Spring 2016

Use of Patchy, Early Successional Slope Habitat Along Coastal Sun-Facing Beaches by the Western Fence Lizard Sceloporus occidentalis at the Species' Northern Geographic Extreme

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Use of patchy, early successional slope habitat along coastal sun-facing beaches by the Western Fence Lizard *Sceloporus occidentalis* at the species' northern geographic extreme

By

Paul Backus

Accepted in Partial Completion of the Requirements for the Degree Master of Science

Kathleen L. Kitto, Dean of the Graduate School

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Date: May 23, 2016
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A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

by
Paul Backus
May 2016
ABSTRACT

Comparisons among core and peripheral populations of animals for patterns of habitat use may be an important step in an area of ecological research: the quest to understand the mechanisms underlying species range boundaries. My research on the Western Fence Lizard, Sceloporus occidentalis, at the northwestern edge of the species' geographic range, is intended to lay the groundwork for future analyses of peripheral populations. Sceloporus occidentalis is a propitious species for studying peripheral animal populations because (1) relative to dryland habitats more typical of the species nearer the core of its geographic range, the peripheral population resides in a relatively unique beach-edge maritime habitat, and (2) it is found in high local abundance, is easy to observe and capture, and has low vagility relative to birds and mammals. My research addresses the habitat preferences, dispersal tendencies, and spatial distribution among individuals of S. occidentalis in a population at the species geographic extreme in western Washington.

In 2013-2014 I captured, measured, and marked 359 lizards on the central beach in an apparent metapopulation along the Washington coast west of Marysville, WA. I recorded detailed habitat characteristics for every 10-meter stretch of beach using the line-intercept method (transect was set perpendicular to beach edge) and used Multidimensional Scaling analysis to correlate habitat characteristics with lizard sighting locations, thereby determining which sections of coastal beach edge were most heavily used by fence lizards. Similarity Percentage (SIMPER) analysis was used to determine which habitat characteristics were associated with most of the difference between occupied and unoccupied habitat areas. These characteristics and their relative influences on habitat differences were: distance to nearest
patch of sun-exposed soil on the slope above the beach (45%), the abundance of nanohabitats (i.e. different substrata or log surfaces) in the log field below the slope (22%), the number of exposed soil patches on the beach slope (16%), the length (between slope base and beach-edge) of the log field on the beach below the slope (10%), and the relative amount of exposed soil in standard plots on the slope above the beach (5%).

Chi-square analysis revealed that lizards were more likely to bask on log surfaces than on sand and leaf litter surfaces, perhaps because (1) body temperature can be more finely regulated on logs by adjusting angle of the body towards the sun, and (2) antipredator cover is nearer when on a log. Hatchling lizards were more likely than adults to be found on sand substratum. Based on proportions of age and sex classes that dispersed and the distances moved, I inferred that younger lizards were more likely to disperse longer distances than adults along Spee-Bi-Dah beach.

Lizard sighting locations were documented in ArcGIS and the degree of overlap in habitat characteristics with lizard locations determined through Analysis of Similarity, which revealed lizards to be clumped around patches of prime habitat. A reasonable inference is that high population density and intraspecific competition in these habitat patches may be pushing lizards to disperse into suboptimal habitat. However, invasive plant species, particularly Himalayan blackberry, rapidly colonize open soil patches on the beach slope, restricting the lizards' access to habitat necessary for nesting and hibernation, and reducing habitat available for population growth or range expansion.

Habitat degradation by invasive species and humans is likely a significant factor in the apparent decline of fence lizard populations along the Washington coast.
ACKNOWLEDGEMENTS

First, I must thank my thesis advisor, Dr. Roger Anderson, for his support and encouragement. Without his guidance and expertise, I may not have completed this thesis. He pushed me to pursue greater ideas, and offered significant effort to help me complete my project. I owe him a great deal. Similarly, I would like to thank the other members of my thesis committee, Dr. Dietmar Schwarz and Dr. David Wallin, for keeping my thesis progress steady and providing much-needed perspective.

This project would not have been possible without funding, so I would like to thank the North Cascades Audubon Society for their support which allowed me to purchase necessary field equipment. I must also thank the Western Washington University Biology Department and WWU Research and Sponsored Programs fund, which helped me to afford travel to-and-from my field sites during summer. The Matthew Freeman Foundation also provided funds that helped cover miscellaneous costs.

I would like to thank Jason Abramo, a fellow graduate student, for his significant help seeking lizards in the field, as well as the dozen undergraduate assistants who graciously volunteered to help with my project. Their assistance was key to gathering my data.

Thank you to the Tulalip Tribe and the beach communities on the reservation for their cooperation with and support of my project. Spee-Bi-Dah, in particular, was very welcoming and residents were always eager to know more about my research.

Finally, thank you to Western Washington University for accepting me into their Graduate Program, to the Biology Department staff for their hard work and support, and to everyone else who made this project possible.
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INTRODUCTION

In this century of climate change and habitat fragmentation, the question of how habitat use, spatial distribution, and dispersal among habitat patches by individuals of a species affect the basic underlying biology of that species’ geographic range boundaries remains unanswered (Sutherland et al., 2013). Unfortunately, the effects of habitat choice and individual dispersal on geographic range boundaries are not well understood and infrequently considered in the literature (Sexton et al., 2009). Moreover, basic research is needed on how dispersal behavior of animals at the periphery of their species’ geographic range may affect population dynamics, how the species range boundary is formed, and how the geographic range boundary shifts in response to climate and habitat changes. Stated more specifically, some of these fundamental questions are (Sutherland et al., 2013): (1) What are the evolutionary and ecological mechanisms that govern species' range margins? (2) How can we upscale detailed processes at the level of individuals into patterns at the population scale? (3) How do species and population traits and landscape configuration interact to determine realized dispersal distances (Dytham, 2009; Sexton et al. 2009)?

Populations occurring at the extremes of the species' geographic range may be particularly vulnerable to climatic variations and habitat given the greater likelihood of sparse and patchy habitat, poor dispersal corridors, and relatively low genetic diversity at range margins. (Foufopoulos, Kilpatrick, & Ives, 2011; Sexton et al., 2009; Williams, Driscoll, & Bull, 2012). For some species, fragmented habitat and increased exposure to edge habitat may force atypical distributions or behaviors (Ries, Fletcher, Battin, & Sisk, 2004). These patchy habitats near the northern edge of a species' geographic range in the northern
latitudes face challenges of a more variable climate, shorter activity seasons, and restricted
gene flow among local populations than in range-center populations (Sexton et al., 2009). It
is also possible that isolated populations may develop novel adaptations at the local scale
which could be important factors in the formation and behavior of range boundaries (Hardie
& Hutchings, 2010; Sexton et al., 2009; Williams et al., 2012). Examining how population
demographics and dispersal at range extremes differ from more central populations could
prove useful in determining how dispersal mechanisms and landscape configuration affect a
species' distribution, and how individuals use differing habitats (Angilletta, Niewiarowski,
Dunham, Leache, & Porter, 2004; Blevins, Wisely, & With, 2011; Walpole, Bowman,
Murray, & Wilson, 2012). An important step in pursuing this line of inquiry requires
documenting these population characteristics at range margins. Despite the fundamental
questions posed above, peripheral populations are less frequently studied than core
populations in the scientific literature (Sexton et al., 2009). Studying peripheral populations
and how individuals interact with their habitats should prove valuable for identifying
populations at risk, for helping conservationists prevent population declines, and laying the
foundation for future research into the organismal mechanistic bases to range margins.

Because peripheral range habitat is often small and fragmented, connectivity among
patches is important for the long-term stability of the peripheral population (Hurston et al.,
2009; Lecomte & Boudjemadi, 2004). According to metapopulation theory, many smaller
populations with sufficient dispersal and gene flow among them can form a stable
population-of-populations (“metapopulation”). Such a population has a higher effective
population size, increasing genetic diversity and decreasing overall extinction risk (Feder et
al., 2010). Study of the spatiotemporal patterns of individual distribution among habitats is the mechanistic foundation for determining the potential connectivity among populations, and thus the potential stability of the metapopulation. Such research may help answer a fundamental question in ecology: how individual dispersal behavior transduces into metapopulation dynamics (Sutherland et al., 2013), and is the focus of my thesis research.

**Background**

Understanding the link between the behaviors of individuals at local scales and the spatiotemporally dynamic patterns observed at the population and metapopulation scales is one of the fundamental challenges facing population ecology (Sutherland et al., 2013). Small-scale studies examining the nature of individual dispersal and distribution are uncommon, but such studies of a few model systems (Clobert, Baguette, Benton, & Bullock, 2012) have the potential to inform large-scale demographic models (Beyer et al., 2010; Bowler & Benton, 2005). How animals choose habitat and the environmental cues used in the animal's decision to disperse typically are not considered in studies of dispersal among populations (Bowler & Benton, 2005; Lima & Zollner, 1996; Sexton et al., 2009). Species wherein individuals have low behavioral tendency to disperse or little physical ability to move far, either within or among habitats, are often purposefully overlooked in favor of species that can be studied using justifiably simplistic models and assumptions of individual behavior and habitat choice to predict population connectivity (Brown, Hoskisson, Welton, & Báez, 2006; Lima & Zollner, 1996). Study of habitat use versus availability at the northern geographic extremes of a species with relatively low vagility, however, provides an
opportunity to study the effects of habitat choice, dispersal, and distribution at a small spatial scale. Because habitats may be more fragmented at the periphery of a species' geographic range, a species with low vagility may face strong climatic and genetic challenges at that periphery (Sexton et al., 2009; Walpole et al., 2012). The study of habitat use, habitat proximity, and dispersal among sub-populations at the periphery of the species' range provide opportunities to study (1) how individual behavior within and among habitats at the micro-local and local scales affect processes and patterns of metapopulation persistence at the regional scale and (2) how species' ranges form and respond to changing climatic conditions (Schippers et al., 2008; Sutherland et al., 2013).

