

AN ABSTRACT OF THE THESIS OF

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Title: Post-breeding Habitat Selection by Songbirds in the Headwaters of the Trask River, Northwestern Oregon

Abstract approved:

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Little is known on the importance of riparian areas to birds near small headwater streams in mesic forests. Progress towards understanding limiting factors that affect bird populations has been difficult because of lack of information beyond the breeding period. I compared bird assemblages between headwater riparian and upland areas throughout the post-breeding period by capturing birds using mist-nets in six paired riparian and upland locations along six headwater streams of the Trask River in northwestern Oregon. In order to assess whether birds prefer headwater riparian areas, I also examined factors affecting habitat selection by juvenile Swainson's thrushes (n=37) using radio telemetry. While riparian and upland locations had similar coarse wood volume and fruiting and tall (> 1.3 m tall) shrub cover, riparian locations had less shrub cover (< 1.3 m tall) and different shrub composition than upland locations. Total capture rate was double that of upland in riparian locations, while bird species richness was similar. Similar numbers of birds were captured in mist-nets oriented perpendicular and parallel to the stream suggesting that birds were not using riparian areas as movement corridors. Adult capture rate was greater in riparian locations than adjacent uplands while results of juvenile capture rates were ambiguous. Riparian locations supported higher capture rates of Swainson's thrushes

and winter wrens than adjacent uplands. Higher arthropod abundance in riparian locations may best explain higher capture rates in riparian locations. Radio-tagged juvenile Swainson's thrushes were more likely to select habitat that was near streams with high proportions of deciduous mid-story cover 1.5 - 15 m in the vertical strata and large volumes of coarse wood; possibly due to cover from predation and sources of food (i.e., fruits and arthropods).

I observed higher survival (97.3%) than reported in previous studies on independent juveniles which suggests that headwater streams contribute positively to the demography of the Swainson's thrush in the Pacific Northwest. In comparison with adjacent upland, headwater riparian areas appeared to be disproportionately used by songbirds during the post-breeding period even though vegetation differences were minimal. To assess if current policies sufficiently protect avian biodiversity, further research should evaluate how manipulation of vegetation affects bird distribution in headwater areas.

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Post-breeding Habitat Selection by Songbirds in the Headwaters of the Trask
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by

Stephanie R. Jenkins

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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CONTRIBUTION OF AUTHORS

Dr. Matthew Betts and Dr. Joan Hagar were involved with the study design of this project and editing all sections of this manuscript. Janel Banks-Sabota analyzed arthropod data.

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CHAPTER I – GENERAL INTRODUCTION

Riparian ecosystems are the vegetative communities and associated wildlife directly and indirectly influenced by streams; these zones constitute the transition between aquatic and dryer upland sites (Knopf and Samson 1994). Riparian forests are critical for the ecological functioning of stream food webs (Wallace et al. 1997) and within drainage basins generally support the most diverse and abundant communities of birds (Stauffer and Best 1980, Knopf and Samson 1994, Bub et al. 2004, Allen et al. 2006), amphibians (Corn and Bury 1989, Sheridan and Olson 2003), small mammals (McComb et al. 1993, Gomez and Anthony 1998), arthropods (Progar and Moldenke 2002, Iwata et al. 2003), and plants (Naiman and Decamps 1997, Pabst and Spies 1998).

However, many studies informing our knowledge of riparian ecology have been conducted in arid and semi-arid climates, where the vegetative transriparian gradient (from streamside to upslope) is pronounced (Gregory et al. 1991, Malanson 1993). Additionally, research has focused on large streams in which the stream-influenced microclimate extends proportionately further upslope relative to smaller streams, therefore affecting a larger total area. These riparian ecosystems typically support high species richness and diversity of vertebrates and has promoted the concept that overall species richness is higher in riparian areas than upland. This concept does not hold up well for forest songbirds in the Pacific Northwest (McGarigal and McComb 1992, Shirley 2005). Relative to riparian areas along large streams or in arid climates, remarkably little is known about wildlife communities in riparian areas in mesic climates, especially in headwater areas, where the difference between riparian vegetation and microclimate to upland is subtle (Pabst and Spies 1998).

Headwater streams are small, perennial and intermittent channels on the outer edges of catchment areas (Richardson et al. 2005). In the Pacific Northwest, headwater streams are generally defined as having an annual stream flow of less than $5.7 \text{ cm}^3/\text{s}$ ($2 \text{ ft}^3/\text{s}$, Orders 1 and 2) and typically do not support fish (FEMAT 1993, Richardson et al. 2005). Headwater riparian areas are an important management concern because they encompass a majority of the harvestable landscape in the Pacific Northwest (Gomi et al. 2002, Olson et al. 2007). Due to abundant groundwater, headwater areas are highly productive and consequently are

economically important for timber (Richardson et al. 2005). Small streams that do not support fish generally receive much less protection from potential impacts related to land use than larger streams. On federal forests, the Northwest Forest Plan (NWFP) requires that riparian buffer widths be equivalent to one site-potential tree height (approximately 30 m) along non fish-bearing headwater streams within the range the Northern Spotted Owl; however, riparian areas along fish-bearing streams in these areas receive twice as much protection (two site-potential tree heights [approximately 60 m]) (FEMAT 1993, NWFP 1994). Further, regulations for state and privately-owned land generally require even less protection of riparian areas of headwater streams than federally-owned land, but this varies widely; in the Coast Range of Oregon, retention of vegetation is not required on headwater streams that are not used for domestic purposes and do not support fish (Lee et al. 2004, OFPA 2010). These conservation mandates have been designed to protect fish and may not be adequate to support habitat for terrestrial species near small fishless streams and where harvesting timber is common. From a management perspective, knowledge of wildlife habitat associations is necessary in order to satisfy multiple use requirements and aid in achieving goals regarding biodiversity conservation. Because little information is known about wildlife in riparian areas along small headwater streams, we first need to understand whether headwater riparian areas that are associated with contiguous mature forest provide unique habitat for terrestrial wildlife.

The Trask River watershed in the mesic Coast Range of northwestern Oregon is dominated by headwater streams and provides an excellent area to conduct research in order to better understand these relationships. Between the Tillamook Burn (three events from 1933-1945) and timber harvest, most of the old-growth coniferous overstory was removed by the 1950s and replanted with Douglas-fir (*Pseudotsuga menziesii*) (TraskWRC 2007). As a result, the majority of the watershed currently contains mature contiguous forest dominated by 40-70 yr Douglas-fir. These fire events also designated property boundaries; burned areas became under state and federal ownership (approximately half of the watershed) and unburned areas generally maintained private ownership. Within this watershed, a collaborative long-term research project began in 2006 (the Trask Watershed Study) to study aquatic and terrestrial ecological functions related to headwater streams in the Oregon Coast

Range (TraskWRC 2007). The Trask watershed contains 4 headwater catchments and each catchment is further divided into four sub-basins. In each of these catchments, baseline information preceding harvest is currently being collected on amphibians, in-stream primary productivity, invertebrates, hydrology, vegetation, and birds (TraskWRC 2007). After baseline information is gathered, this watershed will be experimentally harvested to assess 1) the effects of forest harvest on the physical, chemical, and biological characteristics of small streams; and 2) the extent to which alterations in stream conditions caused by harvest along headwater channels influence the physical, chemical and biological characteristics of downstream conditions. One headwater catchment will remain unharvested to provide a control catchment. The other 3 headwater catchments will contain one sub-basin that will remain unharvested while the remaining three sub-basins will be treated with varied riparian buffer widths and harvesting within riparian areas. Within this research framework, I focused on relationships between headwater riparian areas and terrestrial wildlife. Specifically, I studied songbird communities because songbirds may function as trophic links between riparian and upslope systems (Wallace et al. 1997, Baxter et al. 2005, Christie and Reimchen 2008). Due to high vagility, songbirds may be more able to rapidly respond to temporal fluxes of aquatic insects than land bound wildlife species (Power et al. 2004, Uesugi and Murakami 2007). Riparian areas have been shown to have greater diversity of invertebrates than adjacent upland areas and as a result may support higher densities of insectivorous birds (Stauffer and Best 1980, Iwata et al. 2003, Christie and Reimchen 2008, Iwata et al. 2010).

However, it appears that differences between riparian and upland bird abundance and species assemblages cannot be broadly generalized and are variable depending on factors such as region, topography, and climate (McGarigal and McComb 1992, Pearson and Manuwal 2001, Shirley 2005). Unfortunately, these studies have primarily been conducted during the breeding season when territoriality constrains movement and habitat use is primarily directed by nesting requirements. Information from other critical periods of the avian annual cycle is lacking (Faaborg et al. 2010).

According to the Breeding Bird Survey, several species that are associated with shrubs in riparian zones are declining regionally (e.g., Pacific-slope flycatcher (*Empidonax difficilis*) [2.9% /yr, $p = 0.04$], Swainson's thrush [1.8% /yr, $p = 0.006$] and Wilson's warbler (*Wilsonia pusilla*) [1.1% /yr, $p = 0.2$]) (Ammon and Gilbert 1999, Lowther 2000, Sauer et al. 2008, Mack and Yong 2000). It is unknown whether such declines are associated with declines in habitat availability on the breeding/post-breeding grounds. Birds have been used widely as biological indicators because they respond rapidly to change and may reflect changes at lower trophic levels (Venier et al. 2004). Information on post-breeding habitat is necessary in order to identify possible mechanisms associated with population declines during periods of the annual cycle beyond the breeding season; subsequently this will benefit conservation of bird species as well as other species that are trophically connected to birds.

Specifically, I wanted to examine habitat associations beyond the breeding period because 1) bird use may change due to seasonal variation in resource availability (Stauffer and Best 1980, Iwata et al. 2010), 2) birds become less territorial and may, therefore, access resources located outside of breeding territories (Whitaker and Warkentin 2010) and 3) juvenile survivorship is often lower than that of adults and may have direct effects on population maintenance (Blomberg and Shine 2001, Sandercock et al. 2005, Gardali et al. 2009). The few existing studies on habitat selection by juvenile birds indicate that they may select different habitat than adults [wood thrushes (*Hylocichla mustelina*)(Anders et al. 1998), Swainson's thrushes (*Catharus ustulatus*)(White et al. 2005), Dupont's larks (*Chersophilus duponti*)(Garza et al. 2005)]. We need to consider all periods of a species lifecycle for effective species conservation.

Studies of songbirds during the breeding season generally estimate relative density of songbirds using point counts. Point counts are used to identify the number of each bird species that is heard or seen within a particular area (primarily singing males) (Pagen et al. 2002). However, during the post-breeding period songbirds are less vocal, and are, therefore, difficult to detect with point count methods. Because of this and because I wanted to identify sex and age structure of songbird populations, I captured birds using mist-nets to sample songbird assemblages in riparian and

upland locations. I compared capture rates and vegetation characteristics to address whether bird assemblages differed between headwater riparian and upland locations during the post-breeding period and if capture rates were correlated with vegetation characteristics.

Capture rates from mist-netting efforts are informative to identify songbird occurrence and habitat use of particular areas. However, mist-net captures document bird occurrence in a given area and do not provide information on habitat selection or individual fitness. In order to identify if birds are selecting a particular habitat that optimizes fitness, I additionally identified habitat selection of a focal species during the post-breeding period. I tracked juvenile Swainson's thrushes using radio telemetry in order to provide information on habitat selection during this critical life stage. The Swainson's thrush is a migratory songbird that occurs in higher abundance in riparian than upland habitats in the Oregon Coast Range during the breeding season (McGarigal and McComb 1992). This species is of conservation interest because populations have been in decline in the Pacific Northwest over the past 40 years (1.78 %/yr, $p=0.006$) (Sauer et al. 2008).

The goal of this research was to provide baseline information on songbird assemblages and habitat selection in headwater areas of the Oregon Coast Range. Specifically, my objectives were to 1) determine if capture rate, bird species richness, and age structure vary between headwater riparian and upland habitats, 2) determine if variation in capture rates was correlated with vegetation composition and structure; and 3) identify habitat selection of juvenile Swainson's thrushes.

Identifying habitat selection by juvenile Swainson's thrushes will provide information to assist managers in maintaining habitat for a declining neotropical migrant bird species in a managed forest ecosystem. Additionally, future studies can use my baseline data to evaluate the response of birds to vegetation manipulation that can be used to inform riparian policies. As riparian areas are generally hotspots for wildlife species diversity [birds (Stauffer and Best 1980, Knopf and Samson 1994, Bub et al. 2004, Allen et al. 2006), amphibians (Corn and Bury 1989, Sheridan and Olson 2003), small mammals (McComb et al. 1993, Gomez and Anthony 1998),

arthropods (Progar and Moldenke 2002, Iwata et al. 2003)]; providing information on ecological indicators such as songbirds in headwater riparian areas will aid understanding on how to maximize the effectiveness of these areas for biodiversity.

