their efforts to eradicate post-settlement (< 150 years old) juniper trees growing in shrub-steppe and juniper savannas (NRCS 2012). While this landscape scale restoration treatment will improve habitat for sage-grouse and other sagebrush obligate species (Cook 2015), the effects on bat habitat from this shift in community structure and composition are unknown.

The western long-eared myotis (*Myotis evotis*) is a widely distributed bat species throughout the western United States and Canada (Manning and Jones 1989), and is often one of the most locally abundant species of bat (Holloway and Barclay 2000, O'Shea et al. 2011). It occurs in an assortment of forested and treeless vegetation associations, including Douglas fir (*Pseudotsuga menzesii*), ponderosa pine (*Pinus ponderosa*), juniper (*Juniperus* spp.), shrub-steppe, scablands, riparian habitats, and agricultural areas (Manning and Jones 1989, Rabe et al. 1998, Chung-MacCoubrey 2005, Rancourt et al. 2005, Arnett and Hayes 2009, Nixon et al. 2009, O'Shea et al. 2011, Snider et al. 2013). Roost site selection by western long-eared myotis

is highly variable among vegetation communities and across spatial scales. Tree cavities, snags, stumps, rock crevices, downed logs, caves, mines, and anthropogenic structures have been documented as roost sites (Manning and Jones 1989, Vonhof and Barclay 1997, Rabe et al. 1998, Chung-MacCoubrey 2003, Rancourt et al. 2005, Arnett and Hayes 2009, O'Shea et al. 2011, Snider et al. 2013). Preference for specific types of roosts appears to be influenced by roost site availability in forested areas, perhaps where roost sites in rock are limited (Waldien et al. 2000, Arnett and Hayes 2009). However, the quality of roosts might influence roost site selection in areas where both tree and rock roost sites are available (Rancourt et al. 2005, Snider et al. 2013). The physical characteristics of selected bat roost sites often differ from random available roost sites. For example, used rock roost sites tend to be surrounded by a higher percentage of rock ground cover (Rancourt et al. 2005) and are higher off the ground (Snider et al. 2013) compared to random rock roost sites. Also, differences between used and available roost sites in coniferous forest included crevice dimensions in stumps (Waldien et al. 2000) and snag diameter at breast height (dbh) (Arnett and Hayes 2009). Forest stand characteristics and landscape features also influence roost site selection. Roosts of western long-eared myotis have been reported in clear cuts (Waldien et al. 2000, Vonhof and Barclay 1997), in second and old-growth forest stands (Waldien et al. 2000, Arnett and Hayes 2009), along forest edges (Rancourt et al. 2005), in close proximity to water (Waldien et al. 2000, Snider et al. 2013), and at some distance from permanent water sources (Rancourt et al. 2005, Arnett and Hayes 2009).

Previous research on roost site selection by western long-eared myotis has focused on females and overlooked potential sexual differences in roost site selection (Waldien et al. 2000,

Rancourt et al. 2005, Arnett and Hayes 2009, Snider et al. 2013). One study that examined roost site selection by lactating females and males did not find any gender differences in roosting home range area, but small sample sizes likely precluded the detection of any such differences (Nixon et al. 2009). Sexual differences in roost site selection have been confirmed in other bat species (Broders and Forbes 2004, Broders et al. 2006, Perry and Thill 2007, Hein et al. 2008, Boland et al. 2009).

In this study, I examined roost site selection of western long-eared myotis in a juniper woodland at three different spatial scales: roost, plot, and home range. My objectives were to investigate and identify roost site characteristics that are important for roost selection by lactating females and males across a range of spatial scales. To do this, I compared roost site selection between lactating females and males at each spatial scale.

At the roost scale, I hypothesized that frequency of use and roost site characteristics of used roost sites would differ between the sexes and by type of roost site substrate (tree vs. rock) due to the different energetic demands and thermoregulatory requirements of lactating females and males (Speakman and Thomas 2003). At the plot scale, I tested the hypotheses that the number of pre-settlement trees and post-settlement trees within 17.8 m of the tree roost site (0.1-ha circular plot centered on the nest site) would differ between lactating females and males. Additionally, I hypothesized the number of available tree roosts within 17.8 m of tree roosts and the number of available rock roosts within 5 m of rock roosts would differ between lactating females and males. Lastly, at the home range scale, I tested the hypothesis that the area of pre-

settlement woodlands (ha) within 1 km of roosts would differ between lactating females and males.

Materials and Methods

Study Area

This study was conducted in the Northern Basin and Range ecoregion approximately 84 km southeast of Bend, OR, and 18 km southwest of Hampton, OR. The study area encompassed 2,397 ha and included two seasonal water sources, which were used as sites to capture bats for radio telemetry (43°63'N latitude, 120°46'W longitude and 43°61'N latitude, 120°47'W longitude). Vegetation in the study area is characterized as a mosaic of pre-settlement western juniper woodlands (*Juniperus occidentalis*), sagebrush-steppe (*Artemisia* spp.*)*, and playa (i.e., seasonal wetlands) plant communities (Appendix A). Pre-settlement juniper woodlands (1,948 ha) are the most abundant plant community in the study area, followed by sagebrush-steppe (412 ha) and playas (37 ha). Juniper woodlands are dominated by pre- and post-settlement trees with a low sagebrush (*Artemisia arbuscula*) − Idaho fescue (*Festuca idahoensis*) understory plant community. Low sagebrush and mountain big sagebrush (*A. tridentata* (Nutt.), ssp*. vaseyana*) occurs with Idaho fescue in the sagebrush-steppe community. Playas are natural depressions on the landscape that are typically inundated annually due to precipitation and surface run-off, creating a unique plant community that has a higher tolerance of moist soils than the adjacent upland vegetation. Playas contain either a plant community dominated by silver sagebrush (*A. cana*) / Nevada bluegrass (*Poa nevadensis*) − beardless wildrye (*Leymus triticoides*) or one dominated by spikerush (*Eleocharis* sp.) − dock (*Rumex* sp.), or both. The study area receives an

annual average precipitation of 28 cm, primarily during November – January in the form of snow and during May – June as rain. Average temperatures during the warmest month (July) reach 17°C, while average temperatures during the coldest month (December) drop to -3°C. Topography in the study area is generally flat with an average elevation of 1,524 m, except for two buttes that reach elevations of 1635 m and 1,729 m, respectively.

Western juniper has expanded into sagebrush-steppe and infilled pre-settlement juniper woodlands, reducing the resiliency and resistance of these plant communities to disturbance from wildfire (Stringham et al. 2003, Briske et al. 2008). The U.S. Bureau of Land Management (BLM) actively restores plant communities that are threatened by western juniper expansion and infill by thinning post-settlement trees. Typically, every post-settlement tree is removed in shrub-steppe treatments and a few (2.5 – 9.8 trees/ha) are retained in pre-settlement woodlands for recruitment. Within the study area, 437 ha were thinned in both shrub-steppe and pre-settlement juniper woodlands. Consequently, juniper spatial structure is not uniform across the study area and areas of pre-settlement juniper woodlands that were thinned have lower juniper density than non-thinned areas. The study area contains 561 ha (24%) with no juniper canopy cover, 669 ha (28%) with 0.1% – 10% juniper cover, 730 ha (30%) with 10% - 20% juniper cover, and 437 ha (18%) with > 20% juniper canopy cover (Appendix B).

Playas were excavated (i.e., dug out) during the 1960s to 1980s in efforts to provide water for cattle and wildlife over longer durations than was provided by natural playas. Water availability in playas is seasonal, typically lasting through mid-August during average

precipitation years when cattle are present. However, all three playas occasionally hold water the entire year during average precipitation years when cattle are absent (CRA, pers. obs.).

Bat Capture and Handling

I captured bats during 10 total nights during July 7 – 20 in 2014 and 2015 by placing mist nets over two seasonal water sources located on playas. The seasonal water source used for bat capture in 2014 was dry in 2015, so I relocated the capture site to a water source 2.7 km south of the 2014 capture site in 2015. For each captured bat, I recorded species, body mass, sex, age class (adult or juvenile), ear length, forearm length, and reproductive status for females. I distinguished between adults and juveniles by the degree of ossification of the phalanges of the third metacarpal (Brunet-Rossinni and Wilkinson 2009). Females were classified as (1) pregnant, if a fetus was present in the abdomen as determined by gently pressing on the lower abdomen, (2) lactating, if milk was secreted from the nipples or if the nipples were erect and hair was not present around the nipples, but no milk was secreted, or (3) non-reproductive, if none of the previous criteria applied (Racey 2009). I attached radio transmitters (Model BD-2X; Holohil Systems Ltd., Carp, ON, Canada) to the upper scapulae of lactating female and male *M. evotis* by trimming hair from a small area, applying Perma-Type surgical adhesive (The Perma-Type Company Inc., Plainville, CT, USA), and pressing the transmitter to the skin. Bats were held for 10 minutes to allow the adhesive to set, and then released at the capture site. I assumed all individual bats in the study area were equally likely to be captured and were a random sample of the population in the study area (Manly et al. 2002). Transmitters weighed 0.34 g or 0.36 g, and transmitter-to-body mass proportions for all radio-tagged bats were < 6.18%. Proportionate tag

mass for five tagged individuals (16%) was < 5% (Aldridge and Brigham 1988, Neubaum et al. 2005), proportionate tag mass for 24 individuals (75%) was between 5% and 6%, and proportionate tag mass for three individuals (9%) was > 6%. All handling and tracking procedures with bats were conducted under permits issued by the Oregon Department of Fish and Wildlife (Permit no. 111-14, Permit no. 084-15), and protocols were approved by the Institutional Animal Care and Use Committee at Oregon State University (ACUP 4469).

Radio Telemetry

I used a handheld receiver (model R-1000, Communication Specialists Inc., Orange, California) and a handheld 3-element Yagi antenna to locate day roosts for approximately 12 consecutive days after each bat was fitted with a transmitter during both years of the study. I confirmed day roost locations by visually observing bats or by using the signal to home-in on the location of the bat. Each roost location was entered into a Trimble Juno 3 Series (Sunnyvale, CA, USA). Because bats sometimes shed their transmitters in day roosts, I eliminated false occupancies by monitoring the radio signals of individuals that had been located in their day roosts during the subsequent nightly foraging bout to ensure that transmitters were still on bats.

Study Design and Model Covariates

I used a retrospective study design to test whether bats selected day roost sites at random from among those available in the study area or based on preference for certain roost site characteristics by comparing day roost sites used by bats to random available day roost sites in the study area. This approach is similar to a Design III study (Manly et al. 2002) at a second-

order availability spatial scale (Johnson 1980). I used ArcGIS 10.2 to define the study area and create random points. I created 810-m and 1,162-m radius buffers around each day roost used by one of my study animals, based on the estimated mean home range size (95% probability contour) for lactating females and males, respectively, using the fixed kernel density estimation method (see Chapter 3). I dissolved all buffers to create one contiguous polygon with the multiple ring buffer analysis tool. I generated random points for tree roost sites within the entire study area, but restricted random points for rock roost sites to locations on the two buttes in the study area because every used rock roost, except one, was located on a butte (Appendix C). I used GPS to locate the random points in the field, laid out a 300-m transect in a random direction, and searched for the first available day roost site within 50 m on each side of the transect. I identified one available day roost site for every used day roost ($n = 92$), and defined available day roost sites as juniper trees or rock features that had at least one cavity or crevice with the dimensions of 2 x 3 x 8 mm or larger. If I did not find an available day roost site along a transect, I moved to the next random point. Random available roosts were not used by individuals fitted with radio transmitters, but might have been used by other individuals in the population, which could bias resource selection function beta coefficients (Keating and Cherry 2004, Johnson et al. 2006). Therefore, I searched the available roosts for signs of bat use (i.e., visual on a bat, guano, bat vocalizations). I compared used and available day roosts sites at three spatial scales (roost, plot, and home range) because several species of bats, including *Myotis evotis*, demonstrate higher roost site fidelity towards areas than they do towards specific roost sites (Weller and Zabel 2001, Broders et al. 2006, Snider et al. 2013). This would suggest that

attributes at broader scales might influence roost site selection more than actual characteristics of the particular roost site.

Roost Scale

I quantified several characteristics at the scale of the roost that have been previously identified as important roost site selection criteria for bats. At each used and available day roost site, I measured roost characteristics that were specific to that type of roost substrate (tree vs. rock). For tree roost sites, I determined whether the tree was alive or dead and whether it was a pre- or post-settlement individual, counted the number of available cavities, estimated canopy cover under the roost tree, measured diameter at breast height (dbh) of the roost tree, and estimated tree height (m). I estimated canopy cover one meter from the base of the tree with a densitometer by averaging estimates from each of the four cardinal directions. I used a dbh tape to estimate tree diameter 1.3 m above the ground and estimated tree height with a clinometer. For rock roost sites, I identified the rock feature as an isolated rock or part of an aggregation of boulders (formation), and crevice configuration as either horizontal or vertical. I measured crevice height above the ground from the middle of the crevice opening. I measured landscape aspect with a compass. At all tree and rock day roosts, I estimated the distance from the day roost to the nearest water source with the Near Analysis Tool in ArcGIS, and I used a 30 m pixel Digital Elevation Model (DEM) to estimate elevation of the roost site.

Plot Scale

At each used and available roost site, I established a 17.8-m radius plot (0.1-ha) centered at the perimeter of the trunk for tree roost sites or centered on the crevice for rock roost sites, and counted pre-settlement and post-settlement juniper trees in each plot. Pre-settlement trees were defined as those trees with two or more of the following characteristics: (1) lacking the typical "cone" shape of younger trees, and having large, spreading, irregular-shaped crowns that are often rounded or flat topped; (2) bark with thick, fibrous, well-developed vertical furrows; (3) dead branches or tops, bark missing, often with abundant yellow or light-green fruticose lichen; (4) large horizontal lower limbs, often twisted; (5) decay and/or hollow areas on main trunk; and (6) leader growth in the upper 25 percent of the tree < 1 in. (Miller et al. 2005). Additionally, I counted the number of trees that had at least one visible potential roosting cavity within 17.8 m of used and available tree roosts. Several rock roost sites were located in boulder fields that made counting available roost sites within 17.8 m of crevice openings, logistically challenging, and induced considerably high error in the outcomes. Therefore, I established a 5-m radius plot (0.008 ha) centered on the crevice opening of rock roost sites to reduce error while counting available rock roost sites.

Home Range Scale

At the home range scale, I used ArcGIS to create 1-km radius buffers around day roost sites and calculated the area (ha) of pre-settlement woodland and shrub-steppe in each buffer. I used the Web Soil Survey (NRCS 2015) to retrieve spatial data for soil mapping units developed in 2013 for Deschutes and Lakeview counties, Oregon (Upper Deschutes River Area, Oregon,

Parts of Deschutes, Jefferson, and Klamath counties (OR620) and Lake County, Oregon, Northern Part, Parts of Lake and Klamath counties (OR635). I also obtained ecological site information, including the historical climax plant community, from the soil mapping data. In ArcGIS, I delineated soil mapping units containing western juniper as the dominant tree in the ecological site description as pre-settlement woodlands (Appendix D), and all other mapping units as shrub-steppe.

Statistical Analysis

I pooled data collected during the 2014 and 2015 field seasons and analyzed tree roosts (i.e., live trees and snags) and rock roosts separately. Initially, I used a Barnard's test and Welch's two sample t-test to calculate univariate statistics to examine the relationships between bat sex and the covariates. I used an unconditional Barnard's test rather than a conditional Fisher's Exact test to compare relative use of roost types (trees vs. rocks) between the sexes because the Barnard's test is more powerful and does not assume fixed totals for columns in the 2 x 2 contingency table (Mehta and Hilton 1993). I used a Welch's two sample t-test because the variance between the grouping variables (lactating female vs. male) was slightly unequal. Tree roost covariates were not statistically different between lactating females and males; therefore, I pooled data for lactating females and males to compare between used and available roost sites (D. Miller, pers. comm.). Because I detected statistically influential rock roost covariates between sexes, I analyzed rock roost sites of lactating females and males separately.

I used logistic regression models to compare used roost sites to available roost sites and to identify covariates that best described roost site selection. Logistic regression models are

useful generalized linear models (GLM) for modeling binary response variables as a function of many covariates (Manley et al. 2002). However, several sources of variation that are controllable but not of interest (i.e., random effects), which the logistic model cannot account for, can influence dependent variables during radio telemetry studies. These should be addressed during analysis. In this study, several bats used more than one day roost site ($\bar{x} = 3.68$ SE $= 2.30$) during the time they were observed, creating unbalanced data among individuals. Furthermore, the day roosts used by individual bats might be expected to be autocorrelated (Miller et al. 2003); thus, considering day roosts as experimental units might violate the assumption of independence for logistic regression. A generalized linear mixed model (GLMM) can be more powerful than a GLM for examining population level habitat selection because of its ability to handle binary data and incorporate random effects (Bolker et al. 2009), thus relaxing issues related to unbalanced data and dependence among roost sites within individuals (Gillies et al. 2006). To determine whether a GLM or a GLMM was more appropriate, I tested for dependence at the individual bat level. If no dependence was detected, a simpler GLM could be used in place of a more complex GLMM that includes the random effect for individual bat. I fit a global logistic regression model (including all model covariates), for tree and rock roosts separately, and examined the residuals of the fitted model against individual bats. The results indicated no dependence among bats (tree roosts $F_{1,44} = 0.086$, $P = 0.771$, rock roosts: $F_{1,100} = 0.369$, $P = 0.545$) and that model fit with logistic regression was adequate (J. Peterson, pers. comm.). This was further supported by the lack of evidence for predictable variation among bats as evidenced by the attempt to fit a random effects model (Bates 2010). Therefore, I used the logistic regression model to identify

independent variables that affect the odds that a particular day roost site was used by *M. evotis* relative to the available day roost sites.