**Habitat at Geographic Extremes**

Greater climatic and seasonal variation at the geographic range margins of a species may lead to more frequent and extreme population crashes and local extinctions (Brown et al., 2006). Compounding this issue, patchy habitats make individual dispersal more difficult in species with modest vagility, such as for small terrestrial mammals and reptiles, further increasing extinction risk of peripheral populations in these vertebrates. How the mechanisms of population dynamics at a species' range margin determine the geographic range boundaries is one of the fundamental unanswered questions of population ecology (Sutherland et al., 2013). Fragmented habitats may (1) increase genetic isolation of the peripheral populations from core populations and (2) produce novel adaptations not seen in core populations, which may, in turn, affect how the species' geographic range will expand or contract in response to major environmental changes (Lecomte & Boudjemadi, 2004; Lens et al., 2002). For smaller
populations, influx of individuals from nearby populations may be important for population stability and improve gene flow among populations, thus reducing the detrimental consequences of inbreeding depression (Excoffier et al., 2009). Identifying individual features and age or sex class factors that affect habitat use, dispersal, and habitat chosen for settlement in peripheral populations will be useful for learning what level of habitat connectivity is required for metapopulation persistence.

At geographic extremes of a species, the demographic characteristics of the populations may differ from the presumably more stable populations nearer the geographic center of the species' range. At the northern edge of a species range in the northern hemisphere, environmental stresses may slow growth, shorten the activity season, and leave less time to forage before annual hibernation, thus delaying maturation and reducing rates of survival before first reproduction (Brown et al., 2006; Rodríguez-Robles, Jezkova, & Leal, 2010). Shorter seasons also truncate the mating season patterns compared to more central populations (Angilletta et al., 2004). Northern populations are also at a higher risk of extinction, and often have less area available for range expansion via dispersal from locales with environmental damage (Smith, Schuett, Earley, & Schwenk, 2009). Rapid changes in habitat availability – such as anthropogenic changes in the landscape – may exacerbate the challenges to dispersal. Dispersal by individuals is affected by habitat size, quality, distance to nearby patches, and the characteristics of the environment between habitat patches (Blevins et al., 2011; Hokit, Ascunce, Ernst, Branch, & Clark, 2009). The degree of isolation of these habitat patches affects the dispersal of individuals among nearby populations, and the apparent “decision rules” organisms employ when dispersing and choosing new habitats
Metapopulation theory predicts that multiple small, fragmented populations, which normally may be too small or insufficiently diverse to survive alone, can interact to form a stable metapopulation, if there are enough corridors available to facilitate individual movement (i.e., gene flow) among the populations (Chan, Fitzgerald, & Zamudio, 2008). Populations without these interactions can experience unstable demographics and are less resilient to environmental stress (Prugh, Hodges, Sinclair, & Brashares, 2008; Schippers et al., 2008) – especially if genetic bottlenecks occur (Broquet et al., 2010). All species living at their geographic extremes – even well-connected populations – are more vulnerable to climate change as part of the higher environmental stresses placed on them (Brown et al., 2006; Rodríguez-Robles et al., 2010). The individuals who populate these range extremes and disperse to less-hospitable habitats may have differences in their genome accounting for these differences in behavior and population structure (Rödder & Schulte, 2010). This combination of increased risk and potentially unique genetics makes peripheral populations worthy of conservation and study. Their unique adaptations may prove to be a factor in habitat choice, dispersal, and how species alter their geographic ranges in response to an ever-changing environment.

**Potential effects of individual movement on habitat use and metapopulation dynamics**

The influence of population traits and habitat distribution across the landscape on habitat use and dispersal distance of most organisms is poorly understood (Hawkes, 2009; Sutherland et al., 2013). Such mechanisms are important for understanding the responses of
species and their geographic ranges to changing climate (Buckley, 2008, 2010; Sexton et al., 2009). In places with highly fragmented habitat—as is the case with *Sceloporus occidentalis* in western Washington State—the formation of a metapopulation is important to the long-term survival of the local subpopulations. Dispersal among habitat patches allows for repopulation of locally extinct fragments and replenishment of declining populations. Dispersal of individuals among populations (i.e. migration) increases the viability of these populations, and aids expansion of a species' geographic range (Kramer & Sarnelle, 2008; Lecomte & Boudjemadi, 2004).

Individual habitat use, choice, and dispersal are the central mechanisms of metapopulation dynamics (Southwood & Avens, 2010). Dispersal, however, is often overlooked in large-scale studies due to (1) difficulties in modeling individual habitat use, dispersal movements, and habitat choice during settlement, (2) relatively few small-scale studies examining habitat use and population density effects on dispersal tendencies. Important features of such small scales studies would be decision rules for when to leave their home patch, how to find nearby habitat patches, and how they decide where to settle (Baguette & Dyck, 2007). It is hypothesized that when the set of available habitat patches are unable to sustain a local animal subpopulation due to insufficient patch size, habitat degradation, or climate shifts, then sufficient connectivity among subpopulations would be critical to the maintenance of the metapopulation (Bowler & Benton, 2005; Heinz, Wissel, & Frank, 2006; Southwood & Avens, 2010).

Local demographics also may influence an individual's use of microhabitat and decisions to seek new habitat (Bowler & Benton, 2005; Kramer & Sarnelle, 2008; Lens et al.,
The features of dispersing individuals (sex, age, relatedness, maturity, physiology) will help determine the mechanisms at the basis of an individual's microhabitat and mesohabitat use and dispersal among habitats (Bowler & Benton, 2005; Hofmann, 2008; Ujvari, Dowton, & Madsen, 2008). Knowing the habitat use and dispersal tendencies among these “classes” of individuals will also aid in estimating how the intervening habitat, functions as a barrier or dispersal corridor.

As a model for ecological systems, lizards that bask in open, sunlit microhabitats—such as the aforementioned *Sceloporus occidentalis*—are useful species for study of animals in peripheral populations. Because most lizards, including *S. occidentalis*, have relatively small body size and modest vagility, study of peripheral lizard populations on a local scale is logistically easier than studying larger and more vagile birds and mammals on a larger geographic scale. Population sizes of small vertebrates with relatively low vagility are often high enough in small islands of varied habit for researchers to explore the tendency of these animals for dispersal—even if a minority of individuals disperse—among habitat islands (Ewers & Didham, 2006; Leidner & Haddad, 2011). Populations of the Western Fence Lizard *Sceloporus occidentalis* are locally convenient populations at the species' geographic extreme. Individuals can be found, observed, and captured with little difficulty, so the species is propitious model system for field research. Moreover, because the geographic range of *S. occidentalis* is relatively large for lizards—stretching from Baja California in the south to the northwestern corner of Washington state—and it can be found in moderately high abundances, it is a useful species for both latitudinal and altitudinal studies with respect to climate change and habitat change. The species typically resides in warm, dry regions
(Bowler & Benton, 2005; Hofmann, 2008; Ujvari et al., 2008), thus one would not expect to see these lizards at their northernmost geographic range to inhabit the coastal maritime climate of Washington. The coastal marine environment presents markedly different ecological challenges from the sagebrush desert habitat of more southern populations of *S. occidentalis*, and this northern population provides the opportunity to investigate habitat use at a geographical extreme. For example, body temperature of field-active *S. occidentalis* is about 35°C (Grigg & Buckley, 2013; McGinnis, 1966), so being warm in the cool, coastal maritime region of northwestern Washington, where forests dominate would seem to present a challenge for this species at its geographic periphery. Understanding how *S. occidentalis* adapts to and utilizes this habitat may be a useful step towards addressing larger ecological questions about geographic range boundaries and how they form and change over time, as well as smaller-scale inquiries on preservation and reintroduction efforts.
The three key questions and associated hypotheses my research addresses are:

1) Which characteristics of beach-edge mesohabitats and microhabitats are most highly associated with lizard habitat occupancy?
   - $H_1$: Habitat use by *Sceloporus occidentalis* is associated only with slopes having sun-exposed soils and patchy vegetation above beach.
   - $H_2$: Habitat use by *Sceloporus occidentalis* is associated only with large, vertically complex log fields.
   - $H_3$: Habitat use by *Sceloporus occidentalis* is associated with complex log fields and slopes with exposed soils and patchy vegetation.
   - Null: Habitat use by *Sceloporus occidentalis* is random.

2) What is the lizard distribution with respect to apparent quality of beach-edge habitat?
   - $H_1$: Lizards are uniformly distributed among all beach-edge habitat islands.
   - $H_2$: Lizards are clumped, associated with patches of prime beach-edge habitat islands.
   - Null: Lizards are distributed randomly along the beach irrespective of habitat quality.