***CHAPTER II - COMPARISON OF POST-BREEDING SONGBIRD
ASSEMBLAGES BETWEEN RIPARIAN AND UPLAND AREAS IN THE
HEADWATERS OF THE TRASK RIVER, NORTHWESTERN OREGON***

Introduction

Riparian ecosystems are the vegetative communities and associated wildlife directly and indirectly influenced by streams; these zones constitute the transition between aquatic and dryer upland sites (Knopf and Samson 1994). The majority of research on riparian wildlife has focused on large streams; primarily in arid and semi-arid regions in which there is high contrast between riparian and upland vegetative communities (Gregory et al. 1991, Malanson 1993). In regards to avian assemblages, because these riparian habitats have higher structural complexity than adjacent upland habitats, they typically support more species and higher diversity (Kondolf et al. 1987). This has promoted the concept that bird species richness is higher in riparian areas than in the upland regardless of ecoregional context. However, in temperate forests, the change in vegetation structure from riparian to upland may be subtle, as are corresponding changes in avian assemblages (McGarigal and McComb 1992, Shirley 2005). Relative to riparian areas along large streams or in arid climates, remarkably little is known about differences in birds communities between riparian and upland areas in mesic climates, especially in headwater areas where differences in vegetation and microclimate may be subtle (Pabst and Spies 1998).

Headwater streams are small, perennial and intermittent channels on the outer edge of a catchment area (Richardson et al. 2005). In the Pacific Northwest, headwater streams are generally defined as having an annual stream flow of less than $5.7 \text{ cm}^3/\text{s}$ ($2 \text{ ft}^3/\text{s}$, Orders 1 and 2) and typically do not support fish populations (FEMAT 1993, Richardson et al. 2005). Headwater riparian areas are an important management concern considering they encompass 70-80% of catchment areas and, therefore, the majority of the harvestable landscape (Gomi et al. 2002, Olson et al. 2007). Abundant subsurface water makes headwater areas economically important for timber production (Richardson et al. 2005).

Riparian management is based on legal mandates to protect endangered Pacific Salmon and has primarily focused on large, perennial fish-bearing streams and adjacent riparian areas (Richardson et al. 2005, Adams 2007). Currently, depending on ownership, regulations vary considerably from complete, to no protection (Olson et al.

2007). Small streams that do not support fish generally receive much less protection from potential impacts related to land use than larger streams. On federal forests, the Northwest Forest Plan (NWFP) requires that riparian buffer widths be equivalent to one site-potential tree height (approximately 30 m) along non fish-bearing headwater streams within the range the Northern Spotted Owl, however, riparian areas along fish-bearing streams in these areas receive twice as much protection (two site-potential tree heights [approximately 60 m]) (FEMAT 1993, NWFP 1994). Further, regulations for state and privately-owned land generally require less protection of riparian areas of headwater streams than federal land, but this varies widely; for state or privately managed forests in the Coast Range of Oregon, retention of vegetation is not required on headwater streams that are not used for domestic purposes and do not support fish (Lee et al. 2004, OFPA 2010). These conservation mandates have been designed to protect fish and may not be adequate to support habitat for terrestrial species near small fishless streams and where harvesting timber is common. Knowledge of wildlife habitat associations is necessary in the broader context of maintaining overall biodiversity which is now incorporated in federal, state, and many private-industrial forest management goals. Little information is known about wildlife in riparian areas along small headwater streams, especially because in many cases they are structurally similar to upland areas (Pabst and Spies 1998). In order to be successful in achieving goals to maintain biodiversity, we first need to understand whether headwater riparian areas that are associated with contiguous mature forest provide unique habitat for terrestrial wildlife.

While, the potential influence of headwater riparian areas on downstream habitat has been recognized (Olson et al. 2007, Wipfli et al. 2007), as has their importance as habitat for unique assemblages of amphibian and arthropod populations (Progar and Moldenke 2002, Richardson et al. 2005, Olson and Weaver 2007, Rykken et al. 2007); little is known about headwater riparian areas as immediate habitat for terrestrial vertebrates. Further, information on ecological processes and habitat relationships related to headwater riparian areas is required to determine whether these mandates are effective in maintaining overall ecological function.

Songbirds are commonly used as ecological indicators because they respond rapidly to change and are relatively easy to detect (Venier et al. 2004, Baxter et al. 2005, Christie and Reimchen 2008). Songbirds can be components of trophic food webs in riparian systems, linking aquatic and terrestrial processes (Nakano and Murakami 2001, Iwata et al. 2003, Iwata et al. 2010). According to McGarigal and McComb (1992), two species are more abundant in headwater riparian areas of the Oregon Coast Range than adjacent upland: the winter wren (*Troglodytes troglodytes*) and the Swainson's thrush (*Catharus ustulatus*). Additionally, several species that are putatively associated with riparian areas are declining regionally (e.g., Pacific-slope flycatcher (*Empidonax difficilis*) [2.9% /yr, $p = 0.04$], Swainson's thrush [1.8% /yr, $p = 0.006$] and Wilson's warbler (*Wilsonia pusilla*) [1.1% /yr, $p = 0.2$]) (Ammon and Gilbert 1999, Lowther 2000, Sauer et al. 2008, Mack and Yong 2000). It is unknown whether such declines are associated with decreasing habitat availability on the breeding/post-breeding grounds. Information on post-breeding habitat is necessary in order to identify possible mechanisms associated with population declines during periods of the annual cycle beyond the breeding period; subsequently this will benefit conservation of bird species as well as other species that are trophically connected to birds and aid in maintaining forest wildlife biodiversity.

It is important to examine habitat associations beyond the breeding period since habitat use may change with seasonal variation in resource availability (Stauffer and Best 1980, Iwata et al. 2010). Unfortunately, studies of habitat use by forest songbirds have primarily been conducted during the breeding season. Information from other critical periods of the avian annual cycle is lacking (Faaborg et al. 2010). I wanted to examine habitat associations beyond the breeding season because 1) bird use may change due to seasonal variation in resource availability (Stauffer and Best 1980, Iwata et al. 2010) and 2) birds become less territorial and may, therefore, access resources located outside of breeding territories (Whitaker and Warkentin 2010).

Specifically, my objectives were to 1) determine if capture rate, species richness, and age structure vary between headwater riparian and upland locations and 2) determine if variation in capture rates, species richness, and age structure was

correlated with vegetation composition and structure. I hypothesized that riparian locations may exhibit higher capture rates and species richness than upland locations due to higher amounts of arthropod prey (Nakano and Murakami 2001, Iwata et al. 2010). However, alternatively, based upon past research in the Coast Range during the breeding period, birds may use upland areas more than riparian areas due to structural features (McGarigal and McComb 1992).

Methods

Study Sites

I conducted this study within the Trask Watershed Study Area (25 km²) in the headwaters of the East Fork of the South Fork of the Trask River in the northwestern Coast Range of Oregon (Fig. 2.1)(TraskWRC 2007). This area is dominated by small, seasonally intermittent and perennial streams (orders 1-2) in the Douglas-fir/Oceanspray (*Psuedotsuga/Holodiscus*) plant association of the Western Hemlock (*Tsuga heterophylla*) forest zone (Franklin and Dryness 1988). The study area is situated slightly west of the Coast Range divide, where water flows east towards the Willamette Valley and west to the Pacific Ocean. Elevation ranges from 275 to 1100 meters. This area is influenced by a maritime climate of mild temperatures and annual rainfall of 180-300 centimeters. The study area is owned primarily by Weyerhaeuser Company and the Oregon Department of Forestry with a small portion managed by the Bureau of Land Management. Due to the Tillamook Burn (three events from 1933-1945) and subsequent timber harvest, most of the original, old-growth conifer overstory was removed by the 1950s. The dominant overstory at the time of my sampling was 40- to 70- yr old conifers, mainly Douglas-fir (*Psuedotsuga menziesii*), with western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and noble fir (*Abies procera*). The riparian overstory was a narrow and patchy strip of mixed conifers and red alder (*Alnus rubra*). Pockets of tall shrubs, mainly vine maple (*Acer circunatum*), and small amounts of beaked hazelnut (*Corylus cornuta*) and Pacific dogwood (*Cornus nuttallii*) were scattered throughout the study area. Species present in the understory included trailing blackberry (*Rubus ursinus*), salmonberry (*Rubus spectabilis*), oceanspray (*Holodiscus discolor*), stinking currant (*Ribes bracteosum*), Oregon-grape (*Mahonia aquifolium*),

huckleberries (*Vaccinium* spp.), devil's club (*Oplopanax horridum*) and sword fern (*Polystichum munitum*).

During the 1990s, Oregon Department of Forestry (ODF) conducted light to moderate thinning to a basal area target ranging from 4.13 – 6.02 m²/ha (110 -160 ft²/ac) in the northwest portion of the study area (TraskWRC 2007). At the time of my study, Weyerhaeuser ownership in the eastern section of the study area was characterized by a predominance of 40- to 70- yr old forest, with a small portion of the landscape (12%) in five year-old regeneration harvests.

Sampling Design

I sampled 6 sites along 6 second-order streams, with paired riparian and upland locations nested within each site (Fig. 2.1). Streams were selected as part of a larger collaborative research project designed to address the ecological function of headwater riparian areas. Three planned harvest treatments were each represented by 2 replicates, for a total of 6 pairs of sampling units. I accounted for environmental variation among sampling units by blocking by site and pairing riparian and upland locations within each block. I selected sites in which it was logistically feasible to set 12 mist-nets in riparian and upland locations within constraints of topography. Within each site, paired riparian and upland locations were selected to minimize differences in vegetation structure that are expected to influence bird distributions [i.e., deciduous vegetation cover (Hagar 2007)]. This enabled us to test the hypothesis that birds are associated with inherent riparian characteristics other than vegetation structure.

We positioned twelve mist-nets at each location. I located all riparian mist-nets within 50 m of both sides of the stream. In order to capture birds moving between riparian and upland areas as well as birds that may be moving parallel to the stream, I positioned half the nets perpendicular and half parallel to stream flow. I positioned upland mist-nets in a similar pattern to riparian arrays and at least 50 m from the outermost riparian mist-net in order to be outside buffer widths of planned harvest treatments. The majority of upland locations were 50-75 m from the outermost mist-net in respective paired riparian locations. However, in two sites, the adjacent upland

locations were approximately 400 m from their paired riparian locations in order to avoid the multitude of small streams common in headwater areas. All mist-net arrays were purposefully set in areas with adequate camouflage of shrub cover. All mist-nets were 3 m high and 6 to 12 m in length (4 mist-nets ranged from 6 - 9 m in length to fit across small streams and between topographical features).

Songbird Sampling

Studies of songbirds during the breeding season generally estimate relative density of songbirds using point counts. Point counts are used to identify the number of each bird species that is heard or seen within a particular area (primarily singing males) (Pagen et al. 2002). Conversely, capturing birds using mist-nets samples non-vocal individuals that may have otherwise gone undetected using traditional point counts (Blake and Loiselle 2001, Derlindati and Caziani 2009). This is especially relevant during the post-breeding period when songbirds are less vocal, and are therefore difficult to detect with point count methods. Lastly, mist-nets can be orientated strategically to attempt to identify movement patterns in relation to topographic features (e.g., streams as movement corridors). For these reasons and because I wanted to identify sex and age structure of songbird populations, I captured birds using mist-nets to sample songbird assemblages in riparian and upland locations.

I captured songbirds in two consecutive post-fledging seasons between early July and mid-August in 2008 and mid-June and early August in 2009 (7/1/2008 to 8/15/2008 and 6/15/2009 to 8/6/2009). I considered this period to be post-breeding since I captured my first juvenile on June 17. I sampled one location (i.e., riparian or upland) per day. I sampled both locations at a site consecutively before moving to the next site, alternating daily between upland and riparian locations to reduce potential bias resulting from environmental factors, such as varying daily weather conditions. I repeated sampling at each site every two weeks so that each site was sampled three times in 2008 and four times in 2009. The first sampling period occurred during the last two weeks of June, the second and third occurred at the beginning and ending of July, respectively, and the fourth sampling period occurred during the first two weeks of August.

All mist-net captures took place between 0545 and 1130 hrs. I checked all nets every 45 minutes and extracted captured birds into breathable cloth bags. Each bird was identified to species, checked for sex-distinguishing characteristics, aged using skull pneumatization and/or juvenile plumage characteristics and fitted with a USGS aluminum leg band. Additionally, I measured body mass using a digital balance (g), and wing chord (mm).