I developed a set of 10 candidate logistic regression models (n = 5 models for tree roost sites; n = 5 models for rock roost sites), with variables chosen for biological importance to bats or usefulness as indicators for making land management decisions regarding juniper management and western long-eared myotis (Dochtermann and Jenkins 2011). Each model was developed *a prior*i with < 4 parameters to reduce spurious results associated with data dredging and over-fitting models (1 parameter/10 roost sites; Burnham and Anderson 2002). For tree roost sites: Tree model 1, I hypothesized that roost site selection would be influenced by characteristics at the roost scale (used/available [U/A] = number of cavities in the tree + tree height + tree dbh + tree canopy cover); Tree model 2, I hypothesized that roost selection would be influenced at the plot scale (U/A = number of available roosts within 17.8 m + number of pre-settlement trees + number of post-settlement trees); Tree model 3, I hypothesized that roost selection would be influenced at the landscape scale (U/A = distance to water + elevation + area of pre-settlement juniper woodlands (ha) within 1 km of roosts); Tree model 4, I hypothesized that roost site selection would be influenced by juniper (U/A = number of pre-settlement trees + number of post-settlement trees + area of pre-settlement juniper woodlands (ha) within 1 km of roosts); and Tree model 5 (generalized model), I selected one variable from each of the first four models based on their strength as explanatory variables (U/A = number of cavities + number of available roosts + distance to water + area of pre-settlement juniper woodlands (ha) within 1 km of roosts). I chose number of cavities from Tree model 1 because western long-eared myotis

switch roost sites frequently (Waldien et al. 2000, Rancourt et al. 2005, Solick and Barclay 2006) and I hypothesized that the number of cavities in a particular tree would positively influence its probability of use. Although in other forested habitats bats tend to select roost trees that are taller and have greater dbh than available trees, presumably due to the thermoregulatory benefits of increased insulation (Kunz and Lumsden 2003, Barclay and Kurta 2007), I hypothesized that these characteristics and tree canopy cover would not be as important to bats in juniper woodlands because juniper trees tend to receive direct sunlight due to low stem densities, relative to other forest habitats. I chose number of available roosts within 17.8 m from Tree model 2 because bats select roosts that are located in areas of high available roost densities (Brigham et al. 1997, Rabe et al. 1998, Waldien et al. 2000, Cryan et al. 2001, Weller and Zabel 2001, Baker and Lacki 2006, Arnett and Hayes 2009). I chose distance to water from the Tree model 3 because free water is a limiting resource for bats in arid environments, particularly lactating females (Adams and Hayes 2008), and water sources are limited in the study area. Finally, I chose the area of pre-settlement juniper woodlands (ha) within 1 km of roosts from Tree model 4 because I hypothesized that pre-settlement woodlands would provide a greater number of potential tree roosts than shrub-steppe; therefore, influence roost site selection at the home range scale.

For rock roost sites, the factors included in rock roost models 2-4 were identical to those included in tree roost models 2-4. Rock model 1 represented the hypothesis that roost selection was influenced by the characteristics of rock roost sites (U/A = single rock vs. formation roost site + vertical vs. horizontal crevice); Rock model 5 (generalized model) represented the best

predictors from the first four models (U/A = single rock vs. formation roost site + number of available rock roost sites within 5 m + distance to water + area of pre-settlement juniper woodlands (ha) within 1 km of roosts). I chose single rock vs. formation from Rock model 1 because western long-eared myotis exhibits flexibility in the configuration of rock roost sites that are used (Chruszcz and Barclay 2002, Rancourt et al. 2005, Solick and Barclay 2006). Prior to analysis, I checked for correlation among continuous variables and decided *a priori* that if the correlation between two independent variables was greater than 0.7, I would remove one of the variables. I did not detect correlation between independent variables greater than 0.64, so I used every variable in the analysis (Appendix E). Additionally, I checked model fit with a Hosmer-Lemeshow goodness-of-fit test and I excluded models that were significantly different from expected model fit ($P < 0.05$) (Appendix F).

I compared models using Akaike Information Criterion with a bias correction term for small sample size (AICc, Burnham and Anderson 2002). I used AICc because the number of observations was relatively small compared to the number of parameters in each model ($n / K <$ 40, where n = sample size and K = number of model parameters; Burnham and Anderson 2002). For AICc, I report the number of parameters in each model (K), AICc values, difference in AICc score between the top ranked model and the subsequent *ith* models (Δ_i), and Akaike weights (w_i = estimated probability of model i being the best model given the data and the set of candidate models). I considered models competitive if $\Delta_i < 2$ (Burnham and Anderson 2002, Burnham et al. 2011). I report the coefficient estimates, standard errors, odds ratios (exponentiation of parameter estimates), and 95% confidence intervals of the top models. I preformed all analyses in R version

3.0.2 (R Development Core Team 2013), using the built-in *Stats*, *GGally* (correlation of independent variables), *Exact* (Barnard's unconditional test), and *MuMIN* (model selection) packages.

Results

I captured 81 individuals of four different species (*Myotis evotis, n = 66; Pipistrelles hesperus, n = 9; Myotis volans, n = 4; Myotis ciliolabrum, n = 2*) and attached radio transmitters to 32 individual *M. evotis* ($n = 15$ lactating females, $n = 17$ males). I located 92 day roost sites ($n = 47$ roosts of lactating females, $n = 45$ roosts of males) for 25 different individuals ($n = 10$ lactating females, $n = 15$ males). Fifty-one percent of the roosts were located in rocks and 49% were located in trees or snags. All but one female exclusively selected one type of roost substrate, either rock or tree, whereas 33% of males selected roosts in both trees and rocks. The relative use of roost site types differed between lactating females and males (Barnard's test, $t = -2.86$, $P = 0.005$). Lactating females selected tree roosts ($n = 8$) less frequently than males ($n = 20$), and rock roosts ($n = 39$) more frequently than males ($n = 25$). Within lactating females, frequency of use was greater for rock roosts (83%) compared to tree roosts (17%), while frequency of use for males was more evenly distributed between tree roosts (44%) and rock roosts (56%).

Four of the 28 tree roosts were in juniper snags; the remaining 24 tree roosts were located in pre-settlement trees with at least one cavity. No tree roost covariates proved significantly different between tree roost sites used by lactating females vs. those used by males (Table 2.1).

For the 64 rock roost sites located, frequency of use of single rock vs. formation rock

roost sites did not differ between lactating females and males (Barnard's test, $t = -0.98$, $P = 0.343$). However, both lactating females (92%) and males (85%) overwhelmingly selected rock roost sites that were part of formations. Rock crevice orientation (vertical vs. horizontal) of roost sites did not differ between lactating females and males (Barnard's test, $t = 1.84$, $P = 0.069$). Lactating females selected rock roosts with a greater number of available roosts within 5 m of roosts sites and less area of pre-settlement juniper woodlands within 1 km of roosts, and were located closer to water and lower elevations compared to rock roost sites used by males (Table 2.1).

For tree roosts, the model that best explained roost site selection was Tree model 5, which included one variable from each of the first four models (Table 2.2). However, closer examination of the odds ratios and 95% confidence intervals indicate the number of available tree roost sites within 17.8 m was the only variable having measurable effects in the model (Table 2.3). The odds of a tree roost being selected by a western long-eared myotis increased by a factor of 1.46 (95% CI = 1.10 to 2.11) with one additional available tree roost site (Table 2.3, Fig. 2.1). The second best model was Tree model 2 ($\Delta_i = 0.195$), and again, the number of available tree roost sites within 17.8 m was the most influential variable in the model. The odds that a bat selected a particular tree roost site increased by a factor of 1.92 (95% CI = 1.03 to 4.47) with one additional available tree roost. The third best model was Tree model 4 ($\Delta_i = 1.32$), and the number of pre-settlement trees within 17.8 m was the only variable having measurable effects in the model. The odds that a tree roosts was selected by an individual bat increased by a factor of 1.28 (95% CI = 1.02 to 1.68) with one additional pre-settlement tree.

The model that best described use of rock roost sites by both lactating females and males was Rock model 5, which included rock presence as a single rock vs. formation, available rock roost sites within 5 m of roost sites, distance to water, and area of pre-settlement juniper within 1 km of roost sites (Tables 2.4, 2.6). Rock model 5 was 42.5 and 53.7 times more likely than the remaining candidate models for lactating females and males, respectively. The number of available rock roosts within 5 m of roost sites and distance to water had measurable effects in the lactating female model. The odds that a rock roost site was selected by a lactating female increased by a factor of 1.07 (95% CI = 1.03 to 1.14) for every additional rock roost site available within 5 m and decreased by a factor of 0.86 (95% CI = 0.73 to 0.97) for every 100 m increase in distance from water (Table 2.5, Fig. 2.2). All four explanatory variables in Rock model 5 were important predictors in the male model. The odds that a particular rock roost site was selected by a male bat decreased by a factor of 0.15 (95% CI = 0.02 to 0.86) if the roost was a single rock compared to a formation of rocks; the odds increased by a factor of 1.14 (95% CI = 1.01 to 1.37) for each additional rock roost site available within 5 m; the odds decreased by a factor of 0.66 (95% CI = 0.44 to 0.87) for every 100 m increase in distance from water; and the odds increased by a factor of 1.61 (95% CI = 1.14 to 2.55) for every 10-ha increase in the area of juniper woodland within 1 km of a roost site (Table 2.7, Fig. 2.3).

Discussion

The frequency of use of tree roost sites vs. rock roost sites differed between lactating female and male bats. Sexual differences in roost site selection have been described for other species of *Myotis* (Broders and Forbes 2004, Perry and Thill 2007), particularly between

reproductive females and males (Boland et al. 2009). Preference among lactating females for roost sites in rock crevices is consistent with previous studies in which reproductive females of western long-eared myotis almost exclusively roosted in rocks, even though tree roost sites were available (Rancourt et al. 2005, Snider et al. 2013). Further, preference for rock roost sites by reproductive female western long-eared myotis has been reported in the Rocky Mountains and prairie-badlands of Canada (Chruszcz and Barclay 2002, Solick and Barclay 2006, 2007). Energetic requirements of lactating females are significantly greater than those of males (Speakman and Thomas 2003). Male bats lack the energetic demands associated with milk production; therefore, they often select roost sites with lower ambient temperatures than those of lactating females, which allows males to enter torpor during the day, thereby conserving energy (Hamilton and Barclay 1994). In contrast, lactating females tend to select roosts with higher ambient temperatures, which helps them maintain higher body temperatures, reduce the energy costs of endothermy, and avoid torpor during lactation (Solick and Barclay 2007), allowing them to reduce the energetic costs associated with raising pups (McLean and Speakman 2000, Barclay and Harder 2003). Several studies have suggested that rock roosts provide thermal environments (e.g., warmer roost temperature) within the thermal neutral zone more than tree roosts, and therefore influence the types of roosts selected by female western long-eared myotis during the reproductive period (Rancourt et al. 2005, Snider et al. 2013).

Except for one occasion when a bat roosted in a solitary rock on a pre-settlement juniper flat, rock roost sites were located on the two buttes in the study area; whereas, tree roost sites were distributed more evenly throughout the study area (Appendix C). Although I did not

compare rock roost site availability between the area on the two buttes and the rest of the study area, during the present study, rock roost site density appeared to be higher on the two buttes than the lower elevation juniper flats. Furthermore, potential solitary rock and rock formation roost sites were common on the two buttes, while, rock formation roost sites rarely occurred in the rest of the study area, but solitary rocks were common (Appendix G).

Despite the propensity of reproductive females to select rock roost sites when they are available, the flexible roosting behavior of this species allows it to occupy areas where rock roost sites are limited (Vonhof and Barclay 1997, Waldien et al. 2000, Arnett and Hayes 2009). For example, in managed conifer forests in the Pacific Northwest, western long-eared myotis used several types of roosts, and selection was strongly associated with the availability of snags, live trees, stumps, and downed logs (Waldien et al. 2000, Arnett and Hayes 2009). Contrary to these studies, bats in the present study primarily selected pre-settlement juniper trees with at least one cavity, even though snags, stumps, downed logs, and bark roost sites were also available (Appendix H). An underlying assumption in roost selection is that individual bats select roosts that will reduce energetic costs while raising pups, provide protection from predators, and space for social interaction to maximize their fitness (Barclay and Kurta 2007). Pre-settlement trees might provide a more stable thermal environment, roost permanency, and protection from predators than the other types of wood substrate roosts (Lewis 1995, Kunz and Lumsden 2003). However, during my pilot study in a location near, but outside the present study area, downed juniper logs and pre-settlement trees were selected with equal frequency, whereas rock crevices were not used as roosts. Although roost site availability was not estimated where the pilot study

was conducted, this area appeared to have fewer available rock roost sites than roost sites in wood substrate, indicating that relative availability of the different types of roost sites is an important component of roost site selection in juniper woodlands. If equal densities of roost sites of various types are available, the quality of roost sites might be more limiting to bat populations than the quantity of roost sites (Barclay and Kurta 2007).

The number of available roosts at the plot level was an important predictor in all of the roost selection models. The odds of use increased with additional available roosts for both tree and rock roosts. These results are consistent with previous studies that reported several species of *Myotis* selected roosts that were located in areas with higher densities of roost sites than random potential roosting areas (Brigham et al. 1997, Rabe et al. 1998, Waldien et al. 2000, Weller and Zabel 2001, Cryan et al. 2001, Baker and Lacki 2006, Arnett and Hayes 2009). Protecting areas with high densities of roosts is an important management objective for conserving existing bat populations (O'Donnell and Sedgeley 1999, Cryan et al. 2001). This might be especially true for species that exhibit low fidelity for particular roost sites, such as western long-eared myotis, which switch roosts an average of every 1.2 to 2 days, regardless of the type of roost used (Waldien et al 2000, Rancourt et al. 2005, Solick and Barclay 2006, 2007). Although individual bats in this study switched roosts frequently, consecutive roosts were not more than a few hundred meters apart, which has been reported in western long-eared myotis (Rancourt et al. 2005, Nixon et al. 2009) and other species of myotis (Weller and Zabel 2001, Bernardos et al. 2004). Fidelity to specific roosting areas potentially reduces energetic costs associated with finding new roost sites in unfamiliar areas, as long as suitable roost sites are readily available

(O'Donnell and Sedgeley 1999, Lewis 1995). Preference for particular roosting areas with many prospective roost sites suggests that individuals can attain the necessary resources (e.g., multiple roost sites, prey, water) to fulfill seasonal requirements during the reproductive period in these areas, while potentially reducing the chances of being discovered by a predator.

Climate models indicate that the reproductive success of many species of bats in the western United States is positively associated with availability of free water (Adams 2010). These models are supported by radio telemetry studies that show bats roosting closer to water sources than predicted by the distribution of available roost sites (Gellman and Zielinski 1996, Ormsbee and McComb 1998, Evelyn et al. 2004). However, studies examining this relationship in western long-eared myotis have produced mixed results. In piñon-juniper woodlands and ponderosa pine forest, bat roosts were located closer to water than random available roost sites (Rabe et al. 1998, Snider et al. 2013). Yet, in Douglas fir and ponderosa pine–shrub steppe communities, proximity of open water was not an important indicator of roost site selection (Waldien et al. 2000, Rancourt et al. 2005). Interestingly, tree roosts were not located closer to water than random roosts, whereas in the present study the odds of lactating females and males selecting a particular rock roost site decreased with increasing distance to a water source, suggesting water is important for individuals that use rock roost sites. Similarly, western long-eared myotis often forage and commute closer to water than expected (Chapter 3, Waldien and Hayes 2001). While this species occurs in both arid and mesic habitats, it is not as efficient at retaining water as other species that exclusively reside in arid habitats (Geluso 1978). Commuting between foraging areas, day roosts, and water sources is energetically costly for

bats; therefore, shorter commuting distances would reduce energy expenditure to meet water needs, all other factors being held constant (e.g., habitat quality, prey abundance; Tuttle 1976).

Western long-eared myotis females have been reported to roost in boulder fields (Solick and Barclay 2006) and under solitary rocks (Chruszcz and Barclay 2002, Rancourt et al. 2005). In this study, the probability of use by male bats increased if the roost site was in a rock formation, rather than in a single rock. An explanation for this result is not apparent, particularly because this result was not found for lactating female bats. Rock formations provide higher densities of potential roosting habitat than solitary rocks, which could reduce energetic costs of roost switching (Lewis 1995). For some bat species, lactating females tend to switch among roost sites less frequently than males and non-reproductive females (Kunz and Lumsden 2003). However, lactating females ($\bar{x}$ = 1.3, SE = 0.09) and males ($\bar{x}$ = 1.3, SE = 0.12) spent a similar number of consecutive days in particular roosts during this study, which is consistent with one other study that examined differences in roost fidelity between female and male western long-eared myotis (Nixon et al. 2009).

The probability of use increased for males that selected rock roost sites with area of pre-settlement woodlands within 1 km of male rock roost sites. These results might be explained by the flexible roosting behavior of males and the tendency to enter daytime torpor during the reproductive season. In this study, one third of tagged males used both rock and tree roosts. Because juniper woodlands support higher densities of pre-settlement trees (i.e., more available tree roost sites) than shrub-steppe communities, males might prefer areas that provide both types of roosts. Availability of both roost site types in close proximity would allow males to reduce

energetic costs associated with roost switching (Lewis 1995). Furthermore, having the choice of both rock and tree roost sites in an area permits males to adjust to fluctuations in ambient air temperature throughout the summer months, thus entering torpor more efficiently and consistently (Hamilton and Barclay 1994).

Tables

Table 2.1. Mean, standard error (SE), and 95% confidence intervals (95% CI) for roost site variables used by lactating female and male western long-eared myotis (M. evotis) in central Oregon, 2014-2015. Degrees of freedom (df), test statistics (t), and p-values (P), are derived from a Welches two-sample t-test comparing lactating females and males.