3) Which age or sex classes tend to be more transient and more prone to dispersal?
   - $H_1$: Juvenile lizards are more likely to disperse longer distances within and among beach-edge habitats.
   - Null: Age at dispersal is random with respect to life stage.
   - Null$_2$: Individuals do not disperse from their hatching location.
Documenting patterns of habitat use by *Sceloporus occidentalis*, including population structure and density in the lizard-occupied mesohabitats, and determining the distribution of those mesohabitats and the potential for lizard dispersal among mesohabitats, should provide a basis for future studies of metapopulation persistence in the linear landscape along the marine shore. One may infer that higher potential for subpopulation connectivity will likely result in a more resilient metapopulation (Heinz et al., 2006) that is likely more stable numerically and is perhaps more genetically diverse. Thus, knowing the habitat used and ostensibly chosen by dispersers will provide a basis for understanding larger-scale population dynamics.
METHODS

Research System

The western fence lizard, *Sceloporus occidentalis*, maintains field-active body temperatures of about 35°C (Grigg & Buckley, 2013; McGinnis, 1966), and although in most of its geographic range its seasonal activity is associated with warm, dry conditions (Bowler & Benton, 2005; Hofmann, 2008; Ujvari et al., 2008), the northern edge of the species' range is located in Snohomish County, WA in beach-edge habitats of cool, maritime forests where it persists as an apparent metapopulation. It has been observed that *Sceloporus occidentalis* reside at and seasonally refuge on primarily southwest- and west-facing beach-edge slopes comprising a mix of exposed soils and patchy vegetation above predominantly southwest-facing beaches that have many driftwood logs quasi-permanently packed at the base of the slope (Powers, 2010). This particular habitat presumably has adequate oviposition sites provided by exposed soil slopes, basking and foraging sites provided by logs on which to perch, and antipredator refugia under the same logs and in the litter beneath nearby vegetation. (L. Anderson & Burgin, 2002; Beyer et al., 2010; Blevins & With, 2011; Powers, 2010). Other *Sceloporus occidentalis* populations that were found along beach-edge habitats of the Washington coast in the last century, are apparently extinct all the way south to Olympia, likely due to habitat loss and invasive species. Thus, these coastal populations west of Marysville, WA may become important for reintroduction efforts between Olympia and Everett, and research exemplars of the extrinsic ecological factors and intrinsic genetically-based factors that influence the formation and change of species' range boundaries.
Field Sites

Data for this thesis were collected from five study sites. They consist of five stretches of beach on the Tulalip Indian Reservation near Marysville, Washington (north to south): Sunny Shores (SS), Tulare Beach (TB), Spee-Bi-Dah (SBD), Tulalip Shores (TS), and north of Tulalip Bay (NTB; Figure 1). Each beach name derives from the beach community at the southeast end. Also, each beach has a point of land on the northwest end with another beach community around the point of land. That is, beach research sites are separated by intervening human beach communities, and most of the beach communities have immediately adjacent to the south a steep and heavily vegetated point of land. These beaches and vegetated points represent potential dispersal barriers of different lengths and character. Given the presumption that substantial and intensive research effort would be required for any one beach, SBD was chosen as the primary research focus because as a relatively long and the most centrally located beach, it was tentatively assumed that most of the requisite data for the thesis largely could be acquired from this single stretch of beach.
Figure 1. Map of study sites on the Tulalip Reservation, near Marysville, WA. My research was focused on the most central beach, Spee-Bi-Dah.
The stretches of beach-edge occupied by lizards are typically southwest-facing slopes with exposed soil mixed with shrub patches, some trees on the slope, and also with driftwood logs at the upper reaches of the beach, (Google Earth Photos of six known lizard locations, Burke Museum Records, WA state herp data base, confirmed in person by R. A. Anderson). *Sceloporus occidentalis* is known to be present at these beaches in high abundance (R. Anderson, personal communication).

### Lizard Sightings and Observation

Sighting data on individual *S. occidentalis* were obtained from mid-to-late spring and through the summer. Lizard activity on coastal beaches becomes common in mid-to-late spring, when air temperatures are suitably warm and skies are less cloudy. During summer, lizards along beaches are active from mid-to-late morning, then may retreat to shaded nanohabitats in the heat of the day, and then resume activity in late afternoon and early evening (Powers, 2010).

Complete data recorded for lizard sightings are detailed in Appendix A. Some of the more salient information included date and times when the lizard was seen, its sex and age/size class, paint code, behavior when first seen (basking, perched in apparent visual search, moving, pursuing prey, engaging in social interaction), substratum type (e.g. log, sand, pebbles, leaf litter) and substratum temperature where it was standing, and habitat (log field, dirt slope, grass, shrub), as well as precise location in relation to small nearby landmarks and GPS location. Many lizard locations were also recorded using digital photography.
Combined with habitat characterization data (below), the foregoing data about lizard sightings allowed me to analyze pieces of beach-edge habitat to determine which habitat characteristics were most strongly associated with lizard abundance (addressing thesis question 1), and which features best correlate with lizard habitat occupancy by age, sex, and time of season. In addition, repeated sightings of individually-marked lizards allowed me to characterize lizard residence sizes.

**Lizard Capture and Measurement**

Lizards were captured using a 12' fishing pole modified with an eyelet on the end and a loose loop of braided fishing line (“noose pole”), using standard noose-at-the-neck technique (Calsbeek & Sinervo, 2002; Powers, 2010; Watters, 2010). Lizard body temperatures were measured within 30 seconds of capture using a T-6000 Cloacal thermometer, inserted approximately 15mm into the individual's cloaca. Recording the body temperature, lizard behavior on sighting (i.e. basking, legs extended or body contacting substrate, or mating display), and the appearance of the skin upon capture (color, darkness) allowed me to determine if the lizard had reached appropriate body temperature to be active, or had recently emerged from its burrow.

Captured lizards were placed into individual cotton bags and stored in ventilated portable food-and-beverage coolers for transport to the laboratory. Lizards were identified by sex and measured for tail length and snout-ventral length (SVL) using a rigid, clear plastic ruler. Lizards were kept at least 24 hours (and no more than 72 hours) in order to ensure complete evacuation of the digestive tract. This allowed for an accurate measurement of body
mass. Captured individuals were toe-clipped for permanent marking (no more than two toes per foot and never the longest toe on a hind foot) and given a unique series of temporary paint marks to allow for easy identification at a distance. Toe-clipping is a standard marking technique for small lizards, and does not significantly affect lizard performance or survival (Olsson & Shine, 2006). After measurement and marking, lizards were released at the site of their capture, recorded via GPS coordinates at capture. Resightings of marked lizards allowed me to examine dispersal distances and tendencies by age/sex classes (thesis question 3).

All capture and measurement techniques were approved by the WWU Animal Care and Use Committee and the Washington Department of Fish and Wildlife.

**Habitat Characterization**

To determine patterns of habitat availability to *Sceloporus occidentalis*, I characterized the central beach habitat (SBD) in detail. To do this, I used the line-intercept method to calculate relative abundance of habitat types in different areas of each beach. Every 10 meters, I used a meter tape to set up a line perpendicular to the water and beach-edge interface, running from the base of the slope towards the water (Figures 2, 3). I used the line-intercept method to determine the type and size of each habitat type for that particular area of habitat (defined as the stretch of beach 5 meters to either side of the line). Characteristics of individual logs in each transect (length, diameter, percentage buried) were also recorded to estimate the nanohabitat density on each transect (Figure 4). Nanohabitat density is an estimate of the number of differently-angle log surfaces that a lizard can occupy in a given stretch of beach, and serves as a measure of the vertical complexity of the log field.
at that location. I also recorded the relative abundance of sun/shade/dappled lighting on these line-intercepts during times of lizard activity. The slope above the beach was characterized in a similar way, as an extension of the line up the slope. In many areas, however, the slope was too steep and unstable (or to easily disturbed by human foot traffic) to allow for up-close measurements of habitats. At these 10-meter intervals, measurements on the slope were documented using digital photography, and included records of relative slope area under vegetated cover vs slope area exposed, number of open patches, and distance upslope to nearest open patch.

Weather conditions (e.g. sky conditions, wind speed, air temperature) were also recorded regularly during field activities. Soil surface and subsurface temperature profiles were measured in several microhabitats over several weeks during the peak lizard activity season utilizing IButton Thermochron temperature recorders, which will be compared with known fence lizard nesting and body temperature preferences.
Figure 2. Diagram of beach-edge habitat with log field. Red lines represent the line-transects for habitat characterization.
Figure 3. Example diagram of habitat distribution along beaches.
Figure 4. Nanohabitat availability varies inversely with the amount of the log buried. Dotted lines represent level of sand or sediment covering a given log. Nanohabitat density (10 designated locations along the log, plus either end of the log, totaling to 12 possible positions) is an estimate of the number of substantially different angled surfaces lizards can adopt (out of the 12) on a log in order to control thermoregulation and exposure.
Analyses

Lizard sighting locations were entered into ArcGIS and overlain on a satellite-imagery map of Spee-Bi-Dah beach (Figure 5). Polygons were constructed over the area represented by each 10m habitat transect, and used to obtain a count of lizard sightings in each transect over two summers. This lizard count data was converted into presence/absence data for each transect where lizards were common (more than two total sightings), or rarely seen (less than two total sightings). Transects that contained only two sightings over the observation period were counted as 'absent' if the sightings were within five days of each other, and counted as 'present' if the two sightings were farther apart in time. All habitat data were transformed with a Log(x+1) function to account for the large differences in scale among variables.