Vegetation Sampling

I sampled vegetation at eight 5-m by 30-m belt transects along a 100-m transect through the middle of each location (Fig. 2.2). Belt transects extended 30 m on either side of the 100-m transect and were oriented perpendicular to the stream channel and hillslope, for riparian and upland locations respectively. Belt transects were spaced every 20 m along the 100-m reach. I adapted De Vries (1974) and Waddell (2002) protocols to measure coarse down wood and tally live and dead trees. I measured coarse down wood volume and tallied live trees and snags using a line-intercept method along one edge of each belt transect. I measured diameter at breast height (DBH) of each tree > 10cm DBH that intersected the line. Coarse down wood was measured 1) if it was > 10 cm in diameter where it crossed the line and 2) if it was not elevated < 45 deg from the ground. I calculated volume of coarse down wood using the formula:

$$Volume_m = (\pi / 2L) ((\pi/4)D^2 l_i / l_i) / 10000 (m^3 ha^{-1}),$$

where L is the total length (m) of the transect, D is the diameter in cm of each piece and l_i is the length of each individual piece.

In 5-m by 5-m plots located both at the beginning and end of each belt transect, I identified shrub species and measured percent shrub cover in 25% increments separated into two strata, > 1.3 m tall and < 1.3 m tall. I measured overstory cover using a spherical densiometer. Readings were taken at 15 m intervals at the center of each plot closest to the 100-m transect.

Statistical Analysis

Bird Capture Rates

No statistical tests were performed on species that were captured less than 20 times. I calculated total, adult, juvenile and individual species capture rates in riparian and upland locations per visit at each site (three sites were sampled three times in 2008 and three additional sites were sampled four times in 2009). I combined adults and juveniles when comparing capture rates of individual species due to low capture rates of juveniles. All capture rates are reported as captures per 100 mist-net hours (C/MNH).

I modeled songbird capture rates as a function of riparian and upland locations using generalized linear mixed models for Poisson distributed data and the log link in PROC GLIMMIX (SAS 2000). In order to include the extra sampling event conducted at three out of the six sites (2009 sites), I first tested an interaction between *location* (riparian and upland) \times *visit* (repeated sampling events at each site) to determine if captures rates changed between riparian and upland locations as the post-breeding period progressed. I chose three visits that corresponded to overlapping periods between years. I accounted for overdispersion, common in Poisson-distributed count data and particularly with small sample sizes, by treating visits as repeated measures and using an autoregressive (AR (1)) covariance structure. If there was no evidence of *location* \times *visit* interaction then I assumed that the extra visit would be similar to the other three visits and included it in my analyses. In this case I combined all visits at each location and averaged capture rates in riparian and upland locations by site.

Out of more than 2400 total hours of effort, I sampled upland locations an additional 53 more hours of effort than riparian locations (riparian: 1178 hr; upland: 1231 hr). Although it is a proportionally small difference, I standardized capture rates between sites by dividing captures by effort hours.

Additionally, I modeled total songbird captures in riparian locations as a function of parallel and perpendicular mist-net orientation relative to the stream using a generalized linear mixed model for Poisson distributed data and the log link in PROC GLIMMIX (SAS

2000). I combined all visits at each riparian location and averaged captures at each perpendicular and parallel mist-net by site.

Species Richness

To compare species richness between riparian and uplands, I pooled captures of each species among all sites and sampling events. I compared species richness and the rate of accumulation of new species using rarefaction curves, given that the number of individuals captured can influence the number of species recorded (James and Rathbun 1981, Gotelli and Colwell 2001). Rarefaction estimates richness from different levels of abundance based on multiple random sampling for each specified abundance level. I constructed rarefaction curves in the program EcoSim700 (Gotelli and Entsminger 2001) using 1000 iterations for each abundance level, increasing abundances in increments of 10 units until the maximum recorded abundance level was obtained. This program calculates a 95% confidence interval for each species richness value. I compared richness results between rarefaction and total records analysis methods.

Vegetation Characteristics

For all habitat analyses, I used total counts of trees and snags, coarse down wood volume, shrub richness and mean percent cover of overstory, tall and low shrubs and tall and low fruiting shrubs. All variables were checked for normality. Coarse down wood volume was logarithmically transformed to satisfy normality assumptions. Individual shrub species often span both tall and low shrub strata; therefore, I tallied the number of species in both strata combined to compare riparian and upland shrub species richness. I tested differences in vegetation variables that I expected to be ecologically important to songbirds that had correlation coefficients where $r < 0.50$ (i.e., total shrub species richness, coarse down wood volume and percent cover of tall shrubs, low shrubs, tall fruiting shrubs and low fruiting shrubs) between riparian and upland locations using a linear mixed model with a split plot block design with a normal distribution and identity link function in PROC MIXED (SAS 2000). To limit the chance of spurious results, I did not test for differences in other vegetation variables that were expected to be of less

biological importance and were highly correlated ($r > 0.50$) with selected variables (i.e., percent cover of overstory and total counts of trees and snags).

I report all means and confidence intervals of logarithmically transformed variables as exponentiated (i.e., capture rates, raw species richness, mist-net orientation captures and coarse down wood volume). The natural log of 0 is 1; therefore 1, instead of 0, signifies no difference between exponentiated means.

I considered all variables significant if $p < 0.05$, but did not discount p-values that were greater than but close to this value (Stoehr 1999). Values provided are $\bar{x} \pm SE$ unless otherwise stated. For all tests I provide the difference in means and the surrounding 95% confidence intervals (CI). Reporting CIs around effect sizes is considered to be superior to retrospective power analysis (Steidl et al. 1997).

Results

Community-level Response by Birds to Headwater Riparian and Upland Locations

I captured 200 birds in total, 68 individuals of 13 species in upland and 132 individuals of 16 species in riparian locations. Eleven species occurred in both locations (Table 2.1). Rarefaction revealed that species richness was affected by the number of captures in riparian and upland locations (Fig. 2.2). Rarefaction curves indicated that species richness was continuing to increase at the maximum number of captures. Based upon the greatest common number of captures (68), species richness was similar between riparian ($\bar{x} = 8.2 \pm 0.7$) and upland locations ($\bar{x} = 9.6 \pm 0.7$, paired t-test, $t_{24} = -1.26$, $p = 0.2$, difference between mean values, 1.3; 95% CI = -3.5 to 0.8) (Fig. 2.3). Additionally, I did not find a significant difference in raw richness averaged by site between riparian ($\bar{x} = 6.5 \pm 0.2$, $n = 132$) and upland locations ($\bar{x} = 4.5 \pm 1.7$, $n = 68$; GLIMMIX, $t_5 = 2.11$, $p = 0.09$; 95%; mean difference 1.4, CI = 0.9-2.2) (Fig. 2.4).

Total capture rate in riparian locations ($\bar{x} = 11.2 \pm 1.1$ C/MNH) was double that of adjacent upland locations ($\bar{x} = 5.5 \pm 1.2$ C/MNH, GLIMMIX, $t_{35} = 4.07$, $p < 0.001$; 95% CI = 1.4-2.9, $n = 200$) (Fig. 2.5). There was no evidence that total capture rates in riparian and upland locations were a function of sampling period as described by an interaction

between *location* (riparian and upland) x *visit* (sampling event) (GLIMMIX; $F_{14}=0.93$, $p=0.4$). Additionally, I did not detect evidence of a difference between the number of birds captured in mist-nets oriented parallel ($\bar{x} = 2.0 \pm 0.2$ captures/net) and perpendicular to the stream ($\bar{x} = 1.7 \pm 0.2$ captures/net, GLIMMIX, $t_{65} = -0.65$, $p < 0.5$; 95% CI = 0.5-1.4, $n = 200$ captures in 144 mist-nets)

Species Response to Headwater Riparian and Upland Locations

Four species (Swainson's thrush, winter wren, Wilson's warbler, Pacific-slope flycatcher) comprised 83% of all captures in the riparian locations and five species (Swainson's thrush, Oregon junco, winter wren, Pacific-slope flycatcher, song sparrow) comprised 80% of captures in the upland locations (Fig. 2.6).

Using total counts, fifty-five percent of species occurring in both locations had more captures in riparian locations (Pacific-slope flycatcher, rufous hummingbird, song sparrow, Swainson's thrush, Wilson's warbler, winter wren) and 36% were captured more frequently in upland locations (brown creeper, hermit warbler, Oregon junco, varied thrush).

Swainson's thrush capture rate was 2.8 times greater (95% CI = 1.5 to 5.2) in riparian ($\bar{x} = 4.5 \pm 1.2$ C/MNH) than adjacent upland locations ($\bar{x} = 1.5 \pm 1.3$ C/MNH, GLIMMIX, $t_{35} = 3.79$, $p < 0.001$, $n = 74$) (Fig. 2.7). Winter wren capture rate was 8.5 times greater (95% CI = 2.7 to 27.0) in riparian ($\bar{x} = 1.8 \pm 1.3$ C/MNH) than upland locations ($\bar{x} = 0.2 \pm 0.06$ C/MNH, GLIMMIX, $t_{35} = 3.79$, $p = 0.0006$; $n = 28$) (Fig. 2.7). Evidence was inconclusive that capture rates of Pacific-slope flycatcher was greater (95% CI = 0.9 to 6.2) in riparian than upland locations ($\bar{x} = 1.4 \pm 1.3$ C/MNH in riparian; $\bar{x} = 0.6 \pm 1.5$ C/MNH in upland; GLIMMIX, $t_{35} = 1.84$, $p = 0.07$, $n = 23$) (Fig. 2.7). However, my statistical power may have been too low to detect a difference in Pacific-slope flycatcher capture rates (Steidl et al. 1997).

Song sparrows, Wilson's warblers, and Oregon juncos were captured less than 20 times each. Seven song sparrows were captured in upland locations ($\bar{x} = 0.2 \pm 2.6$ C/MNH) and 7 captured in riparian locations ($\bar{x} = 0.2 \pm 2.6$ C/MNH). Wilson's warblers

were captured primarily in riparian locations ($\bar{x} = 1.2 \pm 1.4$ C/MNH, $n=15$) with 2 captures in uplands ($\bar{x} = 0.2 \pm 2.0$ C/MNH, $n = 2$) and Oregon juncos were captured primarily in upland locations ($\bar{x} = 1.5 \pm 1.3$ C/MNH $n = 18$) with 1 capture in riparian locations ($\bar{x} = 0.1 \pm 2.7$ C/MNH, $n = 1$).

All species captured only in either riparian (black-throated gray warbler, chestnut-backed chickadee, golden-crowned kinglet, orange-crowned warbler, warbling vireo) or upland (hairy woodpecker) locations had ≤ 2 captures (Table 2.1).

Age Structure in Headwater Riparian and Upland Locations

Adult capture rate in riparian locations ($\bar{x} = 9.1 \pm 1.1$ C/MNH) was 1.9 times greater (95% CI = 1.4 to 2.8) than upland locations ($\bar{x} = 4.7 \pm 1.2$ C/MNH, GLIMMIX, $t_{35} = 3.74$, $p < 0.001$, $n = 165$) (Fig. 2.8). I could not conclude that juvenile capture rate was greater (95% CI = 0.9 to 5.8) in riparian ($\bar{x} = 1.7 \pm 1.3$ C/MNH) than upland locations ($\bar{x} = 0.7 \pm 1.5$ c/MNH, GLIMMIX, $t_{35} = 1.85$, $p = 0.07$, $n = 29$) (Fig. 2.8). However, my statistical power may have been too low to detect a difference in juvenile capture rates (Steidl et al. 1997).

Sixty-five percent of all adults were captured in riparian locations and 35% were captured in upland locations. Similarly, 69% percent of juveniles were captured in riparian locations and 31% percent in upland locations.

I captured adults of 16 species, 4 of which were only captured in riparian locations (black-throated gray warbler, chestnut-backed chickadee, orange-crowned warbler, warbling vireo) and 2 were only captured in upland locations (brown creeper, hermit warbler). Ten species were captured in both locations (Table 2.1).

I captured juveniles of 12 species, 6 of which were only captured in riparian locations (black-throated gray warbler, brown creeper, golden-crowned kinglet, hermit warbler, Pacific-slope flycatcher, winter wren) and 3 species were only captured in upland locations (Oregon junco, hairy woodpecker, varied thrush). Juveniles of 3 additional species were captured in both locations (song sparrow, Swainson's thrush, Wilson's warbler) (Table 2.1).