Variable	Lactating females			Males			df	t	P
	$\bar{X}$	SE	95% CI	$\bar{X}$	SE	95% CI	df	t	P
Tree roosts sites[a]									
Cavities	5.38	0.96	3.1-7.7	4.35	0.63	3.0-5.7	13.45	0.890	0.389
Height	6.52	0.52	5.3-7.7	5.86	0.52	4.8-6.9	20.40	0.894	0.382
Dbh	70.17	7.75	51.8-88.5	68.87	7.39	53.4-84.3	19.54	0.121	0.905
Canopy cover	47.69	3.94	38.4-57.0	49.67	6.60	35.6-63.7	21.69	-0.258	0.799
Available roosts	3.75	0.88	1.7-5.8	4.10	0.98	2.1-6.1	22.32	-0.266	0.793
Pre-settlement	4.63	0.96	2.4-6.9	3.50	0.66	2.1-4.9	13.97	0.965	0.351
Post-settlement	15.38	5.13	3.2-27.5	6.85	2.07	2.5-11.2	9.37	1.541	0.156
Distance to water	1743.49	55.63	1611.9-1875.0	2214.60	313.05	1559.4-2869.8	20.16	-1.482	0.154
Elevation	1503.12	3.88	1494.0-1512.3	1508.15	13.78	1479.3-1537.0	21.76	-0.351	0.729
Pre-settlement (1000 m)	304.15	5.94	290.1-318.2	294.69	4.52	285.2-304.2	15.53	1.267	0.224
Rock roosts sites[b]									
Height	107.35	24.49	57.5-157.2	95.23	40.23	11.8-178.7	37.76	0.257	0.798
Available roosts	41.711	4.63	32.3-51.1	17.48	3.75	9.7-25.2	61.00	4.068	<0.001
Pre-settlement	3.21	0.52	2.2-4.3	4.64	1.06	2.4-6.8	35.46	-1.207	0.235
Post-settlement	21.816	1.52	18.7-24.9	20.80	2.52	15.6-26.0	41.13	0.345	0.732
Distance to water	949.41	100.52	745.9-1152.9	1284.96	66.66	1147.3-1422.5	60.31	-2.782	0.007
Elevation	1583.80	6.42	1570.8-1596.8	1629.28	10.84	1606.9-1651.7	40.63	-3.610	<0.001
Pre-settlement (1000 m)	197.35	8.69	179.8-215.0	255.15	5.86	243.1-267.2	60.58	-5.513	<0.001

[a]Tree roost data: Tree height in meters, Dbh in centimeters, canopy cover in percent, distance to water in meters, elevation in meters, Pre-settlement in hectares.
[b]Rock roost data: Crevice height above ground in centimeters, distance to water in meters, elevation in meters, Pre-settlement in hectares.

Table 2.2. Model variables, number of parameters in the model (K), difference in AICc between the ith and the top ranked model (Δ_i), and Akaike weights (w_i = estimated probability of model i being the best model given the data and the set of candidate models) for candidate models developed to explain differences between used tree roost sites of western long-eared myotis and available tree roost sites in central Oregon during July, 2014 and 2015.

Model	K	AICc	Delta	Weight
Cavities + avail_tree + dist_water + pre_set_hr	5	60.80	0.000	0.386
Avail_tree + pre_set + post_set	4	60.99	0.195	0.350
Pre_set + post_set + pre_set_hr	4	62.12	1.319	0.200
Dist_water + elevation + pre_set_hr	4	65.30	4.504	0.041
Cavities + height + dbh + tree_cc	5	66.42	5.627	0.023

Table 2.3. Top models that best explained roost selection in trees for western long-eared myotis (n=12) in central Oregon during July, 2014 and 2015. Variable, coefficient estimates, standard error, odds ratios, and 95% confidence intervals for the best fitting model (plot model) and the global model (based on $\Delta_i < 2$ from the best model from AICc). Akaike's weights (*w*) are provided in parentheses.

Variable	Coefficient	SE	Odds Ratio	95% CI
Best-fitting model ($w_i = 0.386$)				
Cavities	0.129	0.126	1.137	0.892-1.478
Available tree roosts	0.379	0.164	1.461	1.103-2.112
Distance to water	0.020	0.038	1.020	0.949-1.103
Pre-settlement 1000 m	0.225	0.137	1.252	0.991-1.717
Second best-fitting model ($w_i = 0.350$)				
Available tree roosts	0.650	0.159	1.916	1.034-4.473
Pre-settlement trees	-0.211	0.310	0.810	0.418-1.407
Post-settlement trees	-0.030	0.036	0.967	0.898-1.037
Third best-fitting model ($w_i = 0.200$)				
Pre-settlement trees	0.249	0.126	1.283	1.017-1.684
Post-settlement trees	-0.033	0.034	0.967	0.900-1.030
Pre-settlement 1000 m	0.217	0.131	1.242	0.993-1.675

Table 2.4. Model variables, number of parameters in the model (K), difference in AICc between the ith and the top ranked model (Δ_i), and Akaike weights (w_i = estimated probability of model i being the best model given the data and the set of candidate models) for candidate models developed to explain differences between used rock roost sites of lactating female western long-eared myotis (n = 7) and available rock roost sites in central Oregon during July, 2014 and 2015.

Model	K	AICc	Delta	Weight
Single_form + avail_rock + dist_water + pre_set_hr	5	60.38	0.000	0.977
Avail_rock + pre_set + post_set	4	67.91	7.534	0.023
Dist_water + elevation + pre_set_hr	4	81.01	20.636	0.000
Single_form + vert_horz	3	85.49	25.114	0.000
Pre_set + post_set + pre_set_hr	4	91.85	31.476	0.000

Table 2.5. Variable, coefficient estimates, standard error, odds ratio, and 95% confidence intervals for the best fitting model (global model) that explained roost site selection in rocks for lactating female western long-eared myotis (n = 7) in central Oregon during July, 2014 and 2015.

Variable	Coefficient	SE	Odds Ratio	95% CI
Single or Formation	-0.673	0.899	0.400	0.062-2.165
Available rock roosts	0.071	0.026	1.074	1.029-1.138
Distance to water	-0.161	0.072	0.863	0.733-0.980
Pre-settlement 1000 m	-0.027	0.087	0.977	0.826-1.171

Table 2.6. Model variables, number of parameters in the model (K), difference in AICc between the ith and the top ranked model (Δ_i), and Akaike weights (w_i = estimated probability of model i being the best model given the data and the set of candidate models) for candidate models developed to explain differences between used rock roost sites by male western long-eared myotis (n = 11) and available rock roost sites in central Oregon during July, 2014 and 2015.

Model	K	AICc	Delta	Weight
Single_form + avail_rock + dist_water + pre_set_hr	5	46.35	0.000	0.967
Avail_rock + pre_set + post_set	4	54.36	8.008	0.018
Dist_water + elevation + pre_set_hr	4	54.68	8.331	0.015
Single_form + vert_horz	3	70.44	24.097	0.000
Pre_set + post_set + pre_set_hr	4	71.80	25.458	0.000

Table 2.7. Variable, coefficient estimates, standard error, odds ratio, and 95% confidence intervals for the best fitting model (global model) that explained roost selection in rocks for lactating female western long-eared myotis (n = 11) in central Oregon during July, 2014 and 2015.

Variable	Coefficient	SE	Odds Ratio	95% CI
Single or Formation	-1.901	0.942	0.149	0.019-0.857
Available rock roosts	0.132	0.077	1.141	1.009-1.365
Distance to water	-0.422	0.170	0.656	0.437-0.872
Pre-settlement 1000 m	0.476	0.200	1.610	1.140-2.550

Figures
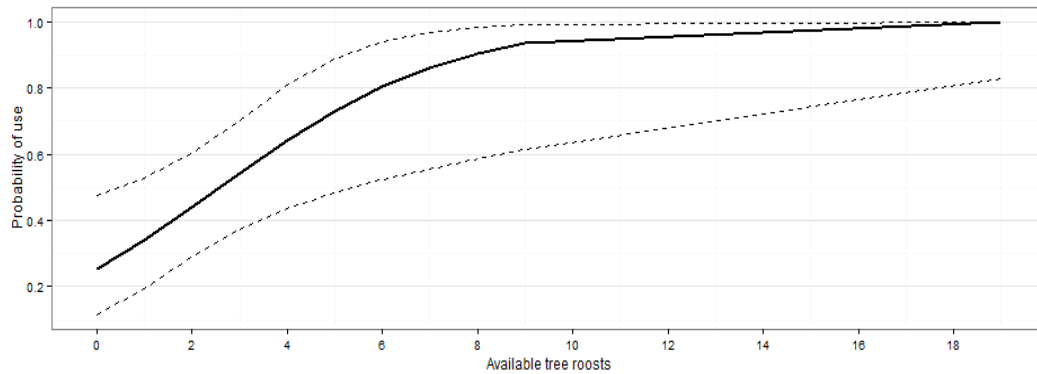
Figure 2.1. Effects of available tree roosts on the probability of western long-eared myotis (n=12) selecting a tree roost site in a western juniper woodland of central Oregon during July, 2014 and 2015. Dotted lines are 95% confidence intervals.
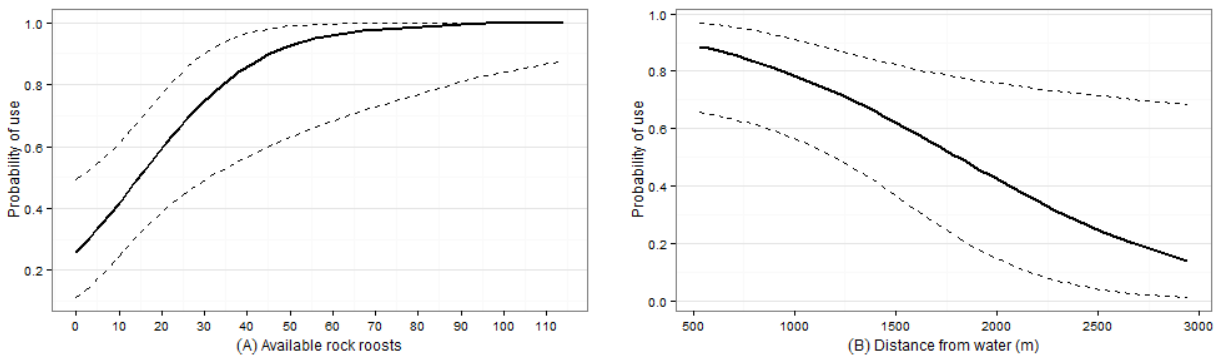
Figure 2.2. Effects of available rock roosts (A) and distance from water in meters (B) on the probability of lactating female western long-eared myotis (n=7) selecting a rock roost site in a western juniper woodland in central Oregon during July, 2014 and 2015. Dotted lines are 95% confidence intervals.
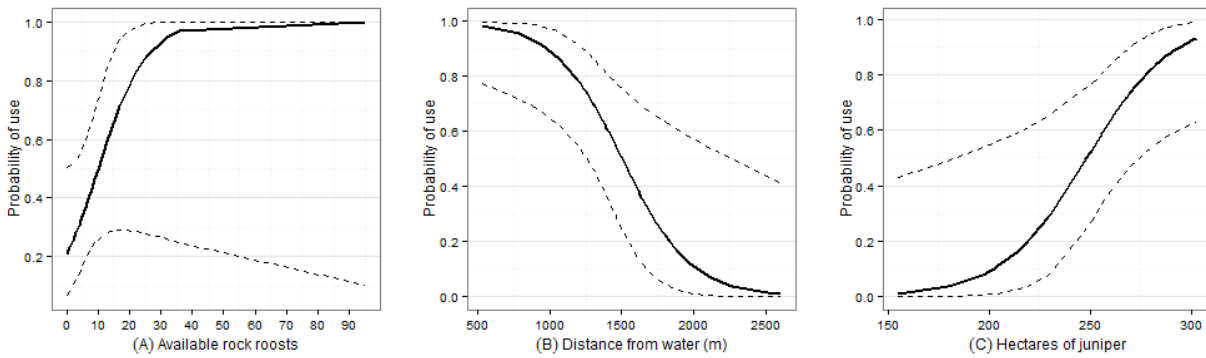
Figure 2.3. Effects of available rock roosts (A), distance from water in meters, (B) and hectares of juniper within 1 km of roosts (C) on the probability of male western long-eared myotis (n=11) selecting a rock roost in western juniper woodland in central Oregon during July, 2014 and 2015. Dotted lines are 95% confidence intervals.

CHAPTER 3: HABITAT SELECTION AND SPACE USE OF *MYOTIS EVOTIS* IN A WESTERN JUNIPER WOODLAND OF CENTRAL OREGON

Abstract

Habitat selection and estimates of home range size provide land managers with information that is required to make informed decisions regarding wildlife conservation and management across multiple spatial scales. However, knowledge of habitat selection and space use is not well understood for bat species in North America, especially in western juniper woodland and shrub-steppe habitats. During the last 150 years, piñon (*Pinus monophylla*) and juniper (*Juniperus occidentalis* ssp. *occidentalis* and *J. osteosperma*) populations have expanded in geographic range and density in the western United States. Attempts to restore habitat for the greater sage-grouse (*Centrocercus urophasianus*) across its range often involves removal of trees with little understanding of the effects on bat populations. I used radio telemetry to examine space use of the western long-eared myotis (*M. evotis*) and habitat selection at two spatial scales (home range and landscape). Mean home range size and mean maximum foraging range did not differ between lactating females and males; however, statistical power to detect differences was low due to small sample sizes. Home range size estimates for lactating females ($\bar{x}$ = 205.85 ha, SE = 47.94) and males ($\bar{x}$ = 424.2 ha, SE = 187.2) are among the largest estimates reported for *Myotis* species in North America. Maximum foraging range for lactating females was $\bar{x}$ = 933 m (SE = 284.9) and males $\bar{x}$ = 1522 m (SE = 532.8). Best habitat selection models for lactating females and males differed across spatial scales, based on Akaike Information Criterion with a bias correction term for small sample size (AICc). At the home range scale, habitat use was

negatively related with distance from water, whereas, males selected areas with > 0-10% canopy cover over areas with no canopy cover. At the landscape scale, habitat use by lactating females and males decreased with increasing distance from roosts and water sources. Additionally, lactating females selected pre-settlement juniper woodlands more than shrub-steppe habitats, but avoided areas with > 20% canopy cover more than areas with no canopy cover at the landscape scale. These results emphasize the importance of managing pre-settlement woodlands that are located near roost sites and water sources for variable tree densities to maintain foraging areas for bats.

Introduction

Understanding the habitat and space requirements of species is critical for wildlife conservation planning across intensively managed landscapes (Morrison et al. 2006). However, complex interactions between wildlife, habitat, and land use make it challenging for land managers to apply wildlife conservation principles across multiple spatial scales because these relationships are often scale dependent (Wiens 1989, Levin 1992). Therefore, management actions at fine scales might not be appropriate at broad scales. Moreover, the ecological patterns and processes that we observe are attributed, in part, to the scale at which they are measured (Wiens 1989).

Species-specific requirements and physiological tolerances determine where animals can live. Johnson (1980) described habitat selection as a hierarchical process that occurs at four distinct spatial scales or selection orders for a given species. The *first order* is the selection of a physical or geographic range; the *second order* is the selection of a home range for an individual or group within the geographic range; the *third order* is the selection of particular patches within

the home range; and the *fourth order* is the selection of fine scale resources or patches of concentrated use (e.g., food items), usually within the third order core. Home range is defined as the extent of an area an individual uses to survive, reproduce, and maximize its fitness during a specified period of time, such as a life stage or season (Kernohan et al. 2001). Habitat selection and home range estimates are two measures that researchers use to gain insight into why individuals use certain areas more than other areas that appear to be available for use. These two measures provide important knowledge for wildlife conservation planning because they are functions of individual-scale behavioral responses and relationships with environment that have implications for reproduction and survival based on species-specific habitat requirements (Johnson 1980, Morrison et al. 2006).

Despite being the second largest order of mammals (Chiroptera), the species-specific habitat and space requirements of bats are not well understood (Racey and Entwistle 2003). This is largely due to their elusive nature and low body mass, which limits radio telemetry studies, of many bat species throughout the world. In North America, most research has focused on either large-bodied bats or species that are currently listed as threatened or endangered under the U.S. Endangered Species Act, or are at risk of being listed (Lacki et al. 2007). Recently, the research focus has shifted to wide-ranging bat species that were historically considered common or abundant (Coleman et al. 2014, Randall et al. 2014), but which are now experiencing significant local and regional population declines due to *Pseudogymnoascus destructans* (White-nose Syndrome) (Frick et al. 2010, Brooks 2011).

Factors such as habitat type, vegetation structure, landscape features (e.g., water sources), and spatial scale affect the selection processes of many *Myotis* species in North America (Lacki 2007). Several species show preference towards specific habitat types (i.e., vegetation

communities), particularly when they are associated with land use and landscape features (Henderson and Broders 2008, Womack et al. 2013*a*, Kniowski and Gehrt 2014). In arid environments, water is a crucial resource that influences the distribution of bat species (Tuttle 1976), and water availability helps conserve existing bat populations (Adams and Hayes 2008). Spatial scale is important because it links the selection processes of individuals to the spatial distribution pattern of specific critical resources. More recent studies have observed differences in the way individuals within populations select areas relative to scale (Ducci et al. 2015), thus potential factors driving intraspecific variation in habitat selection should also be investigated.

Myotis evotis (western long-eared myotis) is often one of the most ubiquitous species of bat where it occurs throughout the western United States and Canada (Manning and Jones 1989, Holloway and Barclay 2000, O'Shea et al. 2011). It inhabits a wide variety of forested and treeless vegetation associations including Douglas fir (*Pseudotsuga menzesii*) forest, ponderosa pine (*Pinus ponderosa*) forest, juniper (*Juniperus* spp.) woodland, shrub-steppe, scablands, riparian habitats, and agricultural areas (Manning and Jones 1989, Rabe et al. 1998, Chung-MacCoubrey 2005, Rancourt et al. 2005, Arnett and Hayes 2009, Nixon et al. 2009, Snider et al. 2013). Few data exist to explain habitat selection and space use requirements for *M. evotis.* In the sole published paper on these attributes, nightly activity areas of female *M. evotis* were closer to water than random areas, but did not differ among forest stand structures in managed Douglas fir forests of western Oregon (Waldien and Hayes 2001).

Native shrub-steppe communities and piñon (*Pinus monophylla*) and juniper (*Juniperus occidentalis* ssp. *occidentalis* and *J. osteosperma*) woodlands throughout the western United Sates have experienced dramatic shifts in community dynamics during the last 150 years due to piñon-juniper expansion and infill into these respective communities (Burkhardt and Tisdale

1969, Young and Evans 1981, Miller and Tausch 2001, Miller et al. 2005, 2008, Johnson and Miller 2006). Piñon-juniper woodlands (tree canopy cover >10 %) and savannas (tree canopy cover < 10%) have increased 10-fold since post-European settlement management began during the 1870's (Miller and Tausch 2001). In Oregon, significant tree expansion has occurred, increasing the range of western juniper (*J. occidentalis*) from 600,000 ha to 2.6 million ha during the last ~85 years (Rowland et al 2008). Prior to post-settlement expansion, western juniper woodlands configuration consisted of small stands with low vegetation production and fuel loads which reduced fire severity, allowing pre-settlement woodlands (> 150 years old) to persist across the landscape (Burkhardt and Tisdale 1969, Young and Evans 1981, Miller and Rose 1999). One exception, where pre-settlement woodlands and savannas formed relatively large stands (> 100 km²), is in the ashy-sandy-pumice soils of central Oregon (Waichler et al. 2001).