Assuming that there is (1) a continuous gradient of habitat quality from ‘optimal’ through ‘suboptimal’ to ‘poor’ quality, and (2) the high population density of fence lizards on Spee-Bi-Dah, where crowding of lizards near optimal habitat may force some lizards into presumably suboptimal habitat, I applied a technique to clarify habitat preference. That is, I removed from the analysis the approximate middle third of transects by lizard sighting count (i.e. transects with 2-5 total sightings, which presumably represent ‘suboptimal’ habitats) to compare the most preferred (presumably optimal) lizard habitats with the least preferred habitats on Spee-Bi-Dah.

When I enrolled in Brian Bingham's Experimental Design class, he introduced me to the virtues of Multidimensional scaling (MDS) analysis. MDS is a powerful analytical tool that plots data points (habitat transects in my case) in n-dimensional space (where n is the
number of variables associated with the samples, see Table 1) based on the similarity of each site. The analysis was performed in the PRIMER 6 statistics package. A similarity matrix, determined by Euclidean distance between samples (i.e. 10m habitat areas), was generated for the analysis. The program then compresses the $n$-dimensional plot into two dimensions, attempting to maintain the relative spatial relationships of the samples; a stress value is given to indicate the level of success achieved in the compression (Carvalho et al., 2014; Heaven & Scrosati, 2008).

MDS analysis is preferred because it has very few assumptions about the input data, and the few assumptions it does have are quite easy to meet. In contract, logistic regression (another commonly used analytical technique in ecology) assumes independence between observations. This is appropriate to a study involving randomly sampled sites, but is not as well-suited to a study involving detailed characterization of an entire habitat area, such as my own (Lagendijk et al., 2015). Another common analytical technique is principal components analysis (PCA), which is similar in function to MDS, though it has additional assumptions regarding linear relationships between sighting data and habitat variables, and tends to produce better results when data is normally distributed. Thus, I chose to use MDS analysis.

The MDS analysis was followed by Analysis of Similarity (ANOSIM) and Similarity Percentage analysis (SIMPER), also in the PRIMER 6 program. Analysis of Similarity identifies any significant separation between treatments (presence/absence of lizards in a 10-meter section of beach) and generates a p-value similar to other statistical analyses. ANOSIM also provides an R-statistic, which ranges from zero to one, and represents the degree of separation between treatment groups. A higher R-statistic (closer to one) represents treatment
groups with clear and distinct separation, whereas a lower R-statistic indicates overlap between treatments. In relation to my thesis, a high R-statistic would represent a population that is heavily clustered around areas of ideal habitat, while a low R-statistic would represent a population that is more diffusely distributed throughout Spee-Bi-Dah beach, with more commonality in regards to habitat characteristics between beach areas (hence a lower R may represent intolerance to extreme spatial proximity among individuals, a result that may be related to hypotheses 1 and 2 in thesis question 2). SIMPER analysis determines which variables are contributing most to the separation between treatment groups, and gives cumulative percentages indicating the relative effect of each variable. Together, these analyses allowed me to examine which habitat characters are most strongly correlated with lizard presence on a stretch of beach.

I also examined differences in habitat preferences by preparing contingency tables which displayed the number of lizard sightings in different substrata (log, litter/debris, sand/soil, pebbles) over all beaches. I prepared tables which compared lizard sightings in different habitats between age and sex classes, as well as a table comparing various lizard behaviors observed in different habitats. Chi-square analysis was used to determine if there were significant differences in habitat preferences. However, chi-square analysis is sensitive to low cell values, which can cause inaccurate test results. In such cases, Fisher's Exact Test was used as a secondary analysis for tables where cell values were too low to provide an accurate p-value via chi-square analysis. Fisher's Exact Test is similar to chi-square analysis, but it is more tolerant of low cell values (Irwin, 1935; Routledge, 2005). Fisher's test is regarded as a conservative test (more Type II errors) with low power (Agresti, 1992; Lin,
Chang, & Pal, 2015). That is, the test has a tendency to falsely produce non-significant results. However, that fact increases confidence in any significant results.

As a follow-up to any significant results from chi-square and/or Fisher's test, I examined tables of standardized residual values. Examining standard residuals is a relatively simple method for determining which cells are contributing most to the deviation from expected frequencies found by the chi-square test (Sharpe, 2015). By examining the positive/negative values of the residuals, it is possible to determine which cell values are higher or lower than would be expected if there were no relationship between habitat and lizard sighting frequency by age/sex/behavior.
RESULTS

Among all beaches studied, 359 lizards were caught and marked out of approximately 1040 total sightings (255 of 359 marked and 800 of 1040 sightings were on Spee-Bi-Dah). Analysis with MDS showed a moderate separation of occupied and unoccupied habitats, with a stress value of 0.11, indicating a reliable conversion of the plot to two dimensions (Figure 6). ANOSIM confirmed a significant separation of occupied and unoccupied transects (p = 0.001), though a low R-stat (0.11) indicated overlap in the data, consistent with the MDS plot. SIMPER analysis showed that 90% of the variation in data was due to five factors (Tables 1 and 2): the upslope distance to the nearest open patch (44.9%), nanohabitat density (22.2%), the number of open patches on the slope above the beach (16.8%), the length of the log field (10.6%), and the amount of open area on the slope relative to the amount of cover (5.5%). Thus, I can conclude that lizard habitat use is associated with both complex log fields and slopes consisting of a mixture of sun-exposed soils and patchy vegetation. This result refutes hypotheses 1 and 2 and the null hypothesis, but supports hypothesis 3 of my first thesis question (“Which characteristics of beach-edge mesohabitats and microhabitats are most highly associated with lizard habitat occupancy?”).
Figure 5. Map of Spee-Bi-Dah with lizard sightings indicated by green dots. Pale rectangles represent habitat transect areas. Inset picture shows close view of transect areas. Red bars show lizard sighting counts by 100-meter sections.
Figure 6. MDS plot of all lizard sightings with 'ideal habitat' selection criterion applied. There is noticeable separation between occupied and unoccupied transects in regards to habitat characteristics, though some overlap is still present. Gray boxes show counts of points in each group (non-overlapping) and in overlap zone.
Table 1. SIMPER analysis results. *S. occidentalis* beach habitat presence is most strongly associated with open soil patches on the slope near the beach, and vertically complex log fields.

<table>
<thead>
<tr>
<th>SIMPER Habitat Variables</th>
<th>Ecological Variable Function</th>
<th>% Contribution to Separation</th>
<th>Lizards Prefer...</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nearest soil patch upslope (m)</td>
<td>Avoid tides</td>
<td>44.88</td>
<td>&lt; 2m</td>
</tr>
<tr>
<td>Nanohabitat density</td>
<td>Refugia</td>
<td>22.24</td>
<td>Higher</td>
</tr>
<tr>
<td># of open slope patches</td>
<td>Nesting, Hibernation</td>
<td>16.81</td>
<td>Lower</td>
</tr>
<tr>
<td>Log field length</td>
<td>Refugia</td>
<td>10.6</td>
<td>Longer</td>
</tr>
<tr>
<td>Relative open area on slope</td>
<td>Foraging</td>
<td>5.48</td>
<td>Lower</td>
</tr>
</tbody>
</table>
Table 2. Average values of SIMPER variables between occupied and unoccupied habitats (± standard error).
Occupied beach habitats have closer soil patches upslope, more vertically complex and longer log fields, and a smaller ratio of open/vegetated areas on slope with more edge habitat available. All were significantly different via two-tailed t-test (p < 0.05) except for nanohabitat density. Average open soil patch size on slope above beach was 14.8 ± 4.4 m² for occupied habitats and 28.5 ± 5.5 m² for unoccupied habitats.

<table>
<thead>
<tr>
<th></th>
<th>Nearest open slope patch</th>
<th>Nanohabitat density</th>
<th># of open slope patches</th>
<th>Log field length</th>
<th>Relative open area on slope</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Occupied</strong></td>
<td>1.06 ± 0.21</td>
<td>76.9 ± 5.7</td>
<td>0.78 ± 0.09</td>
<td>634.3 ± 15.6</td>
<td>0.38 ± 0.04</td>
</tr>
<tr>
<td><strong>Unoccupied</strong></td>
<td>1.89 ± 0.19</td>
<td>69.3 ± 4.9</td>
<td>1.31 ± 0.13</td>
<td>525.8 ± 26.6</td>
<td>0.56 ± 0.05</td>
</tr>
</tbody>
</table>
I repeated the MDS and related analyses after partitioning the lizard sighting data by age/sex class, and by early/late season. However, none of these tests show significant results at the 0.05 level except for the 'early season' set (May-July), which is likely due to the majority of sightings occurring during that period. SIMPER results were almost identical to the overall set of lizards for the 'early season' dataset. The smaller number of sightings in the other datasets likely contributed to the lack of statistical significance.