Vegetation in Headwater Riparian and Upland Locations

Total shrub species richness was lower in riparian ($\bar{x} = 2.5 \pm 0.4$) than upland ($\bar{x} = 3.8 \pm 0.4$), but this difference was not statistically significant (MIXED; $t_5 = -2.39$, $p = 0.06$; mean difference = -1.3, 95% CI = -2.8 to 0.1).

There was evidence that cover of low shrubs (<1.3 m) was significantly different between riparian and upland locations. Low shrub cover was less in riparian ($\bar{x} = 8 \pm 4$ %) than upland locations ($\bar{x} = 24 \pm 4$ %, MIXED, $t_5 = -2.78$, $p = 0.04$; 95% CI = -31 to -1 %, (Fig. 2.9). Additionally, the composition of low shrub vegetation communities were different between riparian and upland; in that salmonberry was the dominant low shrub species in the riparian locations accounting for 87% (± 14 %) of total low shrub cover overall. In the upland, low shrub cover was dominated by 3 species: trailing blackberry ($\bar{x} = 41 \pm 20$ %) vine maple ($\bar{x} = 20 \pm 16$ %) and huckleberry spp. ($\bar{x} = 15 \pm 15$ %) (Fig. 2.11).

Evidence was inconclusive that tall shrub cover was greater in riparian ($\bar{x} = 33 \pm 8$ %) than upland locations ($\bar{x} = 21 \pm 8$ %, MIXED, $t_5 = 1.56$, $p = 0.2$; 95% CI = -8 to 31%) (Fig. 2.9). Vine maple was the dominant tall shrub in both riparian and upland locations, accounting for 69% (± 19 %) of total tall shrub cover overall (Fig. 2.10).

I detected no evidence of a difference between riparian and upland locations in percent cover of tall fruiting shrubs (MIXED, $t_5 = 1.89$, $p = 0.1$; mean difference = 7 %, 95% CI = -2 to 16%, Fig. 2.12), low fruiting shrubs (MIXED, $t_5 = -1.87$, $p = 0.1$; mean difference = -9 %, 95% CI = -21 to 3 %, Fig. 2.12) and coarse down wood volume (MIXED, $t_5 = -1.3$, $p = 0.3$; mean difference = 0.49 m³/ha, 95% CI = 0.12 to 2.01 m³/ha).

Discussion

In this study, capture rates of all species of birds combined was disproportionately high in riparian locations in comparison with adjacent upland in headwaters of the Coast Range in northwestern Oregon. Additionally, capture rates of Swainson's thrushes and winter wren were greater in riparian locations relative to upland. My results provide further support for the aforementioned hypothesis that birds may be in higher abundance near streams possibly due to disproportionate food availability (Nakano and Murakami

2001, Iwata et al. 2010). This research is the first to study birds during the post-breeding period in headwater areas with minimal difference between riparian and upland vegetation. The importance of riparian areas to forest birds is evidenced by overall greater capture rates in riparian than in adjacent upland locations, especially considering the minimal vegetation differences between these locations. Higher capture rates in riparian areas were also documented in the only other study to date that measured songbird activity with mist-nets during the post-breeding period along small streams in temperate forests; however distinct vegetation differences between riparian and upland areas may have played a role in capture rates [Upper Michigan Peninsula (Akresh et al. 2009)]. Additionally, Mosley (2006) found greater capture rates in riparian areas of large streams than adjacent upland forest during the post-breeding period in mixed-wood forest of Northeastern Ontario. While these studies demonstrate the importance of riparian areas as songbird habitat during the post-breeding period, combining results of post-breeding research with information gathered during the breeding period in mesic forests will provide understanding of potential implications relating to the value of riparian habitat throughout the annual cycle and, ultimately, aid in species conservation.

My results indicating higher capture rates in riparian areas are similar to findings during the breeding season in the southern Cascades and coastal ranges of Washington. In this study, Pearson and Manuwal (2001) found that no species was more abundant in upland areas, and species associated with deciduous plants and shrubs, including Pacific-slope flycatchers and winter wrens, were more abundant near streams. While my results are inconclusive regarding Pacific-slope flycatchers, I captured winter wrens with greater frequency in riparian locations to that of upland locations. In contrast, other studies conducted during the breeding season in the Pacific Northwest have indicated that total abundance and species richness is the same or even higher in uplands to that of riparian areas (McGarigal and McComb 1992, Shirley 2005). I found no evidence of a difference in species richness between riparian and upland locations, similar to Shirley (2005) and Pearson and Manuwal (2001). Though Shirley (2005) found that riparian locations do not support higher densities of birds than uplands during the breeding period along streams of varying sizes, she found that the Swainson's thrushes were more abundant near streams, consistent with my disproportionately higher capture

rates of Swainson's thrushes during the post-breeding period in headwater riparian locations. McGarigal and McComb (1992) found that upland areas had higher abundance and species richness compared to riparian areas along headwater streams in the Oregon Coast Range. In their study, only two species, Swainson's thrushes and winter wrens, occurred in greater abundance in riparian areas. My results indicate that Swainson's thrushes and winter wrens were strongly associated with riparian locations during the post-breeding period. Taken together, this indicates that riparian areas in mesic forests are habitat in both the breeding and post-breeding period for Swainson's thrushes and winter wrens; therefore, headwater riparian areas may contribute positively to the conservation of these species.

Despite similarities in habitat use between breeding and post-breeding periods of Swainson's thrushes and winter wrens, inconsistencies are apparent between the breeding and post-breeding period concerning bird abundance and species richness in riparian areas. During the breeding period, some studies indicate greater abundance in riparian areas over non-riparian areas in largely intact mesic forest (Pearson and Manuwal 2001, Palmer and Bennett 2006, dos Anjos et al. 2007). In contrast, others indicate equal or higher abundance in upland areas (Stauffer and Best 1980, McGarigal and McComb 1992, Bub et al. 2004, Shirley 2005). I submit three primary reasons for variability between my findings with others, specifically aimed at addressing differences among research conducted in the Pacific Northwest.

First, I constrained my study to small headwater systems (orders 1 and 2), whereas other studies in the Pacific Northwest were executed on a range of stream sizes between orders 1 through four. Riparian areas of large streams (e.g., orders 3 and 4) typically have more pronounced transriparian gradients in vegetation than headwater riparian areas (Naiman et al. 1993), subsequently increasing songbird abundance and richness. The transriparian gradient in vegetation between headwater riparian and upland areas is generally subtle (Pabst and Spies 1998). This is primarily due to high soil moisture content from the multitude of small streams throughout these systems, and the relatively small difference in microclimates between headwater riparian and upland areas in (Moore et al. 2005, Richardson et al. 2005). Given the similarity in vegetation

structure and microclimate, it is not surprising that bird species richness was similar between headwater riparian and upland locations. However, surprisingly, I found that capture rates in riparian locations were double those in upland locations, consistent with higher bird abundance during the breeding period in the coastal ranges and Cascades of southern Washington (Pearson and Manuwal 2001).

Secondly, individuals I captured during the post-breeding period may be using different resources than during the breeding period, likely to acquire energy for pre-migratory fattening or winter survival and/or cover from predation during molt (Vega Rivera et al. 1999, Vega Rivera et al. 2003). Mosley (2006) captured more birds in mist-nets positioned perpendicular to streams than those positioned parallel to streams and suggested that birds may be using streams as movement corridors during the post-breeding period, possibly to acquire energy resources or perhaps to prospect for future breeding habitat (Mitchell et al. 2010). In my study, however, I did not detect a difference in bird captures between parallel and perpendicular mist-nets. This coincides with habitat selection of juvenile Swainson's thrushes (Chapter III) that that did not appear to follow stream direction, but were generally centered near headwater streams indicating that birds were not using headwater riparian areas as movement corridors. Since cover of both high and low shrubs was similar or greater in upland locations in my study, it is unlikely that the higher capture rate I found in riparian locations can be explained by the predator avoidance or movement corridor hypotheses. This increases the likelihood that food availability may explain high capture rates in riparian locations.

Food resources change over the breeding and post-breeding periods due to differences in phenology of fruiting shrubs and both terrestrial and aquatic invertebrate hatches (Stauffer and Best 1980, Iwata et al. 2003, Iwata et al. 2010). Birds are expected to forage in an energy efficient manner and, therefore, should optimize opportunities to forage in areas where available food resources are the highest (Zach and Falls 1976, Zach and Falls 1979). After breeding, and as songbirds become non-territorial and food resources may be no longer optimal within breeding habitat, it is possible that songbirds may supplement diet or shift habitat use entirely towards optimal

food resources. This could explain differences in my results with studies conducted during the breeding season in the Oregon Coast Range (McGarigal and McComb 1992).

Although bird abundance has been correlated to cover of fruiting shrubs (Pearson and Manuwal 2001), it is unlikely that birds during the post-breeding period used riparian areas based upon fruit availability locations unless birds prefer particular species of fruiting shrubs, as I found no difference in total cover of fruiting shrubs between riparian and upland. Specifically, salmonberry was disproportionately high in riparian locations and may have contributed to the higher capture rates in riparian locations by providing both fruit and arthropod prey (Shirley 2005). However, salmonberry ripened in mid-July and the fruit availability hypothesis does not explain the high capture rates in riparian locations after fruit production has passed. From a physiological standpoint, salmonberry may host high densities of arthropods because of its easily digestible leaves (Shaw et al. 2006).

A possible explanation of why capture rates were higher in riparian than upland locations may be that riparian areas offered increased forage opportunity for arthropods, probably due to greater cover of vegetation species shown to host invertebrates that are favored prey for songbirds (Doolittle 2000). Additionally, both terrestrial and emergent aquatic insect prey were more abundant streamside than 50- to 400 m upslope (Hagar et al. 2010 unpublished data). Even when dry, seasonally intermittent streams still exhibit similar pulses of emerging aquatic insects as larger streams (Dieterich 1992, Banks et al. 2007), and may supplement trophic food webs for insectivorous birds (Nakano and Murakami 2001). We know that terrestrial and aquatic insects are in higher abundance near streams which may attract songbirds to riparian areas during the post-breeding period (Mosley et al. 2006, Iwata et al. 2010).

Anecdotally, I captured Wilson's warbler ($n=17$) primarily in riparian locations. We know that flies and beetles occurred in high frequencies in Wilson's warbler diets elsewhere in the Coast Range (Hagar et al. 2009), therefore, higher captures of Wilson's warblers in riparian locations are possibly due to higher abundance of flies and beetles near streams in my study area (Hagar et al. 2010 unpublished data).

Lastly, our sampling method differed from studies conducted during the breeding season that generally employ point counts to sample songbird populations by recording vocal and visible individuals. Conversely, mist-net sampling tends to capture cryptic species and secretive individuals that would otherwise go unnoticed with traditional point count methods and is especially useful during the post-breeding season as birds become less vocal (Rappole et al. 1998, Derlindati and Caziani 2009). Point counts and mist-netting have been shown to sample different components of the bird community (Whitman et al. 1997, Blake and Loiselle 2001). Mist-netting provides the opportunity to document information on age-structure, which is not well-documented with traditional sampling techniques. In study, the capture rate of Pacific-slope flycatcher in riparian locations was influenced primarily by juvenile captures. These juveniles would likely have gone undetected using point count methodology. On the other hand, my study focused on shrub- and forest-floor associated species, and did not adequately sample canopy-dwelling species.

Overall, differences in juvenile capture rates between riparian and upland were inconclusive, likely due to low sample size and high variation in capture rate, resulting in low statistical power. Nevertheless, the mean difference in capture rates suggest juveniles may have been captured more frequently in riparian than upland locations. My observation of higher capture rates of adults and juveniles together does not support an age-related ideal despotic distribution hypothesis (Fretwell 1972), so it is unlikely that adults are 'pushing' juveniles into lower quality habitat.

Limitations

If songbird capture rate is correlated with a particular vegetation variable, such as cover of low shrubs, it may be more useful to quantify shrub distribution from a volume perspective rather than the planar cover assessment. I assume that I measured habitat variables appropriately; however, it is important to define habitat variables according to bird use in order to avoid potentially obscuring important habitat relationships.

Additionally, it is possible that higher capture rates in riparian locations may have been a result of greater concealment of mist-nets by shrub cover. While tall shrub cover

was not statistically different between riparian and upland locations, cover of low shrubs was greater in uplands. However, after removing shrub species that would not have aided in camouflaging nets (e.g., trailing blackberry, dwarf rose, and Oregon-grape) and combining shrub strata; I found no difference in mist-net concealment between riparian and upland locations (MIXED, $t_5 = -0.29$, $p=0.79$; \bar{x} difference = -2%, 95% CI = -24 to 19 %). Furthermore, Oregon juncos were primarily captured in upland locations, indicating that mist-nets were adequately camouflaged in upland locations. Therefore, my results are unlikely to be biased by the amount of shrub cover that would serve as camouflage for mist-nets in riparian and upland locations.