Tree expansion into shrub-steppe communities alters ecological processes (i.e., nutrient cycles; Doescher et al. 1987) and degrades understory vegetation composition and structure (Miller et al. 2000), yet the impacts to wildlife populations are not well known. Species that have evolved in a treeless, shrub-steppe landscape, such as greater sage-grouse (*Centrocercus urophasianus*), will likely experience negative impacts (Baruch-Mordo et al. 2013), but bat populations might benefit from increased roosting habitat (i.e., tree cavities and under bark). Several federal and state management agencies, plus private landowners, are attempting to remove all post-settlement (< 150 years old) juniper trees in shrub-steppe communities to restore sage-grouse habitat across its range (NRCS 2012) with little understanding of the effects on bat populations.

I examined the habitat selection and spatial responses of *M. evotis* in a juniper woodland at two spatial scales, (1) home range selection on the landscape and (2) resource selection within

the home range. I hypothesized that the mean home range size for lactating females would differ from the mean home range size of males. I predicted that lactating females would use smaller home ranges than the males because lactating females would presumably return to day roosts at night to nurse pups (Henry et al. 2002, Murray and Kurta 2004) and this central place foraging would limit the distances they would travel from the day roost to forage. For similar reasons, I tested the hypothesis that the mean maximum foraging range of bats differed between lactating females and males. I predicted the mean maximum foraging range that lactating females traveled from their day roosts each night would be less than the mean maximum foraging range for males. Lastly, I tested the hypothesis that habitat selection was influenced by spatial scale and would be directly related to habitat type, canopy cover, distance to day roosts, and distance to water. I predicted the probability that a bat would use an area more than availability was influenced by one or all four covariates. To test this hypothesis, I developed three models or hypothesis tests. In the first model, I tested whether all four covariates (global model) influenced habitat selection. In the second model, I tested the effects of habitat type and tree canopy cover. Finally, in the third model, I tested whether the two distance variables (distance to roost and distance to water) influenced selection.

Materials and Methods

Study Area

This study area, which is managed by the Bureau of Land Management (BLM), is located in the Northern Basin and Range ecoregion, approximately 84 km southeast of Bend, OR, and 18 km (11.2 miles) southwest of Hampton, OR. The study area encompassed 3,720 ha and included four seasonal water sources, two of which were used as sites to capture bats for radio telemetry

(43°63'N latitude, 120°46'W longitude and 43°61'N latitude, 120°47'W longitude). Vegetation in the study area is characterized as a mosaic of pre-settlement western juniper woodlands (*Juniperus occidentalis*), sagebrush-steppe (*Artemisia* spp*.)*, and playa (i.e., seasonal wetlands) plant communities. Pre-settlement juniper woodlands (2,536 ha) are the most abundant plant community in the study area followed by sagebrush-steppe (998 ha) and playas (186 ha). Juniper woodlands are dominated by pre- and post-settlement trees with a low sagebrush (*Artemisia arbuscula*) and Idaho fescue (*Festuca idahoensis*) understory plant community. Low sagebrush and mountain big sagebrush (*A. tridentata* (Nutt.), ssp*. vaseyana*) occurs with Idaho fescue in the sagebrush-steppe community. Playas are natural depressions on the landscape that are typically inundated annually due to precipitation and surface run-off, creating a unique plant community that has a higher tolerance of moist soils than the adjacent upland vegetation. Playas contain either a plant community dominated by silver sagebrush (*A. cana*) / Nevada bluegrass (*Poa nevadensis*) – beardless wildrye (*Leymus triticoides*) or one dominated by a spikerush (*Eleocharis* sp.) – dock (*Rumex* sp.), or both. The study area receives an annual average precipitation of 28 cm, primarily during November – January in the form of snow and during May – June as rain. Average temperatures during the warmest month (July) reach 17°C, while average temperatures during the coldest month (December) drop to -3°C. Topography in the study area is generally flat with an average elevation of 1,524 m, except for two buttes that reach elevations of 1635 m and 1,729 m, respectively.

Western juniper has spread into sagebrush-steppe and infilled pre-settlement juniper woodlands, reducing the resiliency and resistance of these plant communities to disturbance (Stringham et al. 2003, Briske et al. 2008). The BLM actively restores plant communities that are threatened by western juniper expansion and infill by thinning post-settlement trees. Typically,

every post-settlement tree is removed in shrub-steppe treatments and a few (2.5 – 9.8 trees/ha) are retained in pre-settlement woodlands for recruitment. Within the study area, 437 ha were thinned in both shrub-steppe and pre-settlement juniper woodlands. Consequently, juniper spatial structure is not uniform across the study area and areas of pre-settlement juniper woodlands that were thinned have lower juniper density than non-thinned areas. The study area contains 1,170 ha (31%) with no juniper canopy cover, 1,030 ha (28%) with 0% – 10% juniper cover, 979 ha (26%) with 10% - 20% juniper cover, and 539 ha (15%) >20% juniper canopy cover.

Playas were excavated (i.e., dug out) during the 1960s to 1980s in efforts to provide water for cattle and wildlife over longer durations than was provided by natural playas. Water availability in dug outs is seasonal, typically lasting through mid-August during average precipitation years when cattle are present. However, all three playas occasionally hold water the entire year during average precipitation years when cattle are absent (CRA, pers. obs.).

Bat Capture and Handling

I captured bats during 10 total nights during July 7 – 20 in 2014 and 2015 by placing mist nets over two seasonal water sources located on playas. The seasonal water source used for bat capture in 2014 was dry in 2015, so I relocated the capture site to a water source 2.7 km south of the 2014 capture site in 2015. For each captured bat, I recorded species, body mass, sex, age class (adult or juvenile), ear length, forearm length, and reproductive status for females. I distinguished between adults and juveniles by the degree of ossification of the phalanges of the third metacarpal (Brunet-Rossinni and Wilkinson 2009). Females were classified as (1) pregnant, if a fetus was present in the abdomen as determined by gently pressing on the lower abdomen, (2) lactating, if milk was secreted from the nipples or if the nipples were erected and hair was not

present around the nipples; but no milk was secreted or (3) non-reproductive, if none of the previous criteria applied (Racey 2009). I attached radio transmitters (Model BD-2X; Holohil Systems Ltd., Carp, ON, Canada) to the upper scapulae of lactating female and male *M. evotis* by trimming hair from a small area, applying Perma-Type surgical adhesive (The Perma-Type Company Inc., Plainville, CT, USA), and pressing the transmitter to the skin. Bats were held for 10 minutes to allow the adhesive to set, and then released at the capture site. I assumed all individual bats in the study area were equally likely to be captured and were a random sample of the population in the study area (Manly et al. 2002). Transmitters weighed 0.34 g or 0.36 g, and transmitter-to-body mass proportions for all radio-tagged bats were < 6.18%. Proportionate tag mass for five tagged individuals (16%) was < 5% (Aldridge and Brigham 1988, Neubaum et al. 2005), proportionate tag mass for 24 individuals (75%) was between 5% and 6%, proportionate tag mass for three individuals (9%) was > 6%. All handling and tracking procedures with bats were conducted under permits issued by the Oregon Department of Fish and Wildlife (Permit no. 111-14, Permit no. 084-15), and protocols were approved by the Institutional Animal Care and Use Committee at Oregon State University (ACUP 4469).

Radio Telemetry

I tracked individual bats for approximately 12 consecutive nights after they were fitted with a transmitter. I attempted to follow individuals from the time they exited day roosts at night until they returned to their roost for the day. We used three mobile telemetry stations to triangulate bats while they were flying and did not include individuals that appeared stationary based on a consistent radio pulse. Each mobile station was equipped with a receiver (model R-1000, Communication Specialists Inc., Orange, California or model R-2000 Advanced Telemetry

Systems, Isanti, Minnesota), handheld 3-element Yagi antenna, handheld radio, and compass. I used the null to null method to bisect the smallest angle while obtaining bearings at each telemetry station (Amelon et al. 2009) and attempted to collect simultaneous bearings at 10-min intervals to ensure consecutive locations were spatially and temporally independent of each other (Swihart and Slade 1985), however, the average minutes between consecutive locations was 30 minutes (SD = 2). I plotted the telemetry station coordinates and bearings in the program Locate III (Nams 2006) while in the field to measure the accuracy of each location fix. I used the maximum likelihood estimator and considered locations unreliable if the size of the 95% error ellipse was > 3 ha. When this occurred, I immediately collected another set of bearings until the 95% error ellipse was below 3-ha threshold.

Home Range and Maximum Foraging Range Estimation

I used the fixed kernel density method to estimate utilization distributions (UD) (Worton 1989) and then calculated 50% and 95% probability contours from the UD for each radio-tagged individual. Kernel density methods calculate UD by applying a kernel function (probability density function), which includes a bandwidth (smoothing parameter) over locations and sums the volume at a fixed percentage under each kernel function (Worton 1989). Bandwidths heavily influence UD estimates with kernel density methods because they control the width of the kernel function (Kernohan et al. 2001, Appendix I). Small widths include fine detail (under-smooth) in the data but potentially inflate Type II error, whereas large widths loosely fit around locations (over-smooth) and can increase Type I error (Kernohan et al. 2001, Kie 2013). I used the ad hoc bandwidth ($h_{ad\ hoc}$) rather than the least-squares cross-validation score (h_{lsvc}) or reference bandwidth (h_{ref}) because 1) the $h_{ad\ hoc}$ allowed me to choose a 95% probability contour that was

one contiguous polygon, as opposed to the multiple polygons that often occur with h_{lsvc} and 2) h_{ref} and h_{lsvc} tend to over-smooth data and inflate home range size estimates (Type I error) based on small samples (Kie 2013). I chose the smallest contiguous polygon of the h_{ref} by reducing the h_{ref} by increments of 0.10 (i.e., $h_{ad\ hoc} = 0.9 * h_{ref}$, $0.8 * h_{ref}$, etc.) and stopping just before the polygon disjointed into multiple polygons (Kie 2013). If the initial home range estimate from the h_{ref} resulted in two or more polygons, I accepted this as the final estimation in the results.

Similar to the choice of bandwidth, there is ambiguity in the minimum number of locations per individual required to accurately estimate UD using kernel density methods (Garton et al. 2001, Kernohan et al. 2001). Seaman et al. (1999) suggested a minimum of 30 locations per individual for unbiased home range estimates, although several home range studies involving bats have included individuals with < 30 locations (Adam et al. 1994, Carter et al. 2004, Morris et al. 2011). To determine whether a minimum of 20 locations was appropriate for analysis, I randomly selected 20 locations from all the individuals with > 30 locations and recalculated 95% probability contours using the same methods as the initial home range estimates based on all available locations. I used a paired t-test to compare the differences between each individual's home range sizes when estimated from 20 locations to that estimated from the full data set.

I included day roost sites and capture sites for home range analysis because they were known locations that were used by bats during the study, but were not obtained through triangulation (Lacki et al. 2007). I used OpenJUMP HoRAE (Steiniger and Hunter 2012) to generate 50% and 95% probability contours for each bat and to provide UD using h_{lsvc} to compare with results of previous studies. I used the 95% bandwidth value to calculate both polygons.

In addition to home range estimates, I included a simple measure of movement in the space use analysis. I estimated the maximum foraging range an individual traveled each night from its day roost by calculating the distance between individual's day roosts and the location that was furthest from its day roost, during subsequent nightly foraging attained with triangulation, with the near analysis tool in GIS.

Study Design and Habitat Selection Model Covariates

I conducted a use-availability comparison to determine the probability of use within each individual's home range and across the study area. This design is similar to a Design III resource selection study in which each used location is compared to a random available location (Manly et al. 2002) at second- and third-order spatial scales of availability, respectively (Johnson 1980). I used ArcGIS 10.2 to define the study area and to create random available points. I dissolved radius buffers around each day roost, which were the estimated home range size for lactating females (810 m) and males (1,162 m), to create one contiguous polygon. For each location, I generated a random point inside the home ranges of individuals and within the study area.

I evaluated the probability of use as a function of four landscape covariates (habitat type, tree canopy cover class, distance to water, and distance to day roosts). To retrieve soil mapping unit spatial data, I used the Web Soil Survey (2015) that was developed in 2013 for Deschutes and Lakeview Counties, Oregon (Upper Deschutes River Area, Oregon, Parts of Deschutes, Jefferson, and Klamath Counties (OR620) and Lake County, Oregon, Northern Part, Parts of Lake and Klamath Counties (OR635). I obtained ecological site information, including the historical climax plant community, from the soil mapping unit data. In ArcGIS, I delineated soil mapping units containing western juniper as the dominant tree in the ecological site description

as pre-settlement woodlands and all other mapping units, including playas, as shrub-steppe. I used these classes as a categorical variable in my models. I reclassified a current stand mapping model for juniper in Oregon (Nielsen and Noone 2014) to four tree canopy percent cover categories (no cover, >0-10%, >10-20%, and >20%). I used the near analysis tool to calculate distance (m) from used and available locations to water sources (i.e., playa dugouts and water troughs) and to day roost sites.

Statistical Analysis

I pooled data from 2014 and 2015 and analyzed lactating females and males separately. I used a Welch's two sample t-test to determine if the mean home range size and the mean maximum foraging range of bats each night from day roosts differed between lactating females and males, respectively. I selected Welch's two sample t-test because the variance in home range size and maximum foraging range for bats was slightly unequal between the grouping variables (lactating female and males).

For the habitat selection analysis, I used either a generalized linear model (GLM) or a generalized linear mixed model (GLMM) to model the binary dependent variable (used-available) as a function of the four independent covariates. The logistic regression model, a type of GLM, is a universal resource selection function because of its ability to model binary data (Manley et al. 2002). A GLMM is a slightly more powerful resource selection function for examining population level habitat selection because of its ability to handle non-normal data and incorporate random effects (Bolker et al. 2008). By including a random effect for individual bats, I was able to relax some of the constraints related to independence among locations within individuals, unbalanced numbers of locations among individuals, and variation among

individuals (Gillies et al. 2006). I used a GLM when the residuals from the global model indicated no dependence among individuals and that the model fit was adequate (J. Peterson, pers. comm.). This was further supported by the lack of evidence of predictable variation among individual bats, as indicated by the attempt to fit a GLMM (Bates 2010). I used the GLMM when these conditions were not met.

I developed three conceptual models for lactating females and males at the home range scale and the landscape scale. I used either the glm function or the glmer function from the lme4 package for R (version 3.0.2, R Development Core Team 2013) to fit each model: (1) global model: RSF = intercept + habitat type + tree canopy cover class + distance to water + distance to day roosts; (2) juniper model: RSF = intercept + habitat type + tree canopy cover class; and (3) distance model: RSF = intercept + distance to water + distance to day roosts. For the categorical variables, I defined habitat type as either pre-settlement woodland (0) or shrub-steppe (1), and created three dummy variables for each cover class and made no cover the reference category. I did not include day roost and capture sites in the habitat selection analysis.

Prior to analysis I checked for correlation among independent variables using the ggpairs function from the GGally package for R. Even though this technique is considered data mining by some authors (Burnham and Anderson 2002), multicollinearity between independent variables can cause estimated coefficients to be unreliable because the standard errors of the coefficients are inflated. I decided *a priori* if the correlation between two independent variables was greater than 0.7 that I would remove one of the variables. I did not detect correlation coefficients between independent variables greater than 0.68, so I used every variable in the analysis (Appendix E). Additionally, I checked model fit with a Hosmer-Lemeshow goodness-

of-fit test and I excluded models that were statistically different from expected fit (P < 0.05) (Appendix J).

I compared models using Akaike's Information Criterion with a bias correction term for small sample size (AICc, Burnham and Anderson 2002). I used AICc because the number of observations was relatively small compared to the number of parameters in each model ($n / K <$ 40, where $n =$ sample size and $K =$ number of model parameters, Burnham and Anderson 2002). For AICc, I report the number of parameters in each model (K), AICc values, difference in AICc score between the *ith* and the top ranked model (Δ_i), and Akaike weights ($w_i =$ estimated probability of model *i* being the best model given the data and the set of candidate models). I considered models competitive if $\Delta_i < 2$ (Burnham and Anderson 2002, Burnham et al. 2011). I used the Laplace approximation from glmer function to calculate coefficient estimates and report the coefficient estimates, standard errors, odds ratios (exponentiation of parameter estimates), and 95% confidence intervals of the top models.

Results

I captured 81 individuals of four different species (*Myotis evotis*, $n = 66$; *Pipistrelles Hesperus*, $n = 9$; *Myotis volans*, $n = 4$; *Myotis ciliolabrum*, $n = 2$) and attached radio transmitters to 32 *M. evotis* ($n = 15$ lactating females, $n = 17$ males). I collected a total of 305 location fixes ($\bar{x} = 30.75$ per individual, SE = 2.26 per individual) from 12 individuals ($n = 6$ lactating females, $n = 6$ males) over an average of 7.56 (SE = 0.52) days (Table 3.1).

Home Range

There was no evidence that the estimated mean home range size differed between estimates based on ≥ 20 locations and those based on > 30 locations (paired t-test, $t_8 = 1.534$, $P = 0.164$). Therefore, I included all 12 individuals with ≥ 20 locations in the home range analysis (Table 3.2). Mean 50% home range size did not differ (Welch's two sample t-test, $t_{5.38} = -0.984$, $P = 0.367$) between lactating females ($\bar{x} = 50.33$, SE = 10.95, $n = 6$) and males ($\bar{x} = 106.68$, SE = 56.17, $n = 6$). Similarly, size of the 95% home range did not differ between lactating females and males (Welch's two sample t-test, $t_{5.653} = -1.129$, $P = 0.304$). Mean 95% home range size for lactating females was 205.85 ha (SE = 47.94) and for males was 424.2 ha (SE = 187.2).

Maximum Foraging Range

The mean maximum foraging range did not differ (Welch's two sample t-test, $t_{5.96} = -0.973$, $P = 0.368$) between lactating females ($\bar{x} = 933$ m, SE = 284.9, $n = 4$) and males ($\bar{x} = 1522$ m, SE = 532.8, $n = 5$).