Chi-square analysis was performed on contingency tables to examine differences in habitat preference among sexes, age classes, and for certain behaviors (Table 3). Significant differences were found in habitat preference for age class and for nanohabitat use by behavior, but not between males and females (p = 0.077). Low cell values based on chi-square distribution can cause unreliable results in chi-square analysis, which was the case in the age and behavior contingency tables. To counter this, Fisher's exact test was used to confirm the results (p = 0.0002 and 0.0005, respectively). As stated above, Fisher's test is more tolerant of low cell values, which suggests a reliable confirmation of the presence of non-random patterns in the age and behavior contingency tables below.
Table 3. Contingency table for chi-square analysis. Significant chi-square results with problematic low cell values are denoted with (**). Significant results with Fisher's Exact Test denoted with (*).

<table>
<thead>
<tr>
<th></th>
<th>Log</th>
<th>Sand/Soil</th>
<th>Litter/Debris</th>
<th>Pebbles</th>
<th>Chi-square p-value</th>
<th>Fisher's Exact Test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td>328</td>
<td>20</td>
<td>6</td>
<td>6</td>
<td>0.08</td>
<td>0.07</td>
</tr>
<tr>
<td>Females</td>
<td>150</td>
<td>14</td>
<td>8</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adults</td>
<td>505</td>
<td>44</td>
<td>19</td>
<td>16</td>
<td>6.4e-5**</td>
<td>0.0002*</td>
</tr>
<tr>
<td>Juveniles</td>
<td>549</td>
<td>29</td>
<td>5</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hatchlings</td>
<td>77</td>
<td>24</td>
<td>3</td>
<td>7</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Behavior**

<table>
<thead>
<tr>
<th></th>
<th>Log</th>
<th>Sand/Soil</th>
<th>Litter/Debris</th>
<th>Pebbles</th>
<th>Chi-square p-value</th>
<th>Fisher's Exact Test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thermoregulation</td>
<td>350</td>
<td>18</td>
<td>3</td>
<td>8</td>
<td>4.03e-7**</td>
<td>3.62e-7*</td>
</tr>
<tr>
<td>Foraging</td>
<td>67</td>
<td>11</td>
<td>8</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Social Interaction</td>
<td>115</td>
<td>22</td>
<td>6</td>
<td>1</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
To determine which factors were contributing to two significant differences seen with the chi-square analysis, I examined tables of standardized residual values. Residuals with an absolute value greater than two are likely to be statistically significant as factors contributing to differences from expected frequencies found in chi-square tests (Sharpe, 2015). In the case of age classes, significant positive deviations were found in cells corresponding to hatchling occupation of sand/soil and pebble nanohabitats, indicating a higher-than-expected frequency of observation (Table 4). This further supports hypothesis 2 in my second thesis question (that lizards are grouped around prime habitat areas) by suggesting that hatchlings are being forced into less-than-ideal microhabitats by competition with older lizards. In addition, lizards were found to have a negative deviation for thermoregulatory behaviors in sand/soil and leaf litter nanohabitats, and positive correlation with those behaviors on logs. I observed higher sighting frequencies of foraging behaviors in leaf litter habitats, but less foraging on logs (Table 5). Social interactions were more common on soils, as seen in Table 5.
Table 4. Standardized residual values for analysis of Age vs Habitat. Significant deviations from expected frequencies in chi-square are denoted with (*). Notably, hatchlings were found on sand and pebbles more frequently than would be expected by chance.

<table>
<thead>
<tr>
<th>Age</th>
<th>Log</th>
<th>Sand/Soil</th>
<th>Litter/Debris</th>
<th>Pebbles</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adults</td>
<td>0.53</td>
<td>-1.79</td>
<td>0.74</td>
<td>-0.29</td>
</tr>
<tr>
<td>Juveniles</td>
<td>0.32</td>
<td>0.10</td>
<td>-1.04</td>
<td>-0.86</td>
</tr>
<tr>
<td>Hatchlings</td>
<td>-1.73</td>
<td><strong>3.95</strong>*</td>
<td>-0.03</td>
<td><strong>2.06</strong>*</td>
</tr>
</tbody>
</table>
Table 5. Standardized residual values for analysis of Behavior vs Habitat. Significant deviations from expected frequencies in chi-square are denoted with (*). Notably, lizards seemed to prefer logs for basking instead of soils or leaf litter, though it was more likely to be found foraging in leaf litter than on logs. Sand and soil seemed to be a common location for social interactions (displaying, mating, chasing).

<table>
<thead>
<tr>
<th></th>
<th>Log</th>
<th>Sand/Soil</th>
<th>Litter/Debris</th>
<th>Pebbles</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thermoregulation</td>
<td>5.07*</td>
<td>-4.09*</td>
<td>-3.81*</td>
<td>0.34</td>
</tr>
<tr>
<td>Foraging</td>
<td>-3.5*</td>
<td>1.49</td>
<td>3.86*</td>
<td>1.04</td>
</tr>
<tr>
<td>Social Interaction</td>
<td>-2.88</td>
<td>3.45*</td>
<td>1.16</td>
<td>-1.25</td>
</tr>
</tbody>
</table>
Given that *S. occidentalis* populations at Spee-Bi-Dah are high, I infer that lizards are competing for prime habitat areas – which supports hypothesis 2 (and refutes hypothesis 1 and the null) of my second thesis question (“What is the lizard distribution with respect to apparent quality of beach-edge habitat?”). The low R-statistic from ANOSIM (which is not unexpected for my study system, but has a significant p-value), as well as the tendency towards juvenile dispersal and apparent competition forcing hatchlings into suboptimal habitat, support this inference on lizard distribution on Spee-Bi-Dah.

I also examined sighting maps of individual lizard which were seen multiple times across weeks and months so that I could (1) get some estimate of the size of a lizard's home territory, and (2) determine which individuals were transient and dispersers. For each apparent lizard dispersal event (see Figure 7), I calculated dispersal distance and summarized the data by age and sex classes (Table 6). Males seemed to disperse in greater numbers than females (approximately 50% more by count), though sex did not appear to be a factor in dispersal distance based on a two-tailed t-test (*p* = 0.78). Juveniles, however, traveled significantly farther than adults when dispersing (*p* = 0.047), which supports hypothesis 2 of my third thesis question (“Which age or sex classes tend to be more transient and more prone to dispersal?”).
Figure 7. Sighting locations of two individuals over 2014 on Spee-Bi-Dah. Dispersing individuals (typically traveling more than 50 meters along the beach) typically have a sighting map similar to the image on the left. Individuals with sighting maps more similar to the image on the right were classified as non-dispersing.
Table 6. Number of dispersing lizards by age and sex categories, with mean dispersal distance in meters ± standard deviation. A 2-tailed t-test shows significant difference between adult and juvenile dispersal distances ($p = 0.047$), but not between males and females ($p = 0.78$). Among age classes, a similar number of individuals were marked. Approximately twice as many males were marked as compared to females.

<table>
<thead>
<tr>
<th></th>
<th>Count</th>
<th>Mean Dispersal (m, ±SD)</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>13</td>
<td>231 ± 229</td>
<td>60 – 727m</td>
</tr>
<tr>
<td>Female</td>
<td>8</td>
<td>252 ± 113</td>
<td>112 – 400m</td>
</tr>
<tr>
<td>Adult</td>
<td>12</td>
<td>176 ± 91</td>
<td>60 – 346m</td>
</tr>
<tr>
<td>Juvenile</td>
<td>11</td>
<td>499 ± 248</td>
<td>65 – 727m</td>
</tr>
</tbody>
</table>
To characterize temporal patterns of temperature compared among microhabitats on Spee-Bi-Dah, I utilized Thermochron IButton Temperature data loggers. Temperatures were logged every 20 minutes for 30 days during August, in a variety of microhabitats; log crevice in sun and shade, open dirt slope in sun and shade for both west- and southwest-facing slopes, and dappled-light NW/SE edge of open slope patch on a southwest-facing slope. For log crevices of sunlit logs, the average temperature over the collection period was 19.0 ± 0.03°C (SE), with a maximum temperature of 27.5°C. In the shade, log crevices averaged 17.7 ± 0.03°C, with a maximum of 20°C. The summarized data for other sites is shown in Tables 7 and 8, below.
Table 7. Average overall soil temperatures for sun-exposed west-facing and southwest-facing slopes, shaded slopes, and NW/SE dappled-light edges of an open slope patch at Spee-Bi-Dah. IButton Temperature loggers were buried up to 20cm in the soil. Data were collected over 30 days in August 2014. Standard errors are shown for each value. The shaded slope 10cm depth data logger failed during the study.