Lastly, only particular songbird species are captured with mist-nets; therefore I cannot report activity of songbird species that do not frequent the lower vegetation strata between the 0.25-3 m from the ground. However, mist-netting was the only sampling method that obtained information on age structure of birds with any reliability, which was one of the central questions of this study.

Future Research

I have provided a baseline of information on capture rates of shrub-dwelling songbirds in headwater riparian and adjacent upland areas of the Trask Watershed in the Oregon Coast Range. In order to identify ecologically based riparian buffer characteristics, future research should evaluate songbird response to manipulation of vegetation structure and composition in headwater riparian and upland areas. Testing hypotheses suggested by my results with manipulative experiments would provide information on how current patterns in shrub-dwelling bird distribution may be affected by varied riparian management practices. Additionally, future work should compare fitness consequences that result from an individual's use of riparian and upland areas. Studying juvenile survival to reproductive status, and habitat selection by identifying disproportionate habitat use on a daily basis would provide important pieces of information to aid in determining differences in quality between riparian and upland habitats (See Chapter III).

Management Implications

The importance of headwater riparian in the Oregon Coast Range as habitat for songbird is evidenced by (a) a doubling of capture rates and (b) greater capture rates for some species (e.g., Swainson's thrush, winter wren) in riparian locations compared to those in adjacent uplands. Given similar vegetation structure between these locations, my results could be explained by higher amounts of arthropod prey in headwater riparian areas. The influence of the stream provides higher moisture availability in riparian areas, resulting in greater vegetation and arthropod productivity (Pabst and Spies 1998). I suggest that maintaining shrub species known to host high abundances of invertebrates that are prey for songbirds near headwater riparian areas will benefit songbirds during the post-breeding period.

Importantly, my research is one out of two existing studies addressing songbird habitat during the post-breeding period in small headwater ecosystems, and the only one specific to the Pacific Northwest. Currently, riparian management regulations primarily provide protection for fish-bearing streams while minimal protection is allocated to small headwater streams. Although riparian areas cover a small proportion of western North America (Kondolf et al. 1987), these areas support high abundance and species richness, some of which only occur in riparian areas. Knowledge of wildlife habitat associations is necessary in the broader context of maintaining overall biodiversity which is now incorporated in federal, state, and many private-industrial forest management goals. Because birds are ecological indicators, it is reasonable to speculate that headwater riparian areas may also provide habitat for unique assemblages of other wildlife species. Indeed this has already been demonstrated for species of amphibians (Sheridan and Olson 2003), small mammals (Gomez and Anthony 1998), and arthropods (Progar and Moldenke 2002, Iwata et al. 2003). Despite the fact that headwater riparian areas provide habitat and contribute to biodiversity, these areas are often affected by anthropogenic activities (e.g., timber harvest). Results of my research will help forest managers achieve goals related to maintaining biodiversity and will provide quantitative data on forest structural features essential to songbirds during the post-breeding period.

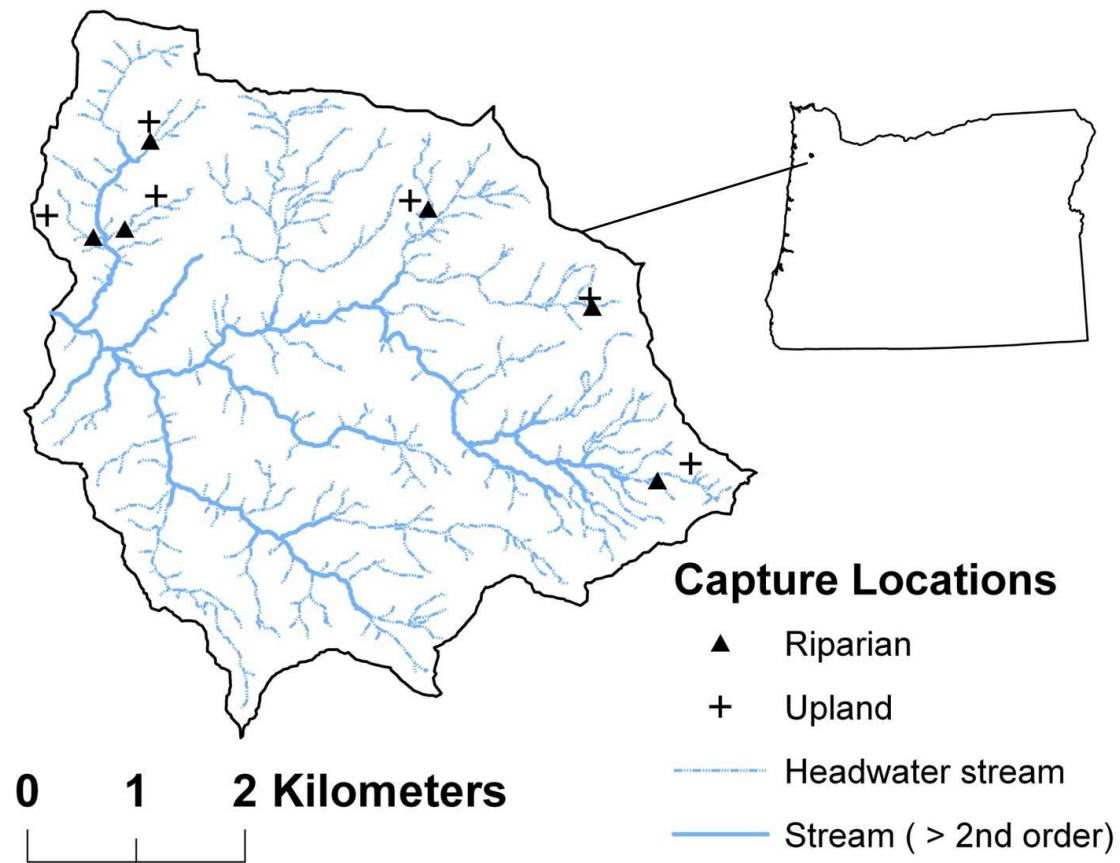


Figure 2.1. Locations of the six paired bird capture sites within the Trask River Watershed, Oregon.

Table 2.1. Total number of captures in headwater riparian (1178 mist-net hours) and adjacent upland (1231 mist-net hours) locations of songbirds captured in the Trask River Watershed, Oregon, 2008-2009.

Species	Scientific Name	Riparian			Upland		
		Total	Adult	Juvenile	Total	Adult	Juvenile
Swainson's Thrush	<i>Catharus ustulatus</i>	54	48	4	20	18	2
Winter Wren	<i>Troglodytes troglodytes</i>	25	18	5	3	3	0
Pacific-slope Flycatcher	<i>Empidonax difficilis</i>	16	11	5	7	7	0
Wilson's Warbler	<i>Wilsonia pusilla</i>	15	14	1	2	1	1
Song Sparrow	<i>Melospiza melodia</i>	7	5	1	6	5	1
Golden-crowned Kinglet	<i>Regulus satrapa</i>	2	1	1	1	1	0
Rufous Hummingbird	<i>Selasphorus rufus</i>	2	2	0	1	1	0
Black-throated Gray Warbler	<i>Dendroica nigrescens</i>	2	1	1	0	0	0
Chestnut-backed Chickadee	<i>Poecile rufescens</i>	2	2	0	0	0	0
Oregon Junco	<i>Junco hyemalis</i>	1	1	0	19	16	2
Brown Creeper	<i>Certha americana</i>	1	0	1	2	2	0
Hermit Warbler	<i>Dendroica occidentalis</i>	1	0	1	2	2	0
Varied Thrush	<i>Ixoreus naevius</i>	1	1	0	2	1	1
American Robin	<i>Turdus migratorius</i>	1	1	0	1	1	0
Orange-crowned warbler	<i>Vermivora celata</i>	1	1	0	0	0	0
Warbling Vireo	<i>Vireo gilvus</i>	1	1	0	0	0	0
Hairy Woodpecker	<i>Picoides villosus</i>	0	0	0	2	0	2
Total		132	107	20	68	58	9

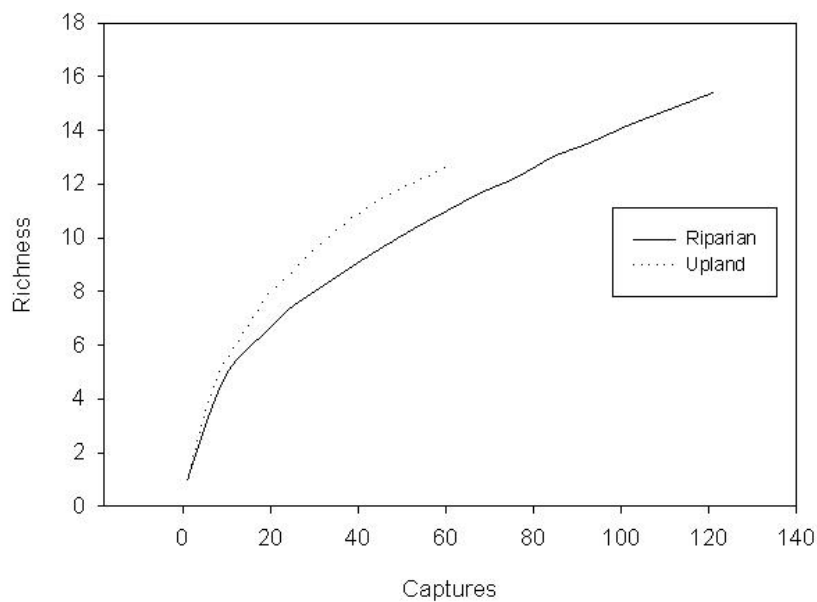


Figure 2.2. Rarefaction curves of species accumulation in headwater riparian and adjacent upland locations as a function of the number of songbirds captured in the Trask River Watershed, Oregon, 2008-2009.

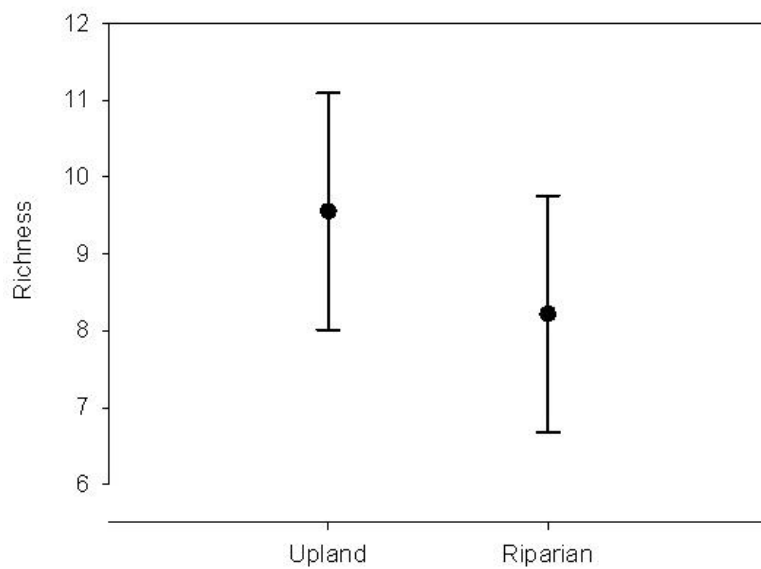


Figure 2.3. Rarefaction estimate of species richness ($\bar{x} \pm 95\% \text{ CI}$) constrained by number of upland songbirds captured ($n = 68$) in the headwaters of the Trask River Watershed, Oregon, 2008-2009

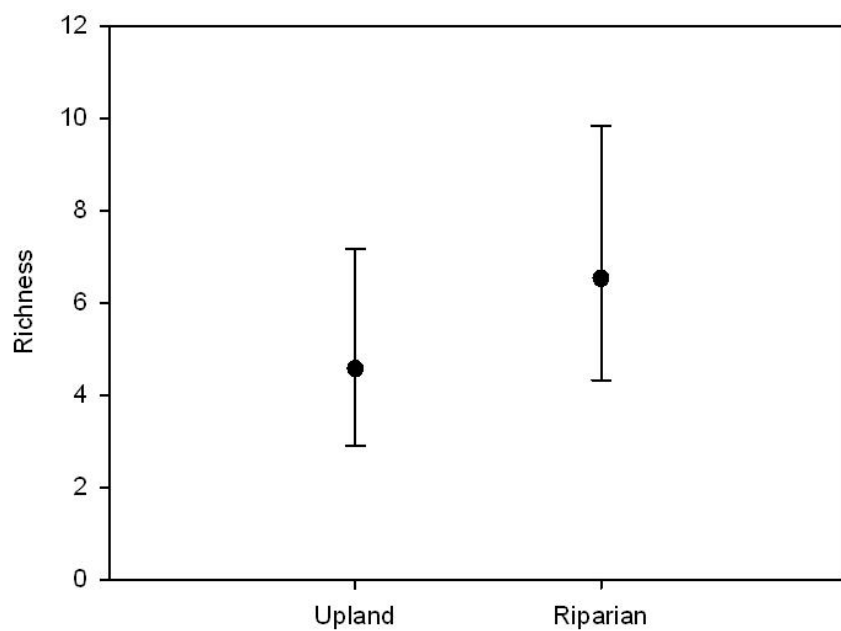


Figure 2.4. Species richness ($\bar{x} \pm 95\%$ CI) of songbird capture rate data averaged by site (captures per 100 mist-net hours) between headwater riparian ($n = 132$) and adjacent upland locations ($n = 68$) in the Trask River Watershed, Oregon, 2008-2009.