Habitat Selection

I included eight individuals ($n = 4$ lactating females, $n = 4$ males) that had > 30 locations in the habitat selection analysis. The best model for lactating females at the home range scale was the distance model that included distance to water and distance to day roosts (Table 3.3). This model had an AIC_c weight of 0.522 and explained the variation in the RSF 2.09 times (0.522/0.250) better than the second best model. The global model ($\Delta_i = 1.47$) and the juniper model ($\Delta_i = 0.1.65$) were the second and third best models, with AIC_c weights of 0.250 and 0.228, respectively. The top model for males at the home range scale was the juniper model,

which included habitat type and tree canopy percent cover. This model had an AIC_c weight of 0.682 and explained the variation in the RSF 2.45 times (0.682/0.278) better than the second best model. The second best model was the global model ($\Delta_i < 2$), with an AIC_c weight of 0.278, and explained the variation in the RSF 6.95 times (0.278/0.040) better than the third model. At the landscape scale, the best model to describe habitat selection by lactating females was the global model (habitat type, tree canopy cover, distance to water, and distance to roost) (Table 3.4). This model had an AIC_c weight of 0.984 and explained the variation in the RSF 61.5 times (0.984/0.016) better than the second best model. There were no other models with $\Delta_i < 2$. The top model for males at the landscape scale was the distance model. The AIC_c weight of this model was 0.681 and explained the variation in the RSF 2.13 times (0.681/0.319) better than the second best model. The second best model was the global model ($\Delta_i = 1.51$) with an AIC_c weight of 0.319.

The odds that a location was selected by a lactating female at the home range scale decreased by 6% for every 100-m increase in distance from water (Table 3.5, Fig. 3.1). The odds that a location was selected by a male were 93% higher when canopy cover was > 0-10% compared to no tree canopy cover. At the landscape scale, the odds that a location was selected by a lactating female decreased by 27% for every 100-m increase in distance from its day roost, decreased by 28% for every 100-m increase in distance from water, and decreased by 82% for shrub-steppe compared to juniper woodlands, and decreased by 88% for canopy cover > 20% compared to no tree canopy cover (Table 3.6). For males, the odds that a location was selected decreased by 15% and by 18% for every 100-m increase in distance from its day roost site and from a water source, respectively (Fig. 3.2).

Discussion

I examined the habitat selection and spatial use of *M. evotis* in a juniper woodland in central Oregon during July, in 2014 and 2015. I expected lactation and pup rearing would restrict the spatial extent of foraging by lactating females compared to males; however, I did not detect a statistical gender difference in either mean home range size or mean maximum foraging range despite best estimates for home range size, for both the 50% and 95% kernel density home range, being twice as large in males compared to lactating females, plus the mean maximum foraging range was nearly 40% greater in males than in lactating females. Furthermore, these estimates of home range size and maximum foraging range are consistent with what I hypothesized. Although several studies have examined sexual differences in space use by North American bat species (Adam et al. 1994, Elmore et al. 2005, Menzel et al. 2005, Morris et al. 2011), only one study detected differences between females and males (Randall et al. 2014). This is surprising because of the differences between the sexes in the physiological and behavioral requirements of reproduction in bats (Speakman and Thomas 2003).

One potential explanation for these results is the small number of samples from these study designs and consequently low statistical power to detect differences between sexes (Type II error). Statistical power and sample size are directly related, thus a decrease in one component lowers the other (Cohen 1992, Steidl et al. 1997). In previous studies of gender differences in space use by bats, fewer than 10 individuals per sex were used in spatial analyses (Adam et al. 1994, Elmore et al. 2005, Menzel et al. 2005, Morrison et al 2011). Similarly, I used only six lactating females and six males in the present study. Therefore, I calculated effect sizes for 50% and 95% probability contours using the compute.es package for R, then conducted a retrospective power analysis (Steidl et al. 1997) using the pwr package for R to determine the

number of individuals (per sex) necessary to detect a difference in home range size at an alpha level of 0.05, power of 0.8, and effect size (50% probability contour = 0.57; 95% probability contour = 0.65). The results from this power analysis suggest that nearly a four-fold increase in sample size would be necessary to detect a difference between the mean home range size of lactating females and males (50%: $n = 49.29$; 95%: $n = 38.12$).

My estimates of home range size for lactating females and males are the largest ever reported for *M. evotis* and are among the largest estimates for any *Myotis* species in North America. Waldien and Hayes (2001) measured activity areas for *M. evotis* of 38 ha and ranged out to 512 m from day roosts within mixed conifer forests of the Cascade Mountains in Oregon. Similar lower estimates were reported from two other *Myotis* species: 46 ha and 14 ha foraging areas for female and male *M. septentrionalis* (northern long-eared myotis), respectively in New Brunswick, Canada (Borders et al 2006); 50 ha for lactating female *M. septentrionalis* in West Virginia (Owen et al. 2003); and 17 ha and 6 ha (90% and 50% probability contours, respectively) for lactating female *M. lucifugus* (little brown myotis) in Quebec, Canada (Henry et al. 2002). Several studies involving *M. sodalis* (Indiana myotis) have reported home range size estimates more similar to the estimates from the present study: 161 ha for lactating females and 116 ha for males in Illinois (Menzel et al. 2005); 1361 ha for lactating females in Missouri (Womack et al. 2013*b*); and 236 ha for lactating females in Ohio (Kniowski and Gehrt 2014). Reported foraging ranges from day roosts to foraging areas of female (5224 m) and male (817 m) *M. lucifugus* were 5.6 times larger and 1.9 times lower than the point estimates from the present study (Randall et al 2014).

Comparing space use estimates with previous studies can be difficult or inappropriate because of differences among the subjects that were examined and the methods used to collect

data (Miller et al. 2003, Amelon et al. 2014). Home range size comparisons across species, sexes, and reproductive status should be carefully examined due to the variability in physiological and behavioral responses to intrinsic and extrinsic factors within these three categories (Miller et al. 2003). For instance, some species appear to have fidelity for particular foraging areas (Rydell 1989, Hillen et al. 2009), while other species are more opportunistic (Brigham 1991, Murray and Kurta 2004), suggesting interspecific differences in foraging behavior. Within species, space use appears to be highly influenced by reproductive status; in particular, lactating females use smaller home ranges than pregnant females (Henry et al. 2002).

Study methods and the type of equipment used to collect data can greatly influence results in studies of space use (Garton et al. 2001, Amelon et al. 2009). In this study, I used three mobile telemetry stations equipped with 3-element handheld Yagi antennas and receivers. I used three R-1000 Communications Specialist receivers the first year and supplemented one of the R-1000's with an R-2000 Advanced Telemetry Systems receiver the second year. I originally attempted to collect data from fixed telemetry stations, but my ability to triangulate consistent location fixes was inconsistent, although two of the stations were positioned near the top of buttes at elevations higher than most of the study area. The maximum range with the R-2000 was approximately 2.5 km and the R-1000 was slightly less, but most of our locations were within ±1.5 km of each station. The more limited range over which I could detect radio-tagged bats required me to incorporate mobile stations in the study design. This approach improved my ability to collect location data for a few individuals. Even with the mobile stations, however, I was unable to follow any individual for an entire night and rarely for more than a few hours because they would move beyond the range of the receivers, indicating my measurements of home range size and foraging range are likely biased low. A recent study that used 5- and 14-

element antennas on elevated towers and mobile tracking stations suggested their study methods and equipment contributed to estimating much larger home range estimates for *M. sodalis* than in two previous studies (Amelon et al. 2014). These examples of our limited ability to fully detect space use by western long-eared myotis should be considered when incorporating estimated home range size and foraging range into bat conservation management practices.

An additional factor that limited the number of successful locations I was able to collect was low ambient temperatures. According to a National Weather Service Cooperative Observer Program station in the study area, the mean air temperature for July 2015 was 12°C and the mean air temperature minimum was 7°C. On several occasions, when the ambient temperature was < 10°C, radio-tagged bats either did not leave the day roost or returned to their day roost after a short foraging bout (< 2 hrs) and did not exit the roost for the remainder of the night, presumably due to low prey densities. Similar behavioral responses to low ambient temperatures has been reported in other bat species: foraging time was reduced or bats did not leave the roost due to low air temperatures and low insect abundance (Rydell 1989, Audet 1990, Catto et al. 1995). One exception was in Yukon, Canada were *M. evotis* foraged throughout the night (6-7 hours) by gleaning insects despite low ambient temperatures (7°C) (Chruszcz and Barclay 2003).

I predicted that vegetation, land use, and landscape variables would influence habitat selection in *M. evotis* at two spatial scales. Incorporating spatial scale into habitat selection studies provides valuable information that can be integrated into wildlife conservation planning (Johnson et al. 2004, Razgour et al. 2011). In this study, I found evidence of distinct selection process for lactating females and males at both the home range and landscape levels. Best models for both sexes suggest this particular population has specific requirements that are associated with vegetation, land use, and landscape features. My results support recent studies

that indicate habitat selection in bats is indeed a hierarchal process (Ober and Hayes 2008*a*, Ducci et al. 2015) that will require detailed cross-scale conservation planning in the future.

Vegetation type and tree canopy cover were important predictors of habitat use for lactating females and males at the landscape level and at the home range level, respectively. Lactating females and males selected pre-settlement juniper woodlands more than shrub-steppe communities, which is consistent with previous studies involving *Myotis* species in which bats used woodland or forested areas more than treeless areas (Audet 1990, Johnson et al. 2004, Murray and Kurta 2004, Rudolph et al. 2009, Womack et al. 2013*a*, Coleman et al. 2014, Kniowski and Gehrt 2014). Woodland areas that are used for foraging sometimes include riparian areas (Grindal et al. 1999, Henderson and Broders 2008), which can provide higher concentrations of prey and less vegetation clutter and cover than adjacent uplands (Downs and Racey 2006), potentially reducing energy expenditure during foraging bouts. However, riparian areas (i.e., playas) in my study area were located in shrub-steppe and were absent from juniper woodlands, suggesting that other factors might contribute to habitat selection in my study area.

Bats employ selective foraging strategies that enable them to conserve energy when prey densities are below optimal thresholds (Racey and Swift 1985). While *M. evotis* consumes prey from several orders of insects, more than 40% of its diet consists of lepidopterans (Lacki et al. 2007). Insect abundance and lepidopteron diversity have been reported to be influenced more by overstory forest canopy cover than understory shrub vegetation (Ober and Hayes 2008*b*, 2010). Furthermore, there is a direct relationship between lepidopteron diversity and overstory canopy cover (Ober and Hayes 2010). In my study area, juniper woodlands (> 10% canopy cover) and juniper savannas (< 10% canopy cover) had more overstory canopy cover than shrub-steppe communities, which were mostly absent of trees except along ecotones where the two

communities converged. Therefore, foraging opportunities for *M. evotis* might have been richer in pre-settlement juniper woodland than in shrub-steppe.

Several species of bats have been reported to show preference for foraging in areas with at least some canopy cover (Menzel et al. 2005, Henderson and Broders 2008, Womack et al. 2013*a*, Kniowski and Gehrt 2014). Certain species, including *M. evotis,* have a strong direct relationship with canopy cover, which is presumably indirectly related to higher prey abundance (Ober and Hayes 2008*a*). I found lactating females selected areas with greater canopy cover compared to areas lacking canopy cover at the landscape scale, whereas males avoided areas with greater canopy cover at the home range level. Males, however, selected areas with > 0-10% canopy cover compared to treeless areas. Wing architecture of *M. evotis* enables the species to use two foraging techniques to capture prey, aerial hawking and substrate gleaning (Manning and Jones, Jr. 1989). On the one hand, low wing loading allows this species to maneuver through vegetation clutter, while its long wings enhance foraging efficiency in more open areas (Norberg and Rayner 1987). Although substrate gleaning requires more energy than aerial hawking, the combination of both foraging strategies might improve overall foraging efficiency in juniper woodlands, which have higher canopy cover and spatial heterogeneity than shrub-steppe communities, particularly when prey densities are low (Ober and Hayes 2008*a*).

Three of the four top models included the predictor variables "distance to roosts" and "distance to water." Distance measures have been identified as important predictors of habitat selection, particularly in the development of habitat suitability models (Rainho and Palmeirim 2011). In this study, the relationship between habitat selection and distance to roosts and water was stronger at the landscape level than the home range level. Home ranges of both lactating females and males were closer to day roosts and water than expected. These results are consistent

with one other study on *M. evotis* where the odds of use and water were indirectly related (Waldien and Hayes 2000). Furthermore, similar outcomes are reported for other *Myotis* species including *M. sodalis* (Kniowski and Gehrt 2014) and *M. septentrionalis* (Broders et al. 2006).

Several behavioral and physiological factors might explain why *M. evotis* selected areas closer to day roosts and water sources than expected. While *M. evotis* occurs in both arid and mesic habitats, it is not as efficient at retaining water as other species that exclusively occur in arid habitats (Geluso 1978). Commuting between foraging areas, day roosts, and water sources is energetically costly for bats; therefore, shorter commuting distances are likely to reduce daily energy expenditure compared to longer distances, given all other factors are held constant (e.g. habitat quality, prey abundance; Tuttle 1976). Ambient temperature influences the amount of energy bats expend to maintain optimal body temperatures (Speakman and Thomas 2003). During cold temperatures, bats tend to reduce nightly foraging time, presumably to balance the cost of flying with the benefit of prey intake (Rydell 1989, Audet 1990, Catto et al 1995). During the present study, radio-tagged bats limited the amount of time they foraged at night during periods of low ambient temperatures. Similarly, the cost of flying greater distances to forage might have exceeded the benefits of energy intake, especially during periods of low density of flying insects due to low ambient temperatures. The energetic requirements for bats vary with reproductive status (McLean and Speakman 2000). Notably, the energy and water demands of female bats increase during lactation compared to pregnant and non-reproductive bats, which requires lactating bats to consume a higher biomass of prey and more water (Kurta et al. 1989, 1990, McLean and Speakman 2000). To maintain water balance, lactating females need to drink nearly 20% of their body mass in water each day, with the remainder of their water requirements coming from intake of preformed and metabolic water (Kurta et al. 1989, 1990, McLean and

Speakman 2000). The constraints associated with simultaneously coping with water stress, low ambient temperatures, and the energetic demands of lactation likely limits the distribution of female *M. evotis* to the proximity of suitable day roost sites and water sources within the study area.

Tables

Table 3.1. Bat number, sex, number of days data was collected, number of locations for 12 *M. evotis* fitted with radio transmitters in central Oregon 2014-2015.

Bat	Sex	Days	Locations
3	Male	7	20
5	Female	NA[a]	22
6	Female	NA[a]	21
10	Female	6	30
12	Male	6	30
20	Female	9	42
22	Male	NA[a]	37
24	Female	10	45
25	Female	6	33
28	Male	9	31
34	Male	8	31
36	Male	7	27

[a]NA = data not available

Table 3.2. Mean 50% and 95% probability contours (ha) and mean foraging range (m) from day roosts for 12 *M. evotis* in central Oregon 2014-2015. Ad hoc and least squares cross validation bandwidths are reported.

Bat	Sex	Ad Hoc (50%)	LSCV (50%)	Ad Hoc (95%)	LSCV (95%)	Range
5	Female	64.40	116.84	218.73	390.60	NA
6	Female	71.25	65.64	378.84	344.25	NA
10	Female	74.72	143.99	275.97	562.45	1654.4±804.6
20	Female	7.94	7.94	45.09	45.09	331.9±75.5
24	Female	27.20	29.90	115.81	128.30	667.2±144.5
25	Female	56.63	29.22	200.73	126.32	1080.9±630.1
3	Male	43.96	18.59	261.10	117.59	NA
12	Male	10.98	9.80	59.05	55.26	265.5±NA
22	Male	3.92	2.33	23.26	12.90	793.5±NA
28	Male	372.99	532.77	1277.16	1833.98	3056.5±628.9
34	Male	97.69	85.76	470.06	414.12	1000.3±521.4
36	Male	110.46	143.01	454.53	558.26	2492.4±445.6

Table 3.3. Model selection of response by lactating female (n=4) and male (n=4) *M. evotis* at the home range (third order) selection level in central Oregon 2014-2015. Model variables, number of parameters in the model (K), difference in AICc between the *ith* and the top ranked model (Δ_i), and Akaike weights (w_i = estimated probability of model i being the best model given the data and the set of candidate models) for candidate models developed to explain differences between used and available locations.

Model[a]	K	AICc	Delta	Weight
Lactating females				
DistRoost + DistWater	3	415.1	0.00	0.52
DistRoost + DistWater + HabType + TreeCC	7	416.6	1.47	0.25
HabType + TreeCC	5	416.8	1.65	0.23
Males				
HabType + TreeCC	5	356.6	0.00	0.68
DistRoost + DistWater + HabType + TreeCC	7	358.4	1.80	0.28
DistRoost + DistWater	3	362.3	5.68	0.04

[a]DistRoost = distance to roost (m); DistWater = distance to water (m); HabType = (0) for juniper woodland and (1) for shrub-steppe; TreeCC = (0) 0%, (1) >0-10%, (2) >10-20%, (3) >20%.

Table 3.4. Model selection of response by lactating female (n=4) and male (n=4) *M. evotis* at the landscape (second order) selection level in central Oregon 2014-2015. Model variables, number of parameters in the model (*K*), difference in AICc between the *ith* and the top ranked model (Δ_i), and Akaike weights (w_i = estimated probability of model *i* being the best model given the data and the set of candidate models) for candidate models developed to explain differences between used and available locations.

Model[a]	K	AICc	Delta	Weight
Lactating females				
DistRoost + DistWater + HabType + TreeCC	7	149.5	0.00	0.98
DistRoost + DistWater	3	157.8	8.29	0.02
HabType + TreeCC	5	409.0	259.49	0.00
Males				
DistRoost + DistWater	4	198.5	0.00	0.68
DistRoost + DistWater + HabType + TreeCC	8	200.0	1.51	0.32
HabType + TreeCC	6	352.9	154.42	0.00

[a]DistRoost = distance to roost (m); DistWater = distance to water (m); HabType = (0) for juniper woodland and (1) for shrub-steppe; TreeCC = (0) 0%, (1) >0-10%, (2) >10-20%, (3) >20%.

Table 3.5. Variable, coefficient estimates, standard errors, odds ratio, and 95% confidence intervals for the best fitting model based on Akaike's Information Criterion for small sample sizes for lactating female (n=4) and male (n=4) *M. evotis* at the home range (third order) selection level in central Oregon 2014-2015.