<table>
<thead>
<tr>
<th>Depth</th>
<th>Sunny SW-facing Slope</th>
<th>Sunny W-facing Slope</th>
<th>Shaded Slope</th>
<th>Open Slope Patch NW Edge</th>
<th>Open Slope Patch SE Edge</th>
</tr>
</thead>
<tbody>
<tr>
<td>0cm</td>
<td>26.0 ± 0.3</td>
<td>25.8 ± 0.2</td>
<td>16.9 ± 0.04</td>
<td>22.4 ± 0.2</td>
<td>20.2 ± 0.13</td>
</tr>
<tr>
<td>5cm</td>
<td>25.0 ± 0.2</td>
<td>24.5 ± 0.15</td>
<td>16.2 ± 0.03</td>
<td>21.8 ± 0.1</td>
<td>20.1 ± 0.08</td>
</tr>
<tr>
<td>10cm</td>
<td>25.7 ± 0.1</td>
<td>24.0 ± 0.1</td>
<td>–</td>
<td>21.0 ± 0.07</td>
<td>19.6 ± 0.06</td>
</tr>
<tr>
<td>20cm</td>
<td>25.0 ± 0.1</td>
<td>23.3 ± 0.06</td>
<td>16.3 ± 0.02</td>
<td>20.3 ± 0.04</td>
<td>19.7 ± 0.04</td>
</tr>
</tbody>
</table>
Table 8. Maximum soil temperature values (°C) observed for each location during August 2014 at Spee-Bi-Dah.

<table>
<thead>
<tr>
<th>Depth</th>
<th>Sunny SW-facing Slope</th>
<th>Sunny W-facing Slope</th>
<th>Shaded Slope</th>
<th>Open Slope Patch NW Edge</th>
<th>Open Slope Patch SE Edge</th>
</tr>
</thead>
<tbody>
<tr>
<td>0cm</td>
<td>65</td>
<td>61</td>
<td>24</td>
<td>59</td>
<td>48.5</td>
</tr>
<tr>
<td>5cm</td>
<td>49</td>
<td>48</td>
<td>21.5</td>
<td>37</td>
<td>37</td>
</tr>
<tr>
<td>10cm</td>
<td>41.5</td>
<td>36</td>
<td>–</td>
<td>29.5</td>
<td>29</td>
</tr>
<tr>
<td>20cm</td>
<td>34.5</td>
<td>29.5</td>
<td>17.5</td>
<td>24.5</td>
<td>24.5</td>
</tr>
</tbody>
</table>
DISCUSSION

Habitat Use

My research supports the notion that *Sceloporus occidentalis* displays preference for certain habitat characteristics on Spee-Bi-Dah beach. Principally, they are associated with wide, vertically-developed log fields and a mixed slope of vegetation and close-by open soil patches. The results from ANOSIM clearly show a significant difference between occupied and unoccupied transects \( p = 0.001 \). However, the relatively low R-statistic in ANOSIM \( (0.11) \) indicates some similarity in habitat characteristics between occupied and unoccupied habitat areas. This can also be seen in the MDS ordination plot, which lacks obvious distinction between groups (though some separation is still observable).

The low R-statistic itself does not invalidate my results, and low R values can still hold ecological significance (Bonato, Delariva, & Silva, 2012; Geheber & Frenette, 2015; Jimenez-Alfaro, Marceno, Guarino, & Chytry, 2015). MDS analysis is often used with plant species or marine invertebrate inventories to examine differences between study sites, and it is in these types of studies, with creatures of relatively low-vagility, where high R-statistics are usually observed (Heaven & Scrosati, 2008; Meyer et al., 2015). In many animal studies with more-mobile subjects, R values more similar to my own were often observed (Bonato et al., 2012; Geheber & Frenette, 2015; Westera, Lavery, & Hyndes, 2003).

The overlap in habitat data, and corresponding low R-stat, may be due to several factors. First, as discussed above, western fence lizards are mobile creatures. Some individuals were found to travel hundreds of meters over a period of weeks while actively dispersing, and even those with a stable territorial range sometimes roamed up to 50 meters,
though most remained with a 10-20 meter stretch of beach. Similarly, a few individuals migrated between adjacent beaches, and there is likely to be a greater number that I was unable to capture, which could increase the noise-to-signal ratio in the data, and therefore lower the corresponding R-statistic.

A second factor that may have contributed to data overlap in relatively occupied and relatively unoccupied features of the habitat is that the high population density of *Sceloporus occidentalis* (Figure 5) may be forcing some lizards to seek out less-than-ideal habitat as more-dominant lizards occupy prime habitat areas. Spee-Bi-Dah and nearby beaches are highly restricted in the amount of habitat area available for population expansion, and my data shows that the number of lizards on even a single beach is very high (even with 359 marked lizards over the study period, only half of the total number of lizard sightings were of previously marked individuals). I was able to corroborate this possible effect by removing moderately-populated habitat transects from the statistical analyses after the initial MDS analysis, but it is possible that there is still some crowding effect occurring even after comparing the ends of the occupancy spectrum. The high lizard population in specific areas compared to others suggests that the lizards are not simply spreading out due to natural tendencies, but more likely due to the aforementioned competition for resources.

Despite the aforementioned confounding factors, the large size of dataset resulted in high statistical power of the ANOSIM. This high statistical power is corroborated by the facts that (1) the MDS analysis revealed no effects of age or sex class, and (2) the majority of lizard sightings occurring during the early season, and (3) SIMPER results were virtually identical to the analysis of the population as a whole.
Together, the MDS, ANOSIM, and SIMPER analyses allowed me to address my first proposed thesis question, “Which characteristics of beach-edge mesohabitats and microhabitats are most highly associated with lizard habitat occupancy?” The SIMPER results show that *S. occidentalis* habitat use is correlated with both log field characteristics (length, nanohabitat density) and with slope habitat characteristics (number of nearby open patches, amount of vegetation), which invalidates my first two hypotheses, but supports my third. I also reject the null hypothesis, based on the statistically-significant ANOSIM results (p = 0.001), which suggest a discernible pattern exists in *S. occidentalis*’ habitat use on Spee-Bi-Dah.

**Habitat Use in More Detail**

The five significant factors that correlate with lizard habitat use as detected by SIMPER analysis can be categorized as pertaining to characteristics of the slope (nearest open patch upslope, number of open slope patches, relative slope open area) or characteristics of the log field (nanohabitat density, log field length). Together, these two sets of characteristics presumably represent habitat requirements for *S. occidentalis*.

Analyses with MDS, ANOSIM, and SIMPER revealed that lizard habitat use correlated with distance to nearest open patch upslope, nanohabitat density, number of open slope patches, log field length, and relative slope openness. These factors all fit with the integrated conclusion that *Sceloporus occidentalis* requires a large and vertically-complex log field and access to relatively open slope habitat above the beach with a mix of vegetation and open sediment. I infer that *Sceloporus occidentalis* have habitat preferences, even within a single beach comprising a high population density of lizards.
Slope Habitat Characteristics

According to the SIMPER analysis, the most important factor in determining lizard habitat use was a slope characteristic – the direct upslope distance to the nearest open patch above the beach (45% of the total effect), which was approximately double the contributing percentage of the next largest factor, nanohabitat density which was a log field characteristic. The 10-meter beach-edge transects with high lizard numbers had smaller average distance to open slope patches compared to those transects with low lizard counts (Table 2). The results fit expectations, as lizards likely require access to open, sunlit sandy areas above the high-tide line (i.e. avoids saltwater flooding) for nesting and hibernation (Angilletta, Sears, & Pringle, 2009; Warner & Andrews, 2002). In the genus *Sceloporus*, average nest depth is approximately 6 cm, and preferred temperatures range from 24-28°C (Angilletta et al., 2009; Warner & Andrews, 2002). The temperature data I collected shows that sunny open slope patches fall within that range, both for west- and southwest-facing beach slopes (Table 7).

Opposite my initial expectations, lizard-occupied transects had lower average values for both number of open slope patches nearby, and relative open area on the slope. These two variables may be correlated to some degree, and thus may represent a single reason for deviation from the expected results. Fence lizards often occupy the edges of dense vegetation patches, as they may require some degree of vegetation cover for protection and as a source for arthropod prey (Diego-Rasilla & Pérez-Mellado, 2003; Watters, 2010). Lizards on Spee-Bi-Dah seem to display preferences for open slope patches that are neither extremely large or extremely small, as most occupied habitat areas fell within the range of 20-40 m² for average exposed soil patch sizes (Figure 8, Tables 1 and 2). It is possible that the largest open slope
areas are more often found too far away from sources of food and refugia for lizards. An example of this phenomenon may be seen in the northwestern section of Spee-Bi-Dah beach, where a landslide created a large contiguous area of open sandy slope approximately 300 meters long, yet lizard populations in that area are quite low (Figure 5). The open slope area in question is separated from the log field below by a 3-meter wide band of a dense stand of Himalayan blackberry. This habitat configuration minimizes the porous, open edge habitat and restricts lizard access to the sandy slope. Moreover, in contrast to the large open patch and average size of least-occupied (lower third of transects representing ‘poor’ lizard habitat) open slope areas (28.5 ± 5.5 m²), the most-occupied (upper third of transects representing ‘optimal’ habitat) open slope habitats have a smaller average patch size (14.8 ± 4.4 m²).
Figure 8. Schematic representation of distribution of open slope patches as related to lizard needs for edge habitat advantages: thermoregulation, refugia, foraging.
It is also prudent to consider the entire suite of variables and variable properties that must be included to determine habitat quality. High-value factors in a given transect can sometimes account for less-ideal qualities in other aspects. Even if a given area does not have as many distinct open slope patches as another, for example, it is possible that the amount of edge habitat available or the quality of nearby cover could account for the observed discrepancy in average open patch size on beach slopes for occupied vs unoccupied habitats.