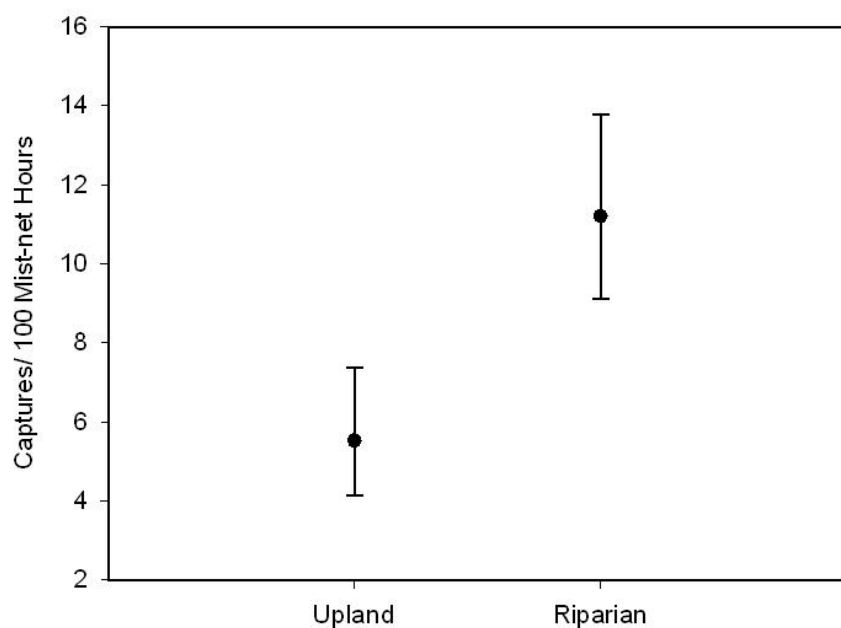


Figure 2.5. Mean captures per 100 mist-net hours $\pm 95\%$ CI for total songbirds captured in headwater riparian and adjacent upland locations in the Trask River Watershed, Oregon, 2008-2009.

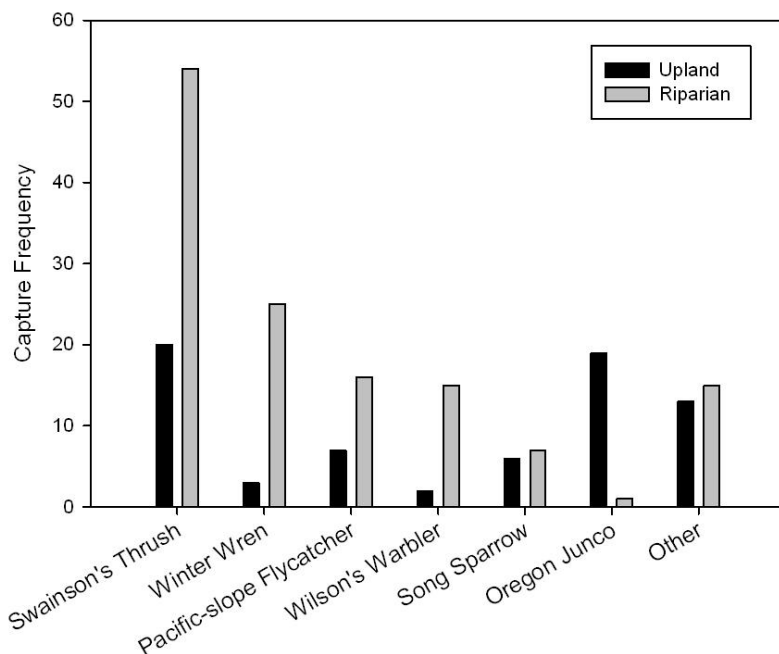


Figure 2.6. Capture frequency of predominate species in headwater riparian (n = 132, 1178 mist-net hours) and adjacent upland locations (n = 68, 1231 mist-net hours) in the Trask River Watershed, Oregon, 2008-2009.

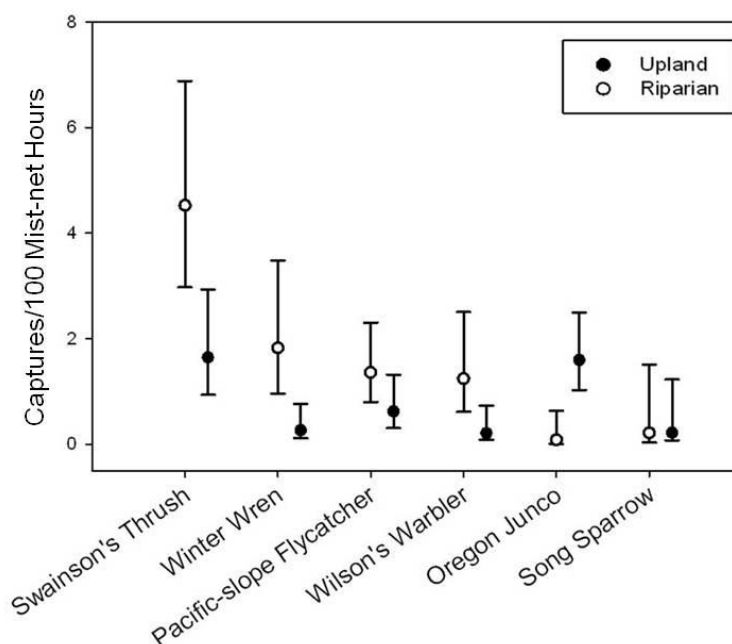


Figure 2.7. Mean captures per 100 mist-net hours \pm 95% CI for predominate songbird species in headwater riparian and adjacent upland locations in the Trask River Watershed, Oregon, 2008-2009.

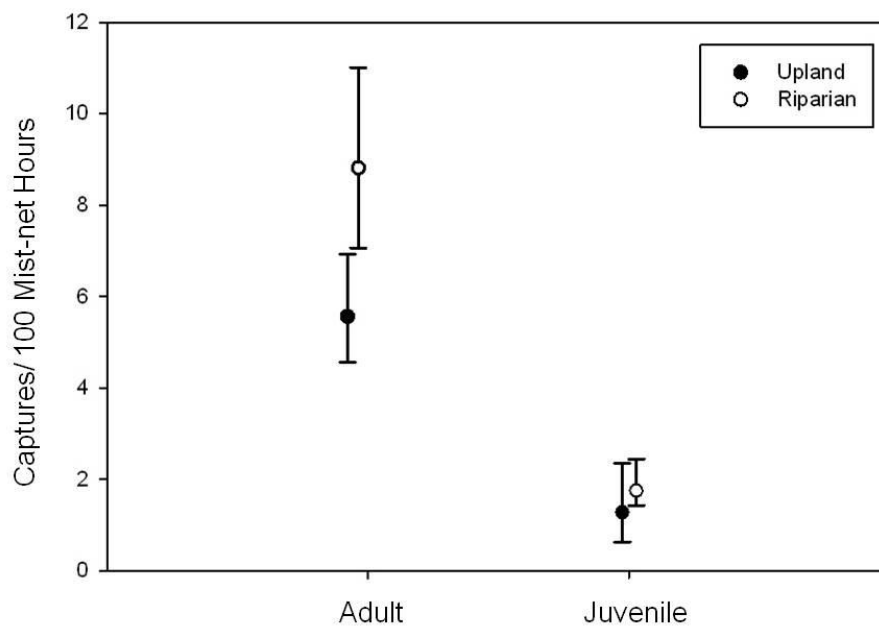


Figure 2.8. Mean captures per 100 mist-net hours (MNH) \pm 95% CI for adult (n=165) and juvenile (n=29) songbirds captured in headwater riparian and adjacent upland locations in the Trask River Watershed, Oregon, 2008-2009

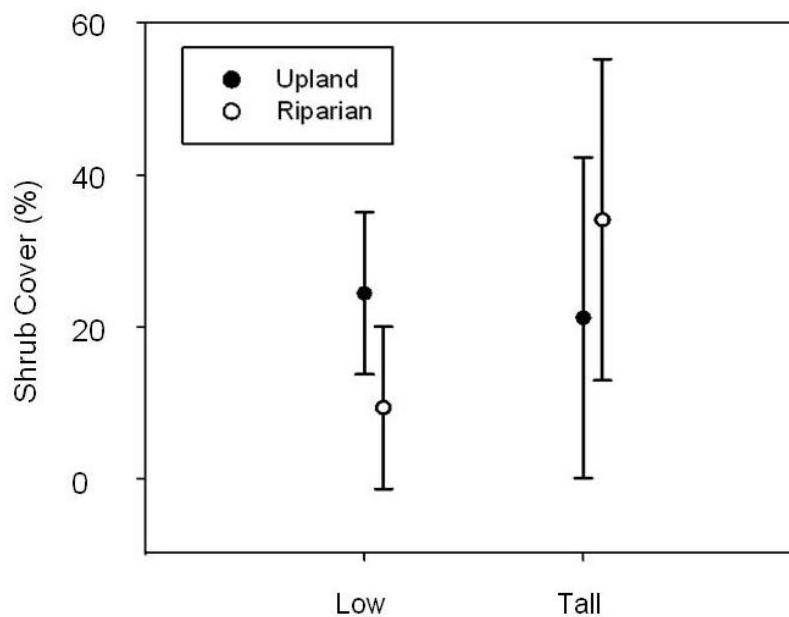


Figure 2.9. Percent cover ($\bar{x} \pm 95\%$ CI) of tall and low shrubs in headwater riparian and adjacent upland locations in the Trask River Watershed, Oregon, 2008-2009.

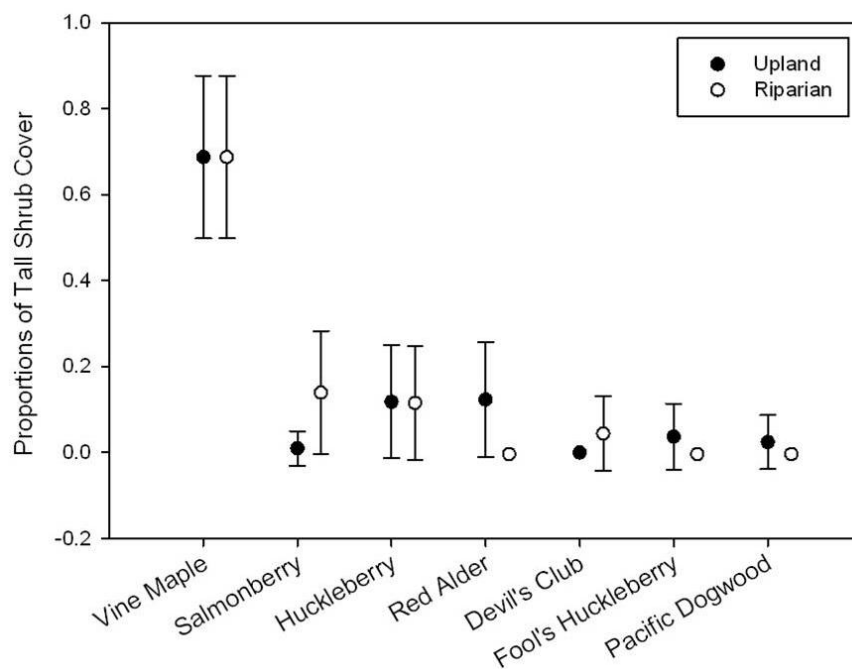


Figure 2.10. Species proportions ($\bar{x} \pm SE$) of tall shrub cover in headwater riparian and adjacent upland locations in the Trask River Watershed, Oregon, 2008-2009