Variable	Coefficient	SE	Odds Ratio	95% CI
Lactating females				
Distance to roost	0.009	0.028	1.009	0.955-1.067
Distance to water	-0.065	0.033	0.937	0.877-0.998
Males				
Habitat type[a]	-0.084	0.314	0.920	0.496-1.708
Canopy cover (> 0-10%)[b]	0.659	0.317	1.932	1.042-3.625
Canopy cover (> 10-20%)[b]	-0.466	0.440	0.627	0.261-1.476
Canopy cover (> 20%)[b]	-0.358	0.498	0.699	0.259-1.845

[a]Habitat type coded as 0 = juniper woodland and 1 = shrub-steppe.
[b]Dummy variables coded as 1, 2, and 3 if the location fell within the defined canopy cover category, 0% canopy cover was the reference category.

Table 3.6. Variable, coefficient estimates, standard errors, odds ratio, and 95% confidence intervals for the best fitting model, based on Akaike's Information Criterion for small sample sizes, for lactating female (n=4) and male (n=4) *M. evotis* at the landscape (second order) selection level in central Oregon 2014-2015.

Variable	Coefficient	SE	Odds Ratio	95% CI
Lactating females				
Distance to roost	-0.316	0.059	0.729	0.641-0.808
Distance to water	-0.324	0.070	0.723	0.624-0.822
Habitat type[a]	-1.706	0.620	0.182	0.050-0.583
Canopy cover (> 0-10%)[b]	-0.136	0.618	0.873	0.249-2.878
Canopy cover (> 10-20%)[b]	0.063	0.817	1.066	0.209-5.274
Canopy cover (> 20%)[b]	-2.142	0.973	0.117	0.016-0.746
Males				
Distance to roost	-0.162	0.024	0.850	0.811-0.891
Distance to water	-0.193	0.034	0.825	0.771-0.883

[a]Habitat type coded as 0 = juniper woodland and 1 = shrub-steppe.
[b]Dummy variables coded as 1, 2, and 3 if the location fell within the defined canopy cover category, 0% canopy cover was the reference category.
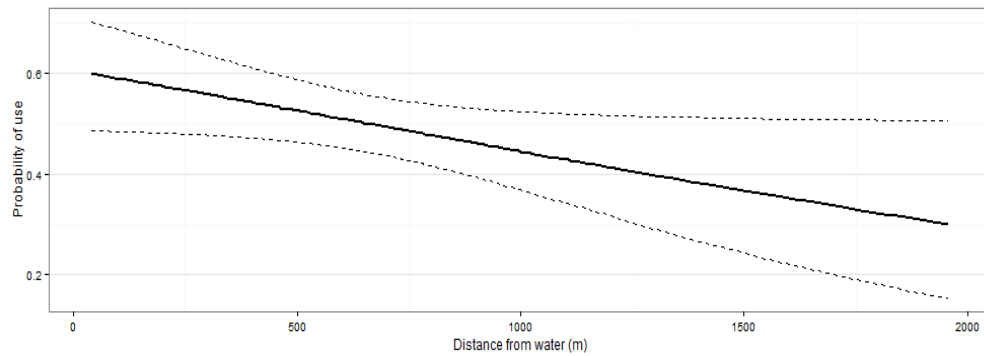
Figures

Figure 3.1. Effects of distance from water in meters on the probability of use of lactating female *M. evotis* (n=4) at the home range level in a western juniper woodland in central Oregon during July 2014 and 2015. Dotted lines are 95% confidence intervals.
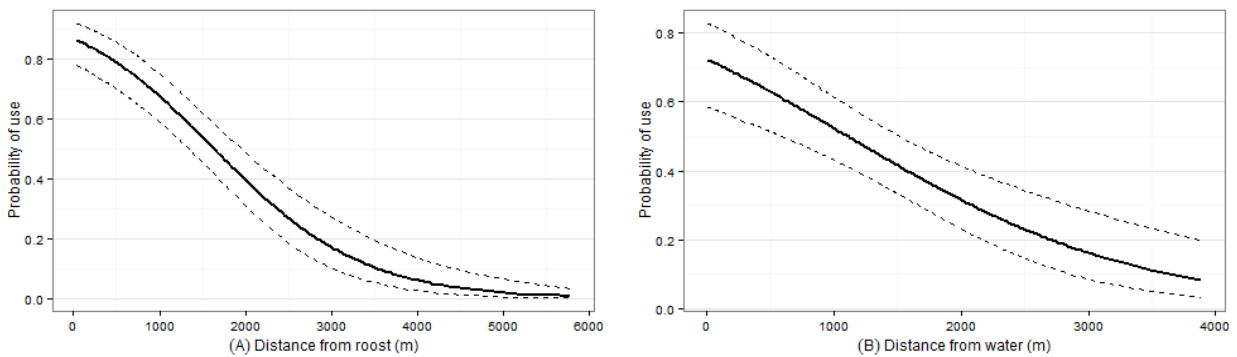

Figure 3.2. Effects of distance from roost in meters (A) and distance from water in meters (B) on the probability of use of male *M. evotis* (n=4) at the landscape level in a western juniper woodland in central Oregon during July 2014 and 2015. Dotted lines are 95% confidence intervals.

CHAPTER 4: SYNOPSIS & CONCLUSIONS

My results support the need to consider spatial scale during conservation planning for western long-eared myotis. I found that roost selection and habitat selection of individuals in this particular juniper woodland is a hierarchical process influenced by several habitat and landscape characteristics. Identifying and protecting these resources both temporally and spatially is necessary to conserve the population of western long-eared myotis in the study area (Hayes 2003).

Roost Selection

I found that lactating females and males differ in roost site selection. Specifically, lactating females preferred to roost in rocks, whereas males roosted in trees and rocks more equally. Species of bats that exhibit low fidelity towards roosts, such as western long-eared myotis, likely benefit from multiple roost substrates because they use the microclimates provided by different roost substrates to respond to varying thermoregulatory demands (Vonhof and Barclay 1997, Chruszcz and Barclay 2002). Areas with both suitable tree and rock roosts will likely increase the probability of use, especially for males. I found evidence supporting the retention of pre-settlement trees during juniper removal treatments to protect bat roosting habitat. Bats rarely roosted in juniper snags, suggesting this type of roost is less important when pre-settlement trees and rocks are available. Furthermore, downed logs and post-settlement trees were not used as roosts by the radio-tagged sample of bats, indicating that these types of roosts are not critical for conserving bat populations when suitable tree and rock roost sites are available. However, less preferred types of roost sites, such as downed logs, snags, and stumps,

might be important roost sites for bats if pre-settlement trees and rocks are unavailable (Waldien et al. 2000, Arnett and Hayes 2009). For instance, stand-replacing wildfire in pre-settlement woodlands would remove roost sites in pre-settlement trees, while creating roosting habitat in the form of snags. Also, post-settlement trees could create roosting habitat after trees are cut during juniper treatments in shrub-steppe communities, by providing down logs and stumps as roost sites where pre-settlement tree roost sites are absent.

Areas with high densities of roost sites that are located in close proximity to water sources are likely to increase the probability of use. Therefore, management strategies designed to protect these areas from disturbance that would diminish roost site availability (e.g., wildfire) will improve summer habitat for western long-eared myotis.

Additional research would improve bat management in juniper woodlands by examining whether lactating females are limited to areas with rocks or whether they exploit other types of roosts when rocks are unavailable. Similarly, are males limited to areas that have multiple types of roosts so they can adjust to varying ambient temperatures? Although previous studies have suggested that tree roost sites maintain lower in-roost temperatures than rock roost sites, there are no empirical data to support this or the potential role of thermal differences between roost site types in determining roost site selection by bats. Furthermore, determining whether bats use juniper woodlands outside the reproductive season would be useful given the insufficient knowledge of bat habitat use outside the summer months for many species of bats in the western Uniteds States. Enhanced animal tracking technologies, such as geolocators, would allow researchers to collect data on bat movements between seasonal habitats, which is a topic in bat ecology that is not well understood (Cryan and Veilleux 2007).

Home Range

The mean home range size estimates for western long-eared myotis from the present study are the largest ever reported for the species and are among the largest for *Myotis* species in North America (Waldien and Hayes 2001, Henry et al. 2002, Owen et al. 2003, Johnson et al. 2005, Menzel et al. 2005, Coleman et al. 2014, Womack et al. 2013*b*, Kniowski and Gehrt 2014). Estimates of mean home range size from the present study did not differ significantly between lactating females and males; however, my statistical power to detect a difference was low due to small sample sizes, which increased the probability of committing a Type II error. Additional research with larger sample sizes would likely reveal sexual differences in home range size given the different energetic and thermoregulatory demands of lactating females vs. males during the reproductive season (Speakman and Thomas 2003).

Habitat Selection

I found evidence that supports the need to manage for variable tree densities in pre-settlement juniper woodlands that are in close proximity to water sources in order to promote suitable foraging habitat for western long-eared myotis. Tree canopy cover appears to be an important characteristic of foraging habitat for bats within pre-settlement juniper woodlands. However, allowing post-settlement juniper trees to infill into pre-settlement woodlands beyond a threshold of 20% canopy cover would likely degrade bat foraging habitat, and areas with > 20% tree canopy cover should be thinned to improve foraging habitat for bats. Removing post-settlement trees from shrub-steppe communities is not likely to negatively affect foraging habitat because bats avoided these areas. Protection of areas that provide high densities of roosts in close proximity to water sources would likely benefit bat populations because the probability of use

increased near these resources. Given the complexity of habitat and spatial requirements of the western long-eared myotis, careful planning is warranted to develop management strategies to identify and protect patches where high densities of bats are likely to occur. Future studies should continue to include a range of spatial scales when examining habitat selection by bats.

Scope of Inference

My thesis research was of necessity an observational study; thus, my results should be considered correlative, as opposed to controlled experimentation. The scope of the study was temporally and spatially limited by the study design, current limitations in the tools available to track individual bats, and the difficulties involved in tracking small, fast-flying study animals at night. The study was conducted during the lactation period (7 July – 3 August) for female *M. evotis*; therefore, inference outside these dates or this reproductive phase of the annual cycle is not recommended. Because climatic conditions influence bat behavior (Adams and Hayes 2008), inference is appropriate only under similar weather conditions to those experienced during the summers of the two years of the study (i.e., precipitation, temperature). Individuals fitted with radio transmitters were assumed to be a random sample from the local population; however, the location where bats were captured was selected due to the presence of water in the playa, rather than a randomly capture site. Therefore, inferences made to other populations, species, and habitats beyond the study area should be made with caution (Miller et al. 2003).

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Appendices

Appendix A. Vegetation communities
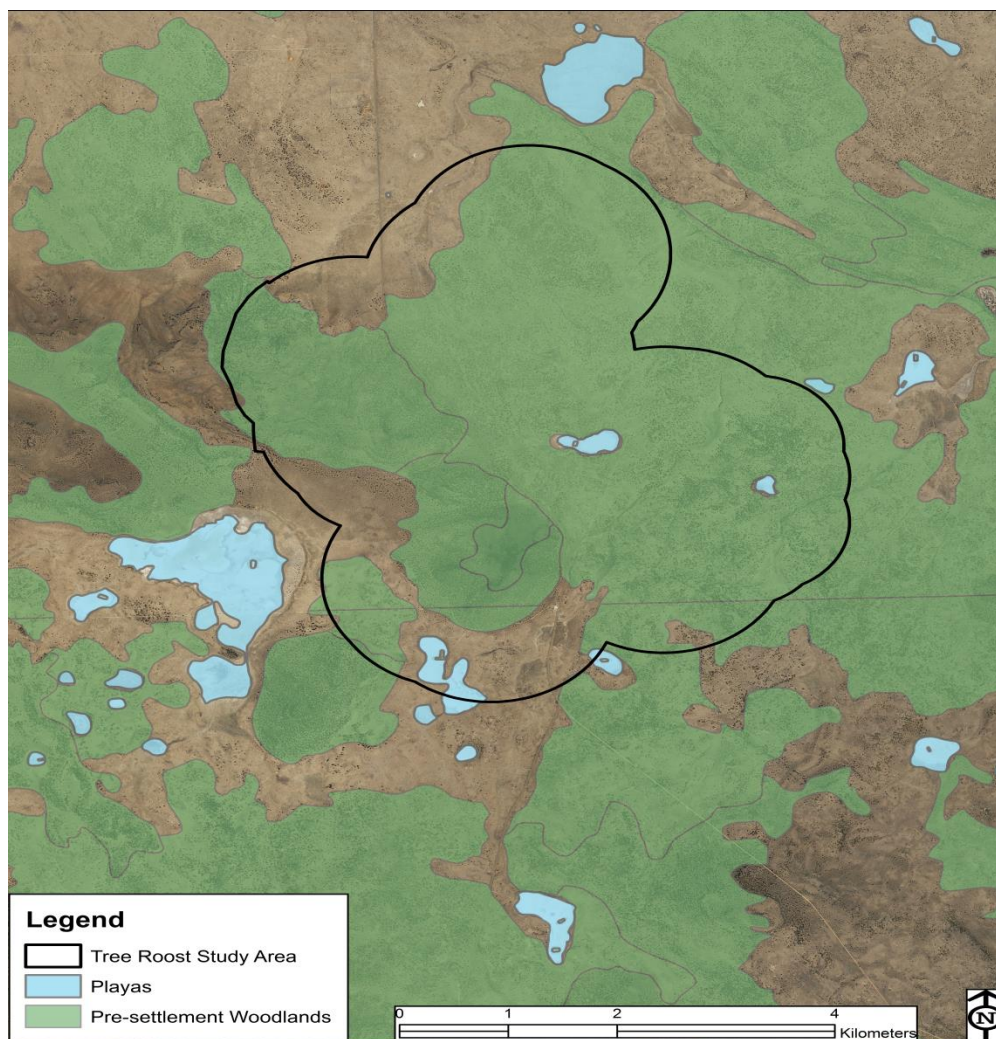
Figure A.1. Vegetation communities in the roost site selection study area. Black line represents the study area, green polygons represent pre-settlement juniper woodland, blue polygons represent playa, and no color represents shrub-steppe.

Appendix B. Tree canopy cover

Figure B.1. Tree canopy cover classes in the roost site selection study area.

Appendix C. Day roost locations
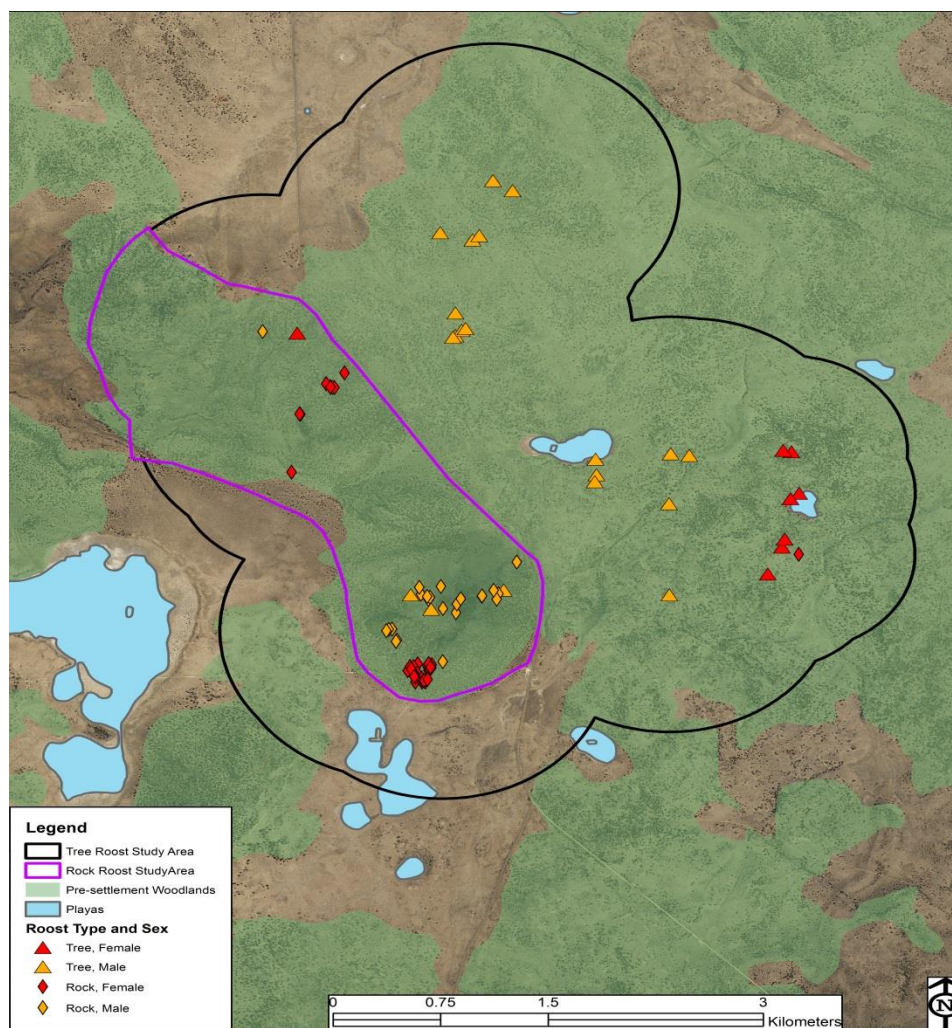
Figure C.1. Day roost sites of lactating female and male western long-eared myotis.

Appendix D. Pre-settlement woodland delineation

Table D.1. Ecological sites developed by the Natural Resources Conservation Service (NRCS) used to delineate western juniper woodlands. Information was attained through the Web Soil Survey (2015).