Overall, I strongly infer that *Sceloporus occidentalis* in western Washington's coastal marine habitats requires beach slopes with a complex mix of vegetation and open patches, and with short travel distance between slope habitat and beach log fields. The apparently optimal combination of features also includes less than two meters between the open slope patches, thereby providing sufficient edge habitat and cover for protection and foraging. I did not observe any occupied habitat area on Spee-Bi-Dah with a distance to nearest dirt patch greater than two meters. Himalayan blackberry is of special concern in Washington for its tendency to grow quickly and thus fill in open slope habitat that is clearly required by *S. occidentalis*.

**Log Field Habitat Characteristics**

Log field length and nanohabitat density were detected by the SIMPER analysis to be two log field characteristics that accounted for the greatest difference (34%) between occupied and unoccupied beach habitats (Table 1). Nanohabitat density, calculated based on the number of different nanohabitats provided by individual logs in a given transect (Figure 4), serves as a measure of the vertical, depth-related complexity of the log field. Deeper log
fields provide a more options for lizards when choosing locations for foraging, basking, displaying, or hiding. Log field length functions similarly to nanohabitat density; some areas, for example, had wide log fields that consisted of relatively few large logs. These areas had correspondingly low nanohabitat density, and supported fewer lizards as a result.

**Habitat Preference by Age and Sex**

Habitat use differences between young vs adult lizards, and between males vs females may be expected, given the purported dispersal tendencies of young lizards and the presumed competition for access to reproductive females among males (Hierlihy, Garcia-collazo, Tapia, & Mallory, 2013; Hofmann, 2008; Ujvari et al., 2008). Thus, I prepared contingency tables that categorized lizard sightings by nanohabitat, and divided lizards into groups based on sex and age class, and behavior when first sighted (Table 3). I found significant effects within the age class and behavior tables, and examined standardized residuals to determine the source of deviation. Statistical patterns matched anecdotal impressions from our observations in the field.

After hatching in mid-late summer, neonate lizards (i.e. hatchlings) were often observed a short distance outside of the log field toward the surf. In contrast, both adults and presume yearlings were rarely seen beyond the log field boundaries. Hatchlings were also observed in microhabitats that were largely unused by more mature lizards, such as small sandy areas at the base of sandstone cliffs with few logs. Typically, these areas were close to other, more useful habitat, but hatchlings were more likely to be found on less-used substrata (Table 4). Hatchlings may have avoided larger lizards or were forced out of the prime habitat areas by larger lizards. I infer from the chi-square residuals, despite the lower sample size,
that hatchlings were less likely to be seen on logs, which otherwise seems to be the preferred adult lizard nanohabitat in the Tulalip metapopulation. The potential competition between lizard age classes supports the second hypothesis (“Lizards are clumped around patches of prime beach-edge habitat”) of my second thesis question: “What is the lizard distribution with respect to apparent quality of beach-edge habitat?”

On the subject of behavioral habitat preferences, most findings fit with expected trends. Lizards were more often found foraging in leaf litter or woody debris, and less often on logs, which is likely due to the availability of insects (R. A. Anderson, 2007; Watters, 2010). Social behavior (displaying, mating, chasing, etc.) was observed more frequently on sand or soil substrates. I found a negative correlation between thermoregulatory behavior and the use of sand/soil and plant litter nanohabitats, and a positive correlation with log habitats, where most basking was observed. Leaf litter is likely a poor substrate for basking due to its relative inability to efficiently hold or reflect heat. As long as sand is not wicking up moisture from below, it can become quite warm from sun exposure, and hence should be suitable for basking. But it is likely that most areas of sand within the log field would receive less sunlight than log surfaces due to partial shading by logs. Moreover, the three-dimensionality of logs permit them to have surfaces that are more likely to have both hot sunlit surfaces perpendicular to the direction of the incoming sunlight—which is suitable for basking—and more tangential sunlit portions conducive to thermoregulation when perched and in visual search for prey (Asbury & Adolph, 2007; McGinnis & Mar, 1970). Logs also provided easy access to cover from predators, whereas leaving the log field to access sun-soaked sand towards the water would leave lizards with few options for cover if the need to flee arises.
Lizard Dispersal

Of 359 marked lizards, twenty were found to have dispersed a substantial distance at some point during the observation period. Dispersal distances ranged from 60 to over 700 meters, over periods ranging from 11 days to more than a month. Four individuals traveled over 400 meters during their observed dispersal, all of which were juvenile lizards, and the top three of which were males. I partitioned these dispersal data by age and sex class (Table 6). Although I found dispersion in all age and sex classes, the longest mean dispersal distance was found in juveniles. A two-tailed t-tests showed that juvenile lizards were more likely to disperse farther than adults ($p = 0.047$). This fits with previous literature on the subject that suggests juvenile lizards tend to more readily disperse, likely due to competition with larger adults (Lecomte & Boudjemadi, 2004; Ujvari et al., 2008). Males and females did not display a significant difference in dispersal distances, though I did find approximately 50% more males dispersing than females. In many lizard species, males tend to be more prone to dispersal in order to search for mates and claim territory (Ujvari et al., 2008). While females can sometimes travel large distances to locate nesting sites, they typically return to their previous living area after nesting (Angilletta et al., 2009). I did not observe this behavior in my study.

The data on lizard dispersal directly addresses my third thesis question (“Which age or sex classes tend to be more transient and more prone to dispersal?”). A two-tailed t-test found greater dispersal distances among juvenile lizards compared to adults, which supports my second hypothesis that juvenile lizards are more likely to disperse farther compared to adult lizards. Additionally, the number of dispersing lizards also shows a bias towards male
dispersal by count, though not by distance traveled (Table 6).

The trend towards juvenile dispersal in *Sceloporus occidentalis* also provides support for the second hypothesis (“Lizards are clumped around patches of prime beach-edge habitat”) of my second thesis question: “What is the lizard distribution with respect to apparent quality of beach-edge habitat?” Juvenile lizards that are forced from prime habitat by competition must travel to seek out other available habitat, at times being forced to utilize less-than-ideal habitat areas. These confounding factors would introduce uncertainty into the analysis. The suggestion of intraspecific competition at Spee-Bi-Dah is supported by the apparent competition between adults and hatchling lizards found through chi-square analysis (Tables 3 and 4). The combined effect of these uncertainties would likely be a dataset with a discernible-yet-obfuscated pattern, similar to what I observed through MDS and ANOSIM. The combination of a statistically significant pattern ($p = 0.001$) and a relatively diffuse dataset ($R = 0.12$) matches what would be expected if *S. occidentalis* were competing for prime habitat patches on Spee-Bi-Dah. Thus, the second hypothesis of my second thesis question is supported. That is, *S. occidentalis* is clumped around areas of prime habitat.
Management Implications

*Sceloporus occidentalis*, as a species, is not endangered. However, range-edge populations in Washington state have been declining in recent decades due to habitat loss by human encroachment and invasive plant species occupying vital landslide habitat. The Washington State Department of Fish and Wildlife and Tulalip Tribe have expressed interest in preserving coastal marine fence lizard populations.

Usable habitat for *S. occidentalis* in western Washington has been declining in recent decades for multiple reasons – among them, habitat loss due to expanding human habitation and slope stabilization activities. Western fence lizards depend on habitat disturbance by small landslides to provide open sandy slope habitat for basking and nesting, as well as hibernation during the winter (Iraeta, Díaz, & Bauwens, 2007; Sears, 2005). Loss of open sandy slope has been exacerbated by the introduction of Himalayan blackberry, an invasive species which quickly colonizes open sandy areas and grows into a thick shrub (Caplan & Yeakley, 2006; Gaire, Astley, Upadhyaya, Clements, & Bargen, 2015). Himalayan blackberry's fast growth blocks access to sandy slope habitat, and their thick root systems make it difficult for lizards to utilize the habitat for nesting or hibernation. A combination of these factors has contributed to the loss of fence lizard populations south of the Tulalip metapopulation. As of 2014, the next closest known population of *S. occidentalis* on the coast is over 200 km to the south, near Olympia, WA. Previously, a number of populations existed on several beaches on the intervening coastline. Understanding the habitat patterns of *S. occidentalis* will be useful to preservation and reintroduction efforts in the state of Washington. Western fence lizards were once common sights on many southwest-facing
beaches around Puget Sound, but have declined due to various factors (described above). In addition to the population's potentially unique genetic adaptations, western fence lizards are a highly visible, charismatic species that is useful in public outreach and education.

Another factor to consider is the presence of complex log fields which *S. occidentalis* depends on. While a minor concern, preservation of these log fields is a factor that conservationists should be aware of, as log fields are occasionally used as resources by various entities. A few, relatively small areas (10-30 meters) of beach were cleared of logs during my study, noticeably reducing the number of lizards observed in those areas after clearing.