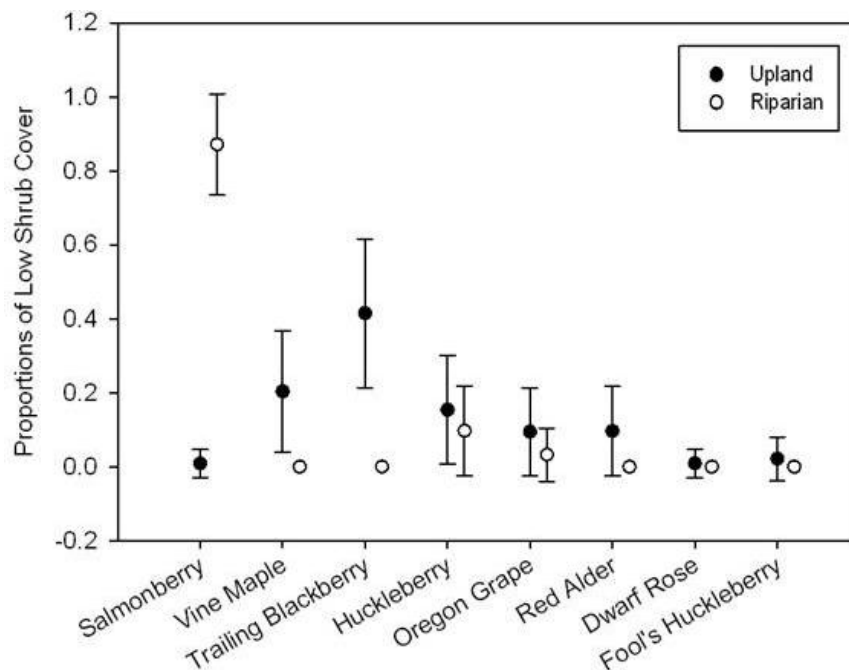


Figure 2.11. Species proportions ($\bar{x} \pm SE$) of low shrub cover in headwater riparian and adjacent upland locations in the Trask River Watershed, Oregon, 2008-2009.

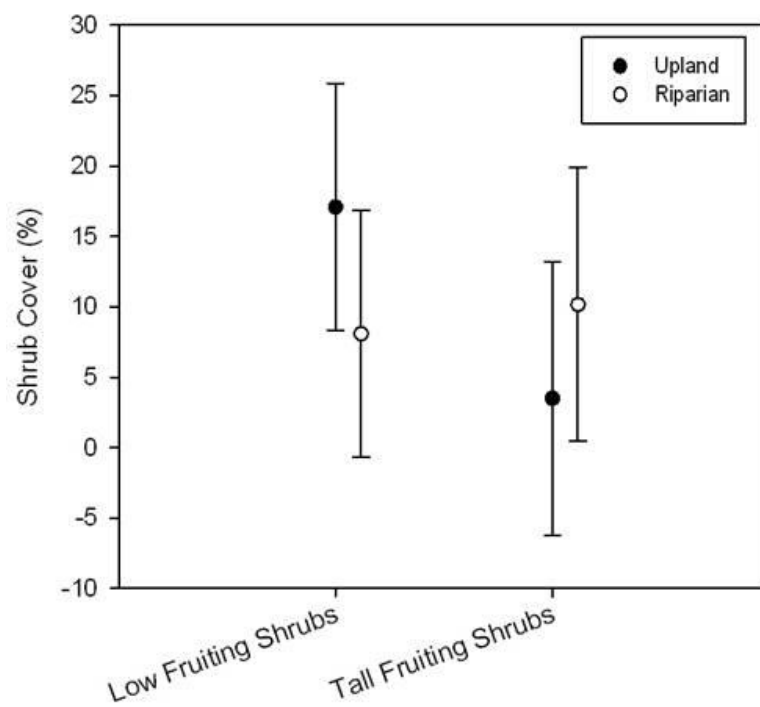


Figure 2.12. Mean cover of low and tall fruiting shrub species \pm 95% CI in riparian and adjacent upland locations in the Trask River Watershed, Oregon, 2008-2009.

***CHAPTER III - HABITAT SELECTION BY JUVENILE SWAINSON'S
THRUSHES (CATHARUS USTULATUS) IN THE HEADWATERS OF THE
TRASK RIVER, NORTHWESTERN OREGON***

Introduction

Riparian forests are critical for the ecological functioning of stream food webs (Wallace et al. 1997), and also often support diverse and abundant communities of birds (Stauffer and Best 1980, Knopf and Samson 1994, Bub et al. 2004, Allen et al. 2006), amphibians (Sheridan and Olson 2003), small mammals (Gomez and Anthony 1998), arthropods (Progar and Moldenke 2002, Iwata et al. 2003), and plants (Naiman and Decamps 1997, Pabst and Spies 1998). As a result, forest policy in many jurisdictions has afforded protection of forested riparian areas (Osborne and Kovacic 1993). However, to date, attention has focused primarily on large, perennial, fish-bearing streams (FEMAT 1993, Adams 2007). Lower order, non fish-bearing streams, often termed 'headwater streams', have received minimal research effort and protection priority. This is of conservation concern given the large proportion of the landscape occupied by riparian areas along small streams and the degree to which they are affected by timber harvest. For example, in the Pacific Northwest, headwater streams constitute a high proportion (83%) of total stream length (Swank 1985). Mandates vary from being unspecified to 45 m in width throughout the United States concerning riparian areas along intermittent streams (Blinn and Kilgore 2001). In the United States and Canada, riparian buffers are intended to conserve ecological function of aquatic systems but are generally less than recommended widths for terrestrial communities (Lee et al. 2004). Conservation policies on federal forest lands mandate riparian buffer widths of one site potential tree height (approximately 30 m) along non fish-bearing headwater streams within the range of the Northern Spotted Owl (FEMAT 1993, NWFP 1994). Currently, in the Oregon Coast Range, retention of streamside vegetation is not required on headwater streams that are not designated as fish-bearing or for domestic use (OFPA 2010).

Vegetation transitions between headwater riparian and upland areas can be subtle in mesic climates of the Pacific Northwest (McGarigal and McComb 1992, Pabst and Spies 1998), so it might be expected that ecological differences are minimal. Yet even along small streams, a decreasing gradient in vegetation diversity has been reported from riparian areas to uplands (Pabst and Spies 1998). Non-coniferous species that provide forage for consumers, such as arthropods (Nakano

and Murakami 2001, Iwata et al. 2003, Hagar 2007), are more abundant in riparian areas. Headwater riparian areas not only influence downstream processes (Gomi et al. 2002, Spies 2002, Wipfli et al. 2007), but may be important habitat for terrestrial vertebrates. For instance, insects emerging from streams may provide forage for birds (Jackson and Fisher 1986, Gray 1993, Baxter et al. 2005) and large amounts of cover of deciduous vegetation in riparian areas may offer protection from predators (White et al. 2005). The spatially continuous nature of riparian areas, along with the abundance of food and dearth of predators may cause them to function as movement corridors for wildlife species (e.g., forest birds) (Mitchell et al. 2010).

Studies on the role of headwater streams as habitat for terrestrial animals is scarce, but existing studies suggest that during the breeding season, the abundance of some migratory bird species (e.g., winter wren, Swainson's thrush) is higher adjacent to headwater streams (McGarigal and McComb 1992). However, these studies have relied on point count methods – which are strongly biased toward detection of singing males (Alldredge et al. 2007). Density of males is not necessarily a good indicator of habitat quality (Van Horne 1983, Bock and Jones 2004). It is also becoming increasingly clear that the demography of migratory species is determined by events occurring throughout the entire annual cycle (Martin et al. 2007). Though studies on the breeding distributions of birds are relatively common, far less is known about habitat selection by juvenile birds during the post-fledging period, directly after independence from parents and before migration (Faaborg et al. 2010).

The juvenile life stage is a sensitive period in which individuals typically incur high rates of mortality (Anders et al. 1997, Kershner et al. 2004, Gardali et al. 2009), probably due to inexperience at foraging and high vulnerability to predation. In this two- to three-month period, individuals must acquire sufficient energy for molt and for long-distance migration (Whitaker and Warkentin 2010). Results of the few studies published to date on habitat of juvenile songbirds have shown that juveniles in the post-fledging period may select different habitat than adults during the breeding season (Anders et al. 1998, Vega Rivera 1998, White et al. 2005, Cohen et al. 2009). Juvenile survival is critical to overall population viability; therefore, protecting habitat for fledgling birds is an important conservation strategy (Faaborg et al. 2010).

My objective was to determine whether headwater riparian areas serve as bird habitat during the post-fledging period. My study species was the Swainson's thrush, a migratory songbird that may occur in higher abundance in riparian areas during the breeding season (McGarigal and McComb 1992) and is of conservation interest; populations of this species have been declining in the last 40 years in the Pacific Northwest (1.78 %/yr, $p = 0.006$). These declines may be due to decreasing habitat availability during the breeding and post-breeding periods (Betts et al. In Press). I hypothesized that juveniles may select headwater riparian areas out of proportion to the surrounding upland, possibly due to the higher amounts of food and cover in these areas (Stauffer and Best 1980, Naiman and Decamps 1997, Iwata et al. 2003, Christie and Reimchen 2008, Iwata et al. 2010). Alternatively, it is possible that variables that are measured and manipulated in forest management (i.e., deciduous and coniferous trees, proximity to stream) may explain habitat selection of juvenile Swainson's thrushes. From a forest management standpoint, understanding how proximity to stream influences habitat selection could inform riparian buffer guidelines. Identifying factors affecting habitat selection by juvenile Swainson's thrushes will provide information to assist managers in maintaining habitat for a declining neotropical migrant bird species in a managed forest ecosystem. Additionally, this will provide information on whether headwater riparian areas function as habitat for this species.

Methods

Study Sites

I conducted my study within the Trask Watershed Study Area (25 km²) in the headwaters of the East Fork of the South Fork of the Trask River in the north central Coast Range of Oregon (TraskWRC 2007). This area is dominated by small, seasonally intermittent and perennial streams (orders 1-2) and is in the Douglas-fir/ocean spray (*Psuedotsuga/Holodiscus*) plant association of the Western Hemlock (*Tsuga heterophylla*) forest zone (Franklin and Dryness 1988). The study area is situated slightly west of the divide where water flows east toward the Willamette Valley and west to the Pacific Ocean. Elevation ranges from 275 to 1100 m. This area is influenced by a maritime climate of mild temperatures and annual rainfall of

180-300 centimeters. The study area is owned primarily by Weyerhaeuser Company and the Oregon Department of Forestry with a small portion managed by the Bureau of Land Management. Due to the Tillamook Burn (three events from 1933-1945) and subsequent timber harvest, most of the original, old-growth conifer overstory was removed by the 1950s. During the 1990s, Oregon Department of Forestry (ODF) conducted light to moderate thins to a basal area target ranging from 4.13 – 6.02 m²/ha (110 -160 ft²/ac) in the northwest portion of the study (TraskWRC 2007). Twelve percent of Weyerhaeuser ownership in the eastern section of the study area was characterized by five year-old regeneration harvests.

The dominant overstory at the time of my sampling was 40- to 70- yr old conifers, mainly Douglas-fir (*Pseudotsuga menziesii*) with western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and noble fir (*Abies procera*). The riparian overstory was a narrow and patchy strip of mixed conifers and red alder (*Alnus rubra*). Pockets of tall shrubs, mainly vine maple (*Acer circunatum*), and small amounts of beaked hazel (*Corylus cornuta*) and Pacific dogwood (*Cornus nuttallii*) were scattered throughout the study area. Species present in the understory included trailing blackberry (*Rubus ursinus*), salmonberry (*Rubus spectabilis*), ocean spray (*Holodiscus discolor*), stinking currant (*Ribes bracteosum*), Oregon-grape (*Mahonia aquifolium*), huckleberry spp. (*Vaccinium* spp.), devil's club (*Oplopanax horridum*) and sword fern (*Polystichum munitum*).