Map Unit Symbol	County	Ecological Site
103E, 550	Deschutes, Lake	R010XA007OR - Juniper Pumice South 9-12 PZ
135C, 189, 579	Deschutes, Lake	R010XA021OR - Juniper Shallow Pumice Hills 10-12 PZ
137E	Deschutes	R010XA026OR - Juniper Pumice North 10-12 PZ
355	Lake	R010XA659OR - Juniper Pumice Plains 8-11 PZ
11 B	Deschutes	R023XA217OR - Juniper Tableland 12-16 PZ
183, 185, 188, 189, 355, 407, 458, 468, 579	Deschutes, Lake	R023XA511OR - Juniper Lava Benches 9-12 PZ

Appendix E. Correlation graphs of continuous day roost variables
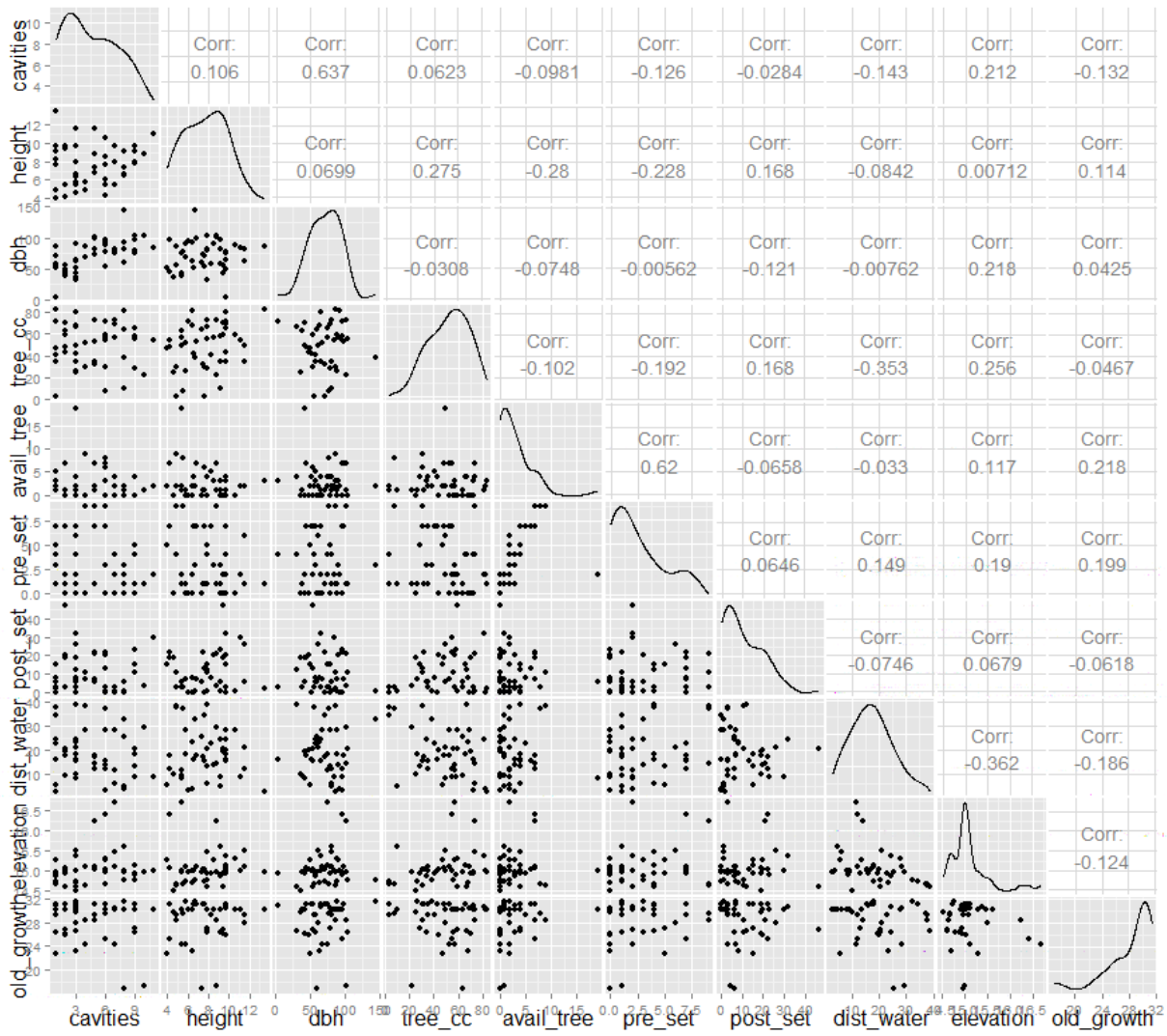
Figure E.1. Correlation graphs of continuous tree roost variables.
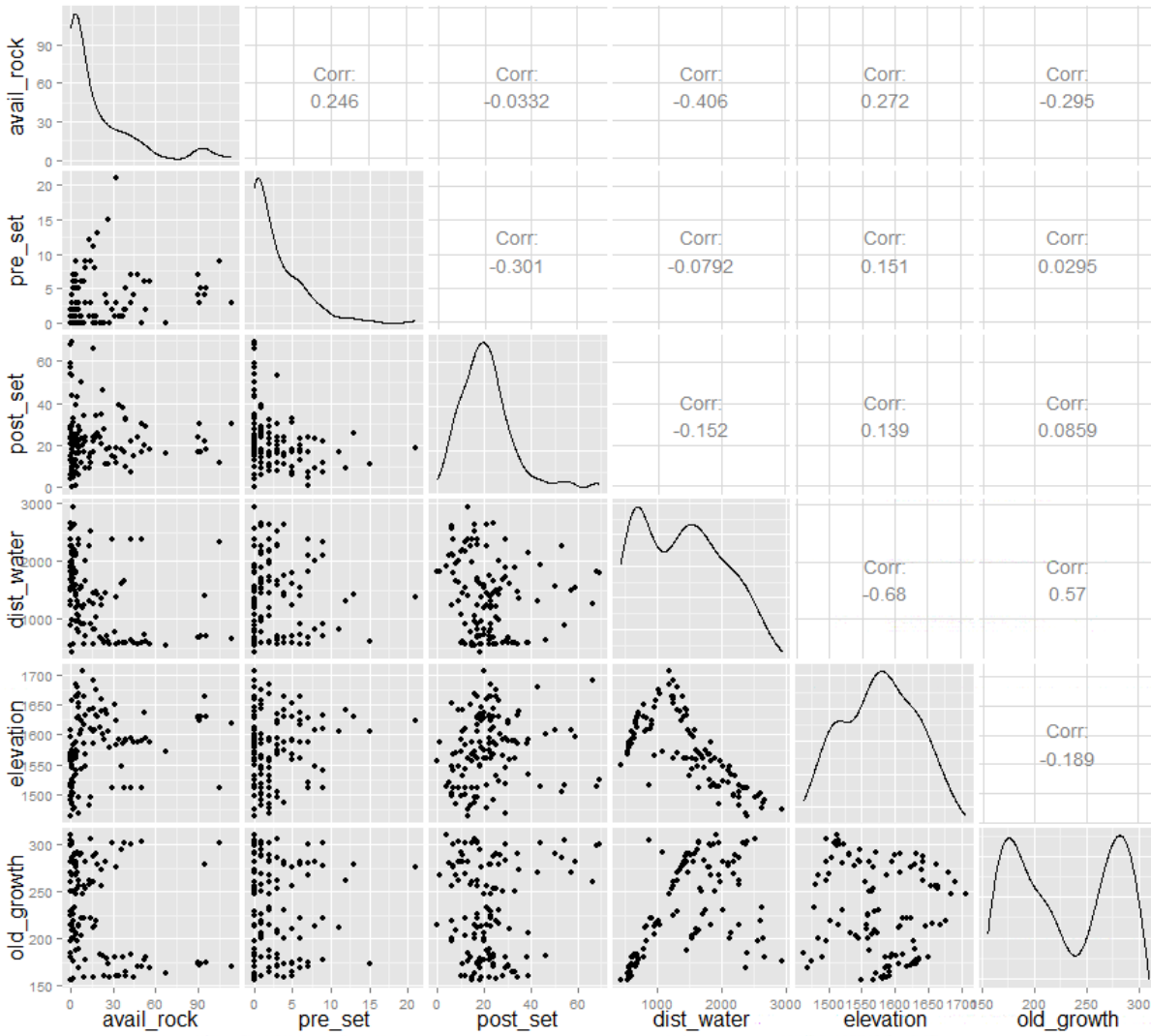
Figure E.2. Correlation graphs of continuous rock roost variables.

Appendix F. Goodness of fit test (roost selection)

Table F.1.Chi-square (X^2), degrees of freedom (*d.f.*), and p-value results for Hosmer-Lemeshow goodness-of-fit test from global day roost models.

Global Model	X^2	*d.f.*	*P*
Tree roost[a]	7.459	8	0.488
Female rock roost[b]	13.019	8	0.111
Male rock roost[b]	5.447	8	0.709

[a]Tree roost models: tree cavities + tree height + dbh + available tree roosts + pre-settlement trees + post-settlement trees + distance to water + elevation + pre-settlement woodlands 1000 m. (n = 12).
[b]Rock roost models: single/formation rock + vertical/horizontal crevice + crevice height above ground + available rock roosts + pre-settlement trees + post-settlement trees + distance to water + elevation + pre-settlement woodlands 1000 m. Lactating female, n = 7; male, n = 11.

Appendix G. Rock roost sites
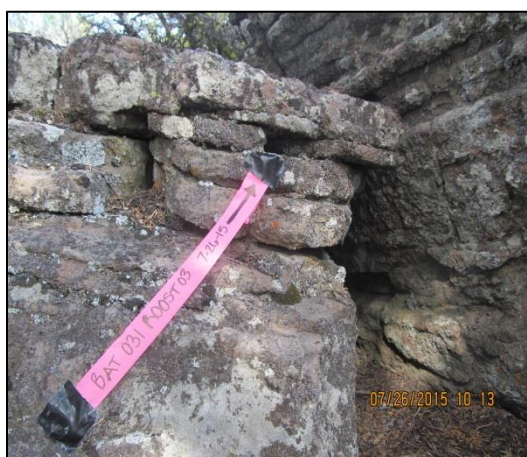
Appendix H. Tree roost sites

Appendix I. Effects of bandwidth on 95% probability contours
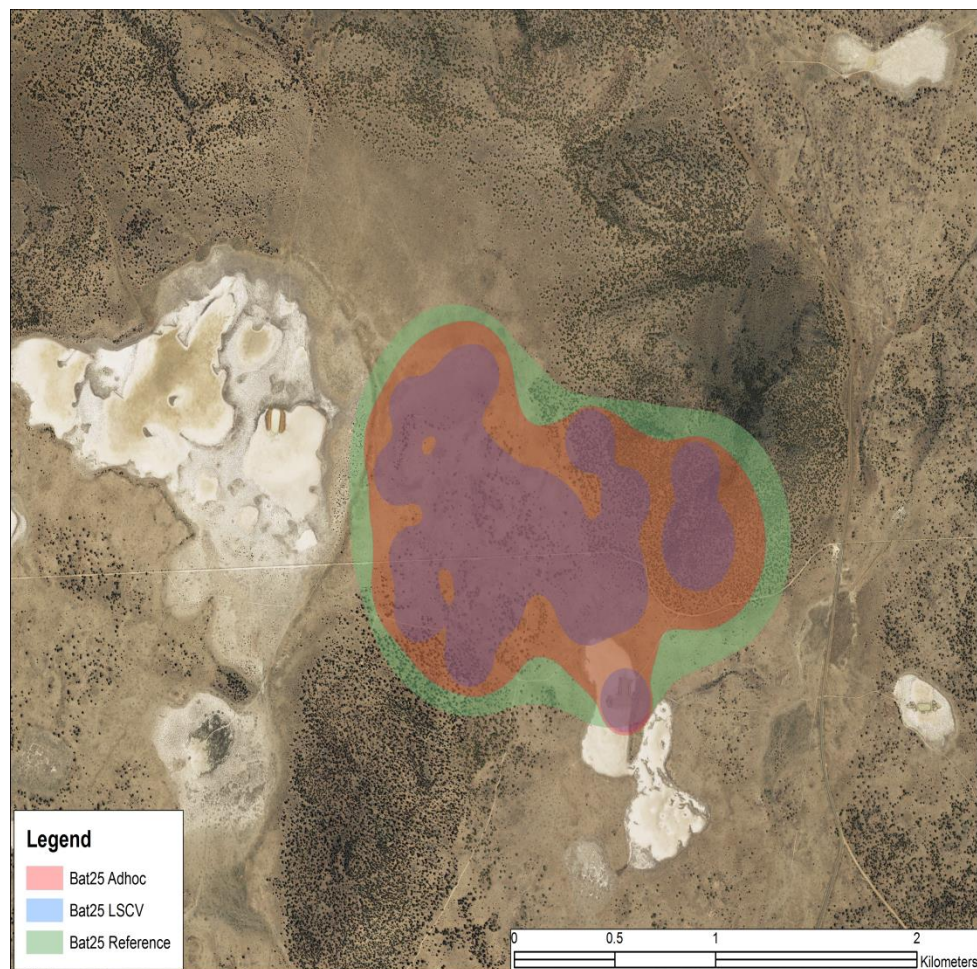
Figure I.1. Example of the effects of bandwidth on 95% probability contours using the fixed kernel density method. Bandwidths are ad hoc, least squares cross validation, and reference.

Appendix J. Goodness of fit test (habitat selection)

Table J.1.Chi-square (X^2), degrees of freedom (*d.f.*), and p-value results for Hosmer-Lemeshow goodness-of-fit test from global habitat selection models.

Global Model[a]	X^2	*d.f.*	*P*
Female home range level	6.675	8	0.572
Female landscape level	3.187	8	0.922
Male home range level	7.449	8	0.489
Male landscape level	11.495	8	0.175

[a]Habitat selection models: distance to roost + distance to water + habitat type + tree canopy cover class (%). Lactating female, n = 4; male, n = 4.

Appendix K. Chapter 2 exploratory analysis
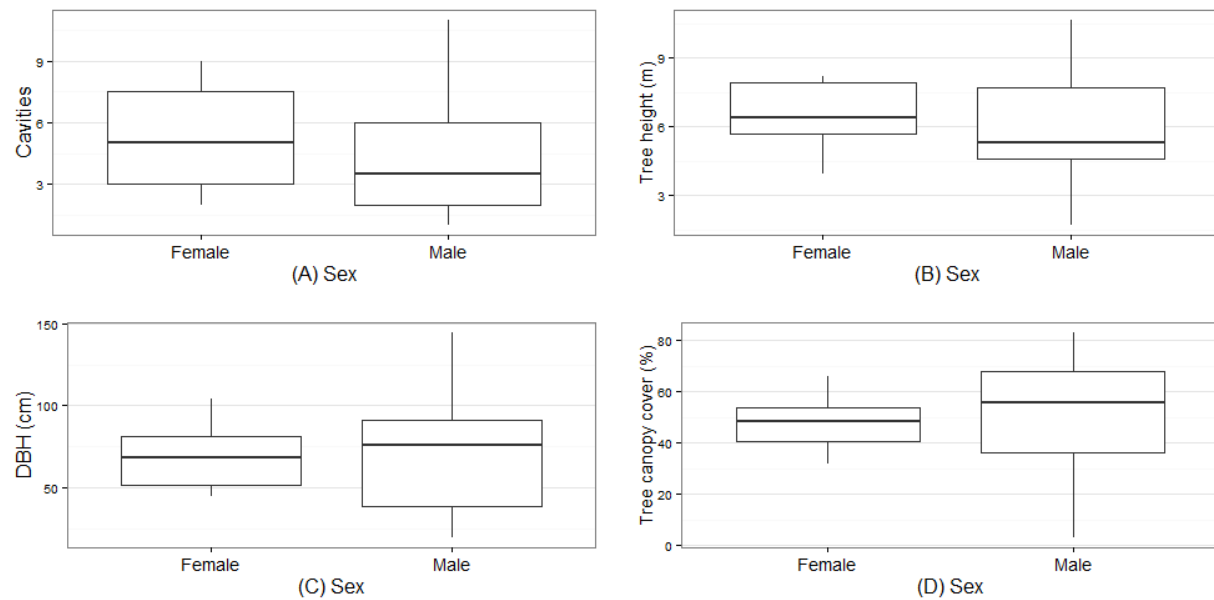
Figure F.1. Relationship between sex and roost level characteristics; tree cavities (A), tree height in meters (B), DBH in centimeters (C), and tree canopy cover in percent (D) for tree roosts.
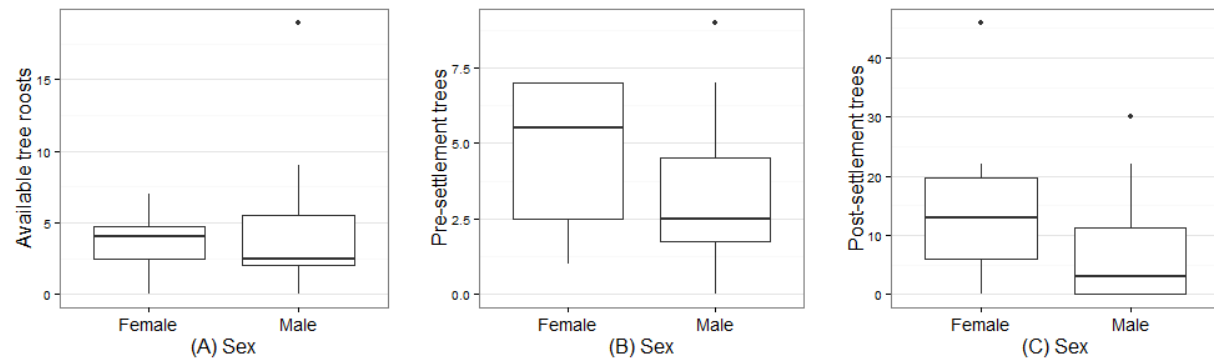
Figure F.2. Relationship between sex and plot level characteristics; available tree roosts (A), pre-settlement trees (B), and post-settlement trees (C) for tree roosts.
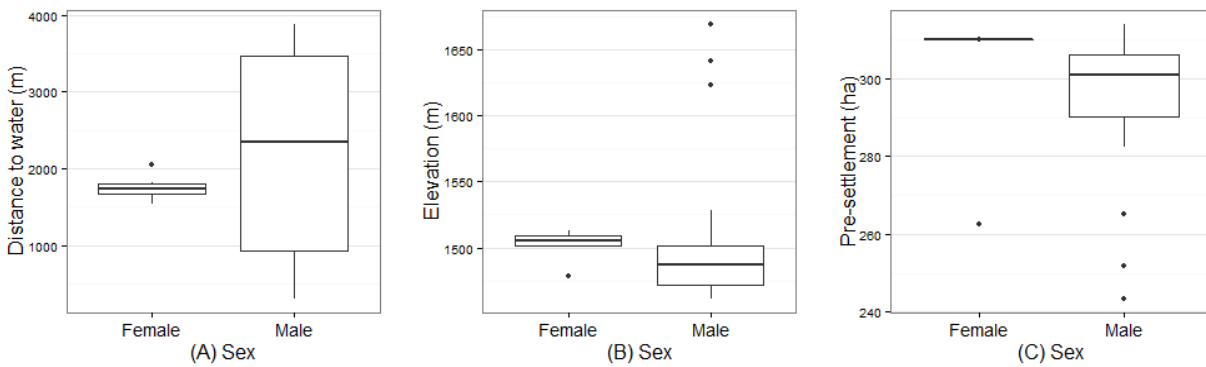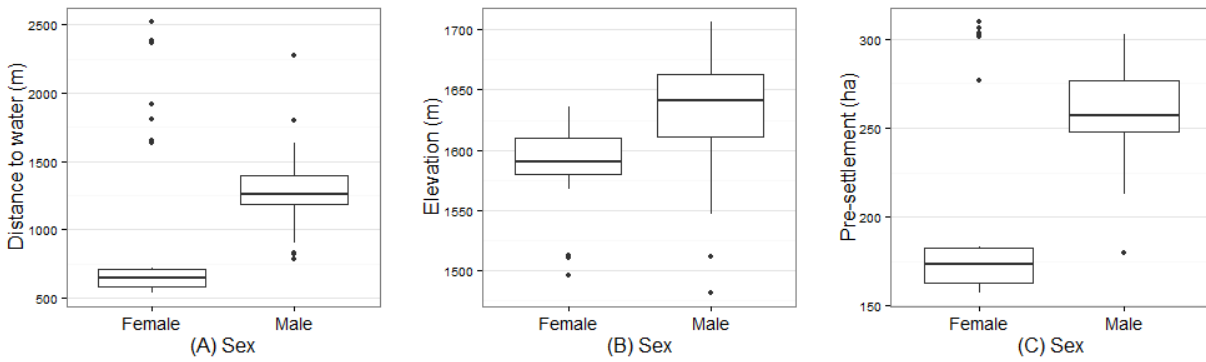
Figure F.3. Relationship between sex and landscape level characteristics; distance to water in meters (A), elevation in meters (B), and pre-settlement woodlands within 1000 m or roosts in hectares (C) for tree roosts.
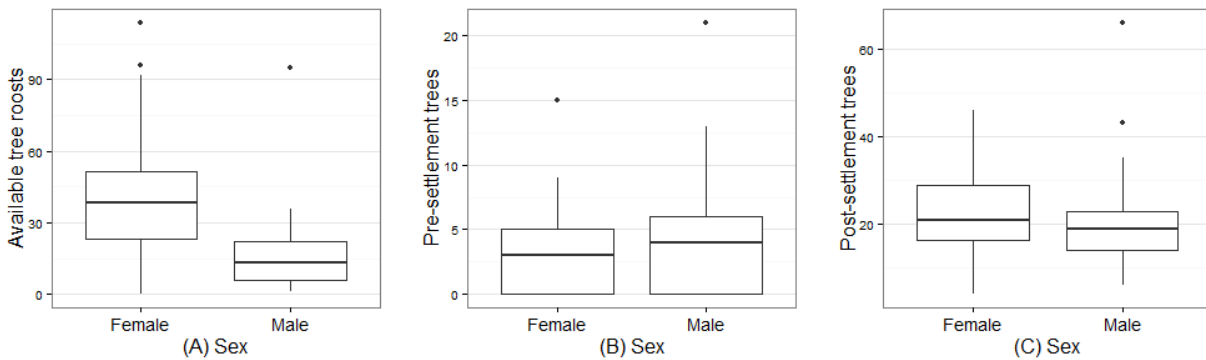
Figure F.4. Relationship between sex and plot level characteristics; available rock roosts (A), pre-settlement trees (B), and post-settlement trees (C) for rock roosts.