It is undeniable that nesting habitat is vital for a population's survival. In the case of *S. occidentalis*, that habitat is open sandy slopes created by landslides. That habitat is under threat from expanding human habitation and slope stabilization efforts, as well as invasive plant species such as Himalayan blackberry. This leads to the conclusion that preservation and reintroduction efforts should focus on suitable, southwest-facing, open sandy slopes with a complex mix of vegetation, as discussed previously. Key tasks should be identifying and preserving suitable lizard habitat, and controlling invasive plant species, which are often capable of recolonizing open land areas more quickly than native vegetation (Caplan & Yeakley, 2006; Gaire et al., 2015). Log field complexity (length and nanohabitat density) should be considered, and maintained where possible.
Implications for Understanding Geographic Range Boundaries

Studying populations at the extreme of their geographic range and documenting their
differences from core populations are valuable for understanding the mechanisms underlying
geographic range boundaries (Sutherland et al., 2013). Range-edge populations have been
studied more often in recent years, though much work remains to be done. The implications
of such studies are even more pressing with the increasingly evident impacts of climate
change putting ever-increasing pressure onto peripheral populations (Rodríguez-Robles et al.,
2010). Additionally, potentially unique genetics in range-edge populations make them
valuable sources of knowledge (Broquet et al., 2010; Excoffier et al., 2009; Ficetola &
Bonin, 2011; Hardie & Hutchings, 2010; Sexton et al., 2009).

My research represents an incremental step towards a better understanding of
geographic range boundaries and their underlying mechanics. By comparing the habitat use
and dispersal characteristics of the Tulalip metapopulation with more centrally-located
populations, it may be possible to uncover differences in genetic, physiological, and
behavioral characteristics that could be important factors in dispersal and adaptation as
geographic range peripheries.

Environmental challenges to peripheral populations are likely to increase in the face
of climate change and the potentially increased prevalence of invasive species (Powers,
2010; Rödder & Schulte, 2010). A species ability to adapt to these changes depends on its
ability to migrate, and availability of habitat to migrate to (Dytham, 2009; Feder et al., 2010;
Southwood & Avens, 2010).
Future Studies

My thesis forms a basis for understanding *S. occidentalis* populations on the Tulalip Reservation and the implications for understanding mechanisms of geographic range boundaries and their interaction with changing climate. An important next step would be the characterization of subpopulations at the edges of the Tulalip metapopulation (Sunny Shores to the north, and NTB to the south). These beaches may be less crowded, and potentially allow for more detailed characterization of habitat use and dispersal of individual lizards. Comparison of these beaches with my own research, as well as more range-center populations, could yield valuable insight into differences between core and peripheral populations.

Another useful study to build on this information would be a detailed examination of the genetic diversity within and between beaches of the Tulalip metapopulation and other regional *S. occidentalis* populations. Such research is currently being undertaken by Jason Abramo under the guidance of Dr. Roger Anderson, and would help researchers understand the genetic history of the metapopulation and more details regarding the connectivity of the sub-populations. Physiological studies are also underway to examine differences among *S. occidentalis* populations in the region, which could lead to greater understanding of the physiological and energetic requirements of different habitat types among lizard populations.

Additionally, comparing the Tulalip metapopulation to other *S. occidentalis* populations in the region would be invaluable in understanding the differences between populations in more detail. Anecdotal evidence suggests noticeable morphological differences between coastal maritime *S. occidentalis* populations in Washington and desert-
dwelling populations in the Alvord Basin in Oregon (Jason Abramo, Roger Anderson, personal communication, 2014). Studying these differences in more detail, as well as genetic and physiological variations, would be quite valuable.
LITERATURE CITED


Appendix A – WA Coastal Lizard Sightseeing and Capture Data to be recorded

Information to document horizontally on top of each pair of facing pages: Notebook ID, Year, Page #

Information to document vertically (lines are numbered), in column, when a lizard is encountered:

1. **Date**

2. **Locale:** state name of beach, such as TB, SBD, TS, NTB, MB, EM (state n or s of beach if in corridor/barrier locale)

3. **Search Type:** SPS for standard plot search, HS for haphazard, wandering search; CE for chance encounter. Also: state NS, # or EW/# for search direction, & your movement speed, & if you视为 a gape or arm movement or other (go to #26) led to sighting.

4. **# Searchers** (if scribe is not really to be searching, then do not list in the number or list as half person)

5. **Initials of Searcher, Scribe is listed first** (if scribe mostly just following & looking less intensively count the scribe as 1/2)

6. **Time of Event or Time of Detection (military time), and Initials of Finder**

7. Detection Method or Event: (note: drop washer/flagging or tie bag flag at 1st sighting location)
   - PS = Begin Search,
   - RS = Resume Search, ES = End Search

8. **Species, Sex, Age/Size Class of Lizard or Snake Detected:**
   - SM, #m = see it moving, in locomotion 1
   - SM, #s = see it moving by slight change in posture or position, < 1 body length
   - D = no shadows, < 1 body length
   - D = dirt patch, GP for wood, and & state size of dark or light
   - D = dirt, GP for wood, and & state size of dark or light
   - D = rock wall, LW for wood, and & state size of dark or light
   - D = log wall, LW for wood, and & state size of dark or light
   - D = log, and state
   - D = under log & state:

9. **Lizard Behavior when first detected:**
   - BA = basking, body pressed to substrate in sun, CO = cooling, body pressed to substrate in shade
   - NM = no moving, HM = head movement only, LO = looking at or looking for something; what, if known in #26.
   - If lizard is BA, CO, or NM, then state also: (note: LO can be added to BA or CO or NM or HM)

10. **Microhabitat:**
    - **S & L** = for search direction, & your movement speed, & if your state name of beach, such as
    - **B & L** = for search direction, & your movement speed, & if your state name of beach, such as

11. **Microhabitat:**
    - **DF** = dirt cliff face, DS = dirt slope, RCF = rock cliff face, RS = rock slope, BRF = boulder/rock field, LF = log field,
    - **GS** = grass slope, SH = shrubs, FO = forest, BB = blackberry; BI = beach intertidal; HH = human habitat; M = mixed, if
    - **meso** size & slope angle
    - **state liz location** in mesohab: liz is: mid, top, bottom, edge of meso, # m from edge & height above slope base.

12. **Microhabitat:**
    - **DF** = dirt patch, GP = grass patch, HP = herbaceous patch, BR = boulder/rock (BRs = isolated, BRp = patch),
    - **Bp** = blackberry patch, **FP** = fern patch, **SP** = scotchbroom patch, **EP** = equestum patch, **IP** = ivy patch, **UT** = under tree,
    - **RW** = rock wall, **AW** = log wall, **Pa** = post. **Lg** = log, **Sn** = snag, or 4-letter **acronym** for plant, near plant (< 20 cm from
    - **perimeter), UDW = if under dead wood. Note:** State **size** of microhabitat & liz location in microhabitat; **i.e., BR state top or side &
    - **state distance from edge; for Lg state end, top, side, base, & height above ground; State distance from p = near perimeter of plant,
    - **but then state which compass-side: N, NE, E, SE, S, SW, W, NW

13. **Lighting on Lizard at first sighting:**
    - **Su** = full, direct sunlight, in open or open patch under plant (state sun patch size), **CI** = Cloudy, no shadows.
    - **LS** = low sun, **d** = direct sunlight on ground, **H** = weak shadows, sunlight reduced by thin clouds or smoke haze.
    - **F** = filtered light through shade of leafy-branches of plant, with no distinct borders between sun and shade, **D** = dappled lighting from plant, and most distinct patches of sun and shade are < 4 cm in diameter,
    - **Sh** = in total shade, **Sh> more in shade,** **Sh< less in shade than in sun**

65
14. $T_{SSL}$ & $T_{2m} = T_{SSL}$ is temperature of substratum at lizard location where lizard was first seen; $T_{2m}$ is temp at 2m in air

15. Location/Coordinates: State the GPS latitude & longitude & Way Point # (WP #) and which GPS unit. State compass direction & distance from prominent, obvious landmark; be sure compass is adjusted to true N; if known. Use two rows for these data.

16. Paint Mark Status: NP = No paint visible, LP = losing paint, but some paint is visible, then, or otherwise, state (place 16 & 17 in same box) paint code using options of W, Y, G, R, B, X (none), in anterior-to-posterior order: neck, mid-back, base of tail.

17. Outcome: CB = captured, bagged; CR = captured, released; CL = captured, lost; A = Abandoned (place 16 & 17 in same box)

18. Time of Outcome (military time)

If Captured or if evaded capture:

19. Tb & Status Tb = body temp, Status: (PB = pressed behaviors or NPB = not pressed, captured in behavior not induced by humans)

20. Toe Clip Status: if lizard is toe-clipped already, write TC or give actual toe clip #; write NTC if it is not toe-clipped

21. Bag #: if released or captured & lost, then provide a dash (---); if bag number was inadvertently unstated, write a question mark: ?

22. Capture Location & Coordinates

23. Capture microhabitat, as above, but if evasion microhabitat (EM) &/or evasion nanohabitat (EN) then identify it & also state distances to closest refugium & to the evasion refugium

24. Capture Lighting

25. Lizard Behavior at Capture

26. Comment #: Comments are placed on nearby page. Include evasion & other behaviors, distance & direction between sighting and capture; be sure to explain when formal search was in pause, but lizards were encountered without search.
Appendix B – Photographs of Mesohabitat Types

Log field near human habitation (acceptable lizard habitat).
Log field with sandy slope above (acceptable lizard habitat).
Very small log field with hard-packed sandstone cliff (poor lizard habitat).
Heavily vegetated log field (poor lizard habitat).
Open upper slope area separated from log field by large Himalayan blackberry patch on lower slope (small log field, restricted access to open slope area = poor lizard habitat).