Figure F.5. Relationship between sex and landscape level characteristics; distance to water in meters (A), elevation in meters (B), and pre-settlement woodlands within 1000 m or roosts in hectares (C) for rock roosts.
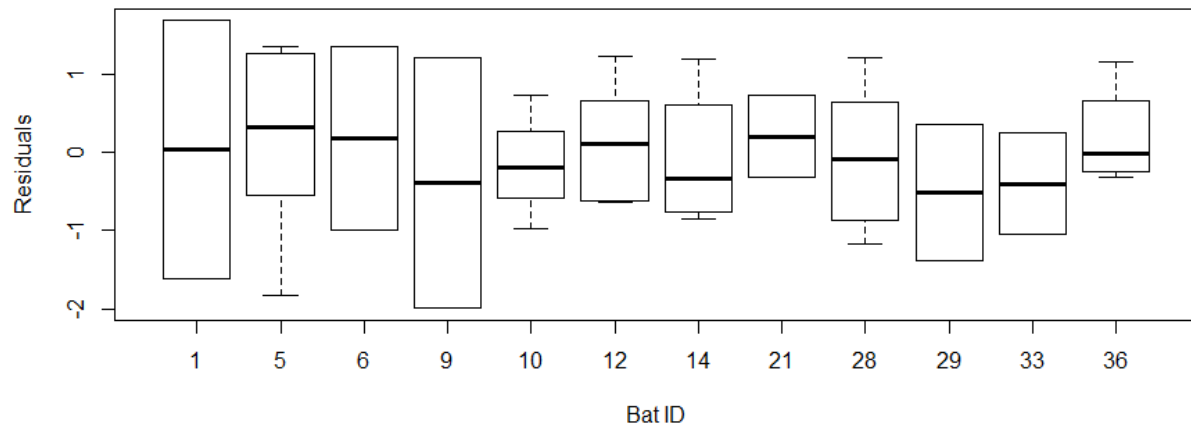
Figure F.8. Effects of individual bat on the residuals of the global tree roost model.
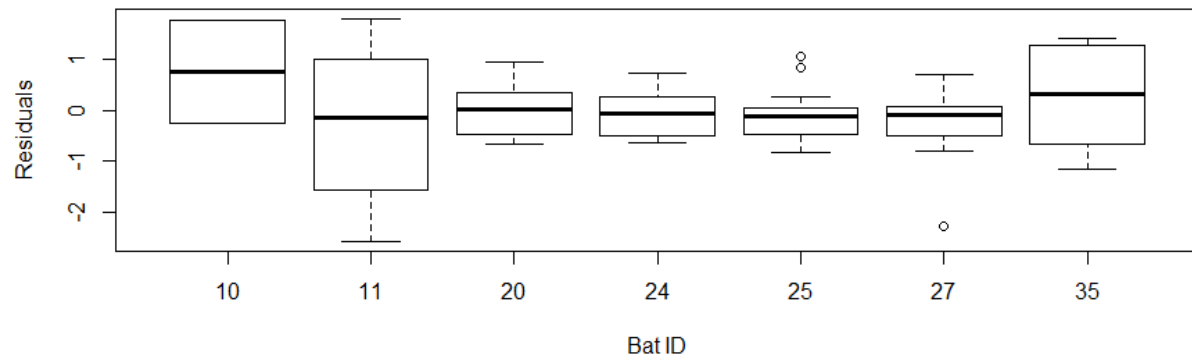
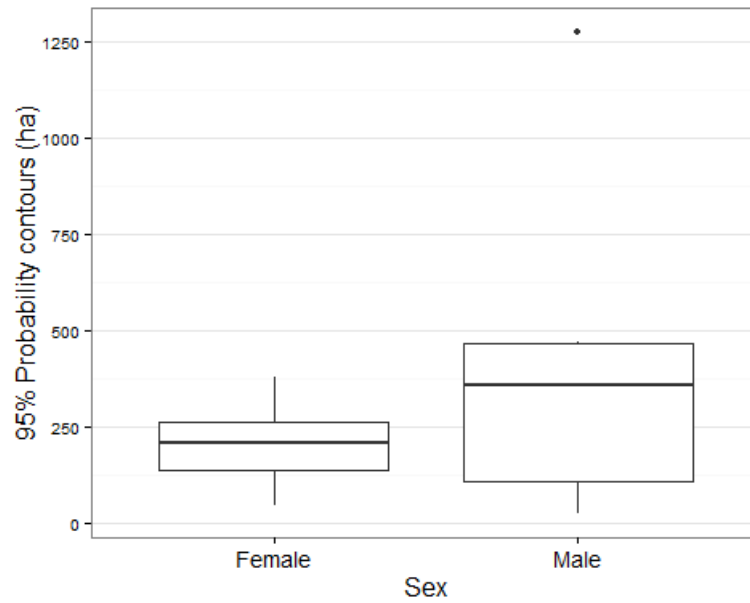Figure F.9. Effects of individual bat on the residuals of the global lactating female rock roost model.
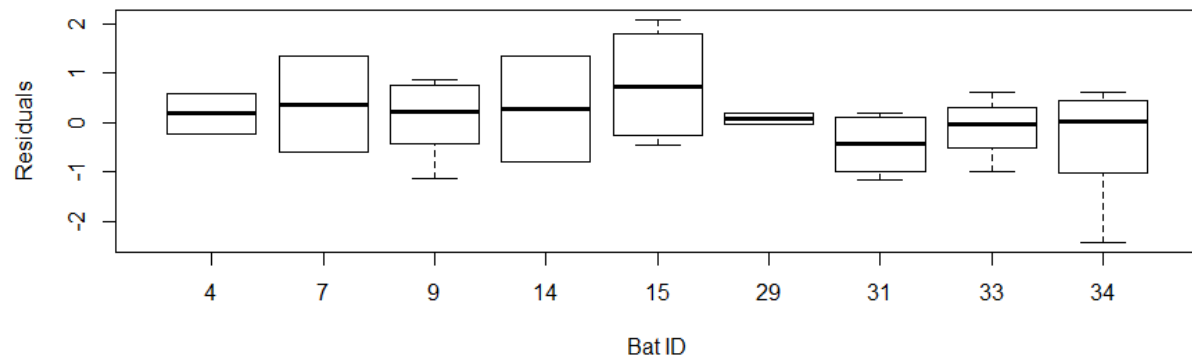
Figure F.10. Effects of individual bat on the residuals of the global male rock roost model.

Appendix L. Chapter 3 exploratory analysis

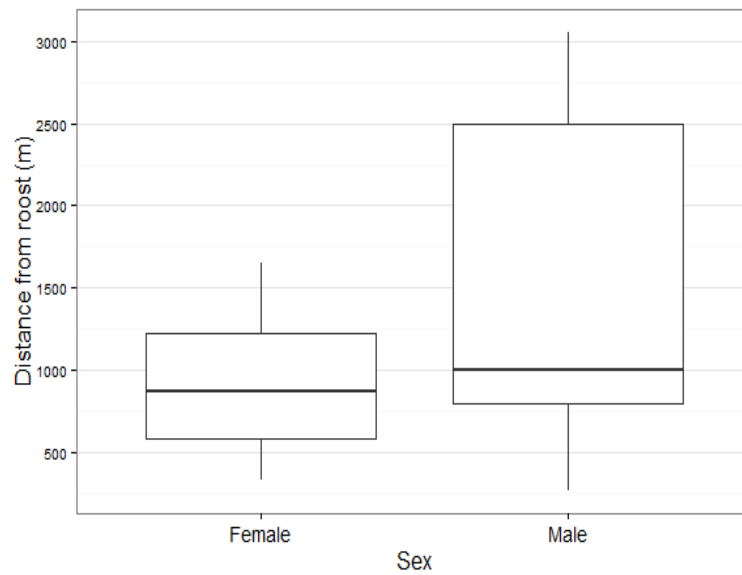Figure G.1. Relationship between sex and home range area size.

Figure G.2. Relationship between sex and mean maximum distance traveled from day roost.
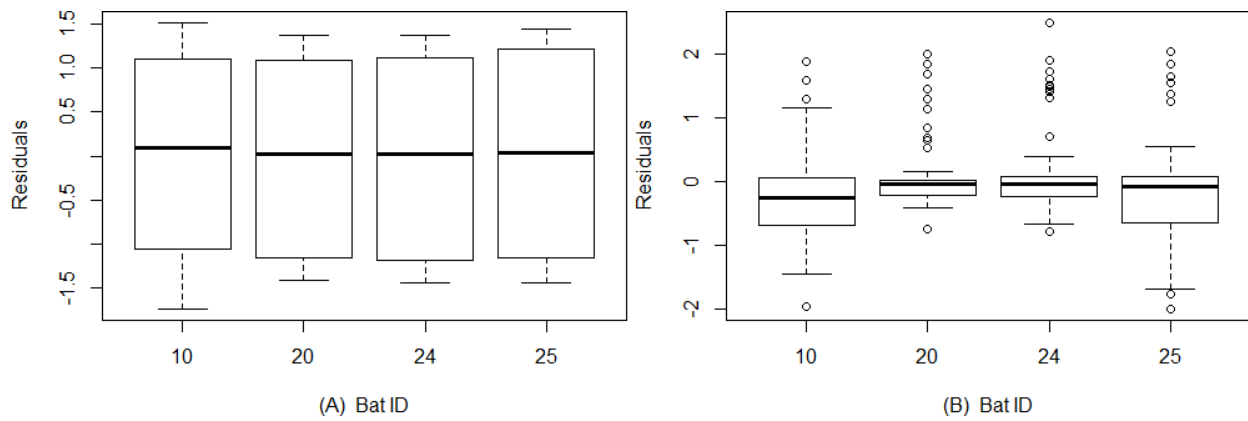
Figure G.3. Effects of individual bat on the residuals of the global model for lactating females at the home range level (A) and landscape level (B).
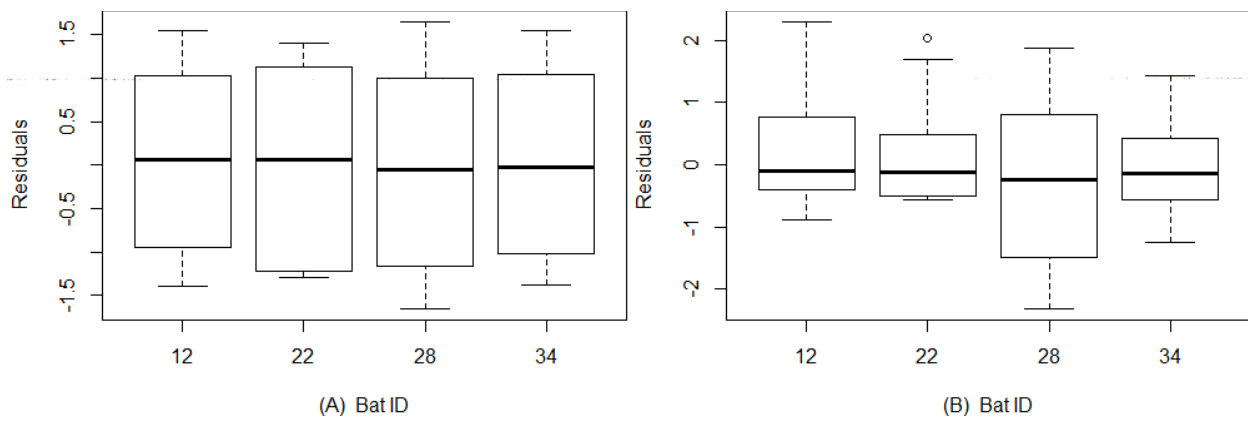

Figure G.4. Effects of individual bat on the residuals of the global model for males at the home range level (A) and landscape level (B).
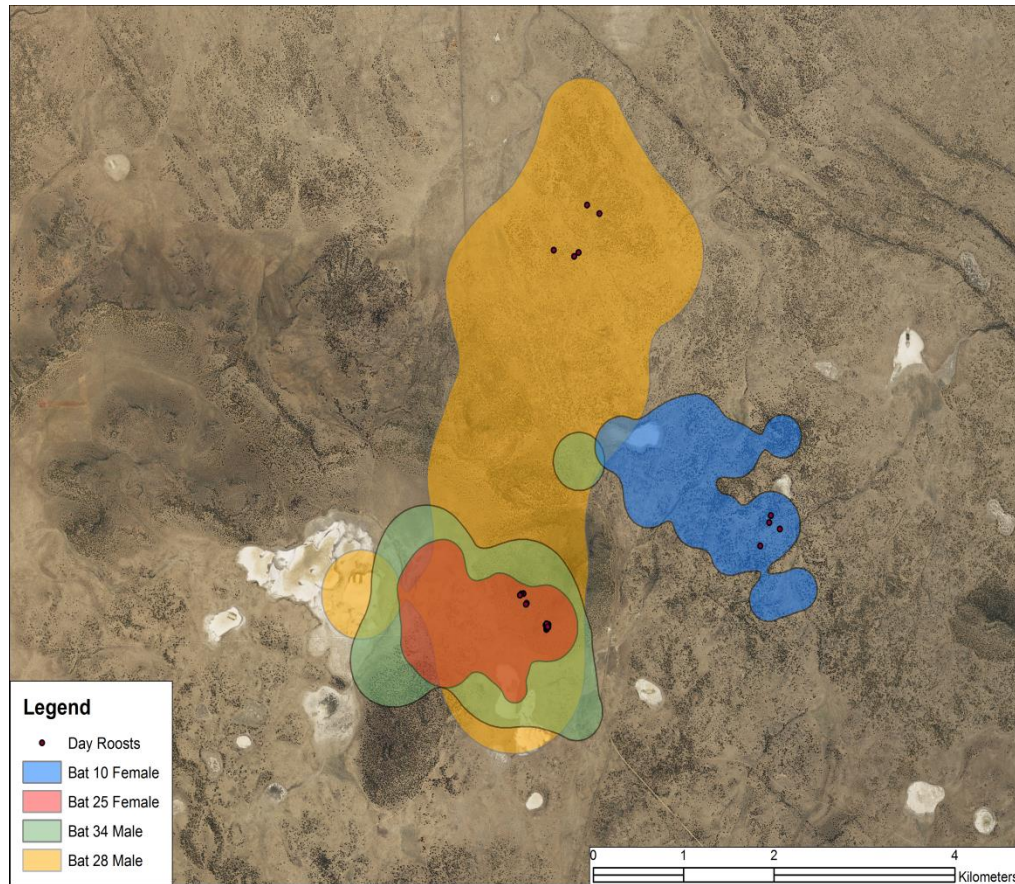
Appendix M. Bat sex and home ranges

Figure M.1. Example of the spatial relationship between day roosts and home ranges for lactating females and males.