Juvenile Capture

I captured and tracked juvenile Swainson's thrushes (hereafter referred to as juveniles) in 2 consecutive post-fledging seasons during early-July and mid-September in 2008 and mid-June and early-September in 2009 (7/1/2008-9/17/2008 and 6/15/2009-9/4/2009). I captured juveniles directly at the nest, or using mist-nets. Mist-net captures resulted from a concurrent study that compared songbird assemblages in six paired headwater riparian and adjacent upland sites where I sampled each riparian and upland pair every two weeks using an array of 12 mist-nets per habitat (Chapter II). All mist-nets were 3-m high and 6- to 12-m in length (4 mist-nets ranged from 6 - 9 m in length to fit across small streams and between topographical features). I located all riparian mist-nets within 50 m of both sides of

intermittent and perennial, non fish-bearing 2nd order streams. I positioned upland arrays in a similar pattern to riparian arrays and at least 50 m from the outermost riparian mist-net and outside of planned riparian buffers. All mist-net arrays were purposefully set in areas with adequate camouflage of shrub cover (See Chapter II for detailed methods). I also captured juveniles opportunistically in dense vine maple pockets near riparian sites, along logging roads and from nests of radio-tagged females. I captured juveniles in both riparian and upland areas, but I captured the majority of juveniles < 40 m from streams in habitat I categorized as 'riparian' (upland = 6 captures, riparian = 31 captures). Nests ranged from 5-41 m from the nearest stream.

All mist-net captures took place between 0545 and 1130 hrs. I placed captured birds into breathable cloth bags. Juveniles were distinguished from adults using skull pneumatization and/or juvenile plumage characteristics (i.e., buffy-tipped primary coverts, length of 10th primary) and fitted with a USGS aluminum leg band. Additionally I measured body mass using a digital balance (g) and wing chord (mm).

Radio Telemetry Attachment

I attached radio transmitters (1.1g in 2008 and 0.9g in 2009; Philip Blackburn, Naganoches, TX) using a combination of eye lash adhesive (Ardell Lash Grip Adhesive, copyrighted) and epoxy in 2008 or a modified Rappole attachment system in 2009 (Rappole and Tipton 1991). I attached radio transmitters to nestlings when they were 10 – 11 d old. Nestlings were returned to the nest where they fledged within 1-2 days. Total transmitter weight was 3-4% of each bird's mass. There has been no evidence that transmitters affect passerine behavior or survival (Powell et al. 2000, Davis et al. 2008) and I did not observe any adverse effects of radio transmitters on daily activities of birds or when I had the opportunity to re-examine them upon recapture.

Tracking Juvenile Birds

I tracked juveniles on foot with a 3-piece yagi antenna and Wildlife Materials 3000 (2008) or TRX100 (2009) receiver. To reduce observer bias, I avoided assigning the same bird to one observer for more than two consecutive days. I

assumed juveniles were independent when they were no longer being fed by their parents or emitting begging calls, and the female was not detected in the area. I followed each independent juvenile for 30 minutes to confirm independence from parents. I recorded UTM coordinates of the location of each juvenile every 1-2 days, alternating between morning and afternoon/evening so each juvenile was monitored during different diurnal periods. On rare occasions, the time between locations of an individual spanned 4 days when signals were temporarily lost or when transmitters fell off an individual but were subsequently reattached upon recapture. I approached juveniles as quietly as possible to identify the precise location without influencing movement from my tracking effort. In cases in which I could not visually confirm the precise location of a juvenile due to thick vegetation cover, I circled the dense patch of vegetation entirely where the radio signal was the strongest and recorded the UTM coordinates at the centermost point. I was able to effectively detect radio signals within a 6-9 km radius of previous locations. I checked each lost radio frequency for the next 5 d and then periodically to verify loss of transmission.

Juvenile Habitat Selection

If juvenile habitat selection is adaptive (i.e., enhances survival and future reproduction), understanding juvenile habitat selection is a first step toward connecting land use patterns with overall songbird demography. Habitat selection is defined as the use of a particular resource or group of resources out of proportion to availability (Johnson 1980, Jones 2001). A common assumption is that random sampling of a landscape provides an accurate assessment of availability for an individual (Aarts et al. 2008). However, this assumption may not accurately represent available habitat according to a focal species' natural history (Aebischer et al. 1993, Jones and Robertson 2001). Here, I defined availability according to typical daily movement distances gathered from pilot data in the same study area for juvenile Swainson's thrushes. Based on this ecological definition, I considered distances <300 m from each previous location to be available to juvenile. I collected habitat data at each juvenile location as well as at a paired random location (termed 'available'), obtained from a random bearing and distance from the juvenile's previous location (30-300 m, even distribution). I omitted from analysis each juvenile's first location

because it was not possible to pair it to an available location based from a previous location. I expect that independent juveniles are highly vagile and likely to be physiologically capable of movement greater than 300 m over 1-2 day periods (maximum distance in my study = 562.8m). Our results are conservative given the inherent spatial autocorrelation in vegetation composition and structure of consecutive locations of juveniles (Schwartz et al. 2003) and, therefore, potentially underestimate the total area available to juveniles.

Habitat Characteristics

In 2008 I sampled habitat characteristics in four 5-m radius subplots centered 20 m at cardinal directions from each juvenile location and at paired available locations. Based on these data, the number of subplots (2 versus 4) did not influence estimates of the means of habitat variables. Therefore, in 2009 I used 2 subplots (5-m radius) per location in order to maximize the number of locations for which I could obtain habitat information. One subplot was centered at the juvenile location with the other subplot centered 20 m away in a random direction. This method was duplicated at the paired available location.

At each subplot I measured percent cover for shrubs (0-1.5 m tall) and deciduous mid-story (from 1.5 - 15 m above ground in vertical strata). I estimated percent cover using 25% resolution (i.e., 0, <25, 26-50, 51-75, 76-100%). I standardized the method for estimating percent cover among crew members at the start and periodically throughout each season by jointly completing vegetation assessments. Within each subplot I recorded the number of live deciduous and coniferous trees >10 cm diameter at breast height (DBH). I categorized deciduous and coniferous species into two size classes, each based upon current harvestable diameters: <25.4 cm and > 25.4 cm for deciduous trees and < 17.8 cm and > 17.8 cm for coniferous trees. For analysis, I simplified tree information to reflect presence or absence of each tree type (deciduous, coniferous) and size category because my plots were too small to accurately calculate tree density (i.e., most plots had \leq large tree). I estimated volume of coarse down wood along a 20-m linear transect between the two subplots at each location. I adapted (1974) and Waddell (2002) protocols to measure down wood. Down wood was measured 1) if it was > 10 cm in diameter where it crossed the

transect and 2) if it was not elevated < 45 deg from the ground. I calculated volume of downed wood using the formula:

$$volume_m = (\pi / 2L) ((\pi/4)D^2 l_i / l_i) / 10000 (m^3 ha^{-1}),$$

where L is the total length (m) of the transect, D is the diameter in cm of each piece and l_i is the length of each individual piece.

To estimate percent overstory cover, I used an ocular tube (PVC pipe fitted with cross hairs, 5 cm in both length and diameter). I recorded the occurrence of deciduous, coniferous, and open canopy that intersected the cross hairs (Emlen 1967). In 2008 I took four ocular tube readings per location, one at the center of each subplot. In 2009 I took 11 ocular tube readings per location, one every two meters on the coarse down wood transect.

I measured distance to nearest stream for each juvenile and available location using the “NEAR” feature in ArcMap 9.3 [Hawthornes Tools,(ESRI 2009)]. I averaged all variables from all subplots for each location. I combined both years of data because habitat remained stable (i.e. no major windstorms, wildfire, or timber harvest) and inter-annual variation in songbird capture rates was negligible in my simultaneous study comparing riparian and upland songbird assemblages.

Statistical Analysis

Juvenile Habitat Selection

I excluded deciduous overstory cover in favor of deciduous mid-story and shrub cover because it was highly correlated with these variables ($r > 0.60$) and because Swainson’s thrushes are ground nesters and generally forage low in the vertical strata (Mack and Yong 2000).

I calculated the relative odds of juvenile occurrence by comparing habitat characteristics of juvenile locations in relation to paired random available locations. All variables are described in (Table 3.1). I developed two *a priori* models for juvenile

habitat selection. One of my main hypotheses was that proximity to stream would influence habitat selection, and therefore this variable is included in both models. One model was based on ecological criteria postulated to be important to juveniles (Stauffer and Best 1980, Naiman et al. 1993, White et al. 2005); this included deciduous mid-story cover, shrub cover, coarse down wood volume and proximity to stream. From an ecological standpoint, inexperienced juveniles may select habitat within close proximity to a stream because it may serve as a 'resource hub' due to high amounts of emergent aquatic invertebrates and deciduous vegetation that provide food and cover (Nakano and Murakami 2001, Iwata et al. 2003). The other model focused on current forest management priorities; it incorporated variables that are measured and manipulated in forest management (i.e., the four tree variables) as well as proximity to stream. From a management standpoint, understanding how proximity to stream influences habitat selection could inform riparian buffer guidelines.

I calculated the relative odds ratio of juvenile occurrence (ROR) using a multilevel mixed effects logistic regression model with PROC GLIMMIX (SAS 2000) for binominal data with a logit link function. I accounted for temporal and spatial autocorrelation among multiple locations for a juvenile by treating each juvenile as a sampling unit [sensu (Mitchell et al. 2010)]. I paired each juvenile and available (random) location since I could not assume all available (random) locations within the spatial extent of all observations were available to a given juvenile at any particular time.

Vegetations Characteristics

I also compared each potential habitat variable between juvenile and available locations in a univariate analysis, using a split plot block design with PROC MIXED (SAS 2000). I accounted for individual variation among juveniles by treating each bird as a sampling unit (block) and paired juvenile and available locations (split plots). Additionally, I used this method to test if the distance between consecutive locations resulted from the time elapsed between consecutive locations. I also tested the effect of observer on the difference estimates between juveniles and available locations, with the assumption that recorders may inadvertently bias cover estimates based upon foreknowledge of juvenile and available locations.

For 2 juveniles, I recorded only 1 location per juvenile before they moved outside the study area. My definition of availability is based upon 300 m from the previous location; therefore, in absence of a previous location, I decided to pair each juvenile location with the available location that normally would have been paired with the subsequent juvenile location. This is logical because the 300-m radius of daily available habitat often overlapped locations for several tracked juveniles. I tested with and without these data, and removing these two juveniles in my analysis did not significantly affect parameter estimates or standard errors.

Additionally, the only 2 pairs of siblings I tracked appeared to select habitat within proximity to one another. I randomly removed 1 sibling from each family and found no significant change in the odds of juvenile occurrence (e.g., proximity to stream [ROR mean change = -0.09 %] and mid-story cover [ROR mean change = -0.04 %]). Therefore, I retained these individuals as independent samples.

I report all means and confidence intervals of logarithmically transformed variables as exponentiated (i.e., ROR estimates and coarse down wood volume). The natural log of 0 is 1, therefore, in order to interpret CIs, 1 instead of 0 signifies no difference between exponentiated means for coarse down wood volume. However, because I have numerous ROR estimates, I subtracted one from ROR estimates and CIs for ease of understanding.

I considered all variables significant if $p < 0.05$, but did not discount p-values that were greater than but close to this value (Stoehr 1999). Values provided are $\bar{x} \pm CI$ unless otherwise stated. Reporting CIs around effect sizes is considered to be superior to retrospective power analysis (Steidl et al. 1997).

Results

Juvenile Daily Location and Movements

I tracked 37 independent juveniles (capture method; nest=6, mist-net=31) for 1 to 22 d (mean number of locations per juvenile 5.1 ± 0.63 (SE), range 1-16). The six individuals captured at the nest achieved independent status 14-16 d after fledging.

Overall, I documented 1 mortality of unknown cause; the remaining 36 juveniles survived to migrate or move outside of my study area.

The distance between consecutive juvenile locations averaged 141 ± 15 (SE) m (range 23 m – 563 m) (Fig. 3.1). The mean amount of time between consecutive locations of individuals was 31.6 ± 2.4 (SE) hrs, but ranged from 4 - 128 hrs. Greater than 60 hrs elapsed between consecutive juvenile locations in 9% of my sample (22/204 locations). Distance between sequential locations was not related to elapsed time (MIXED; $F_{88} = 1.05$, $p = 0.4$) (Fig. 3.2).

Habitat Selection

Overall, the ecological model was more useful for explaining juvenile habitat selection; this model contained more statistically significant variables (i.e., proximity to stream, deciduous mid-story cover, coarse down wood volume) than the management model (i.e., only proximity to stream). Juveniles selected locations that were closer to streams and had greater amounts of deciduous mid-story cover and coarse down wood than available locations (Table 3.2). The effect of shrub cover on the odds of juvenile occurrence was inconclusive (Table 3.2). Management-oriented variables (i.e., the presence of deciduous or coniferous trees separated into harvestable and non-harvestable size classes) were not useful for discriminating juvenile from available locations (Table 3.3). Juvenile locations were characterized by a mean deciduous mid-story cover of 52% (CI = 46 - 57%, range 0-100%, Fig. 3.4) and 30 m from a stream (CI = 24 – 38 m, range 0-175 m, Fig. 3.5). Available locations were characterized by a mean deciduous mid-story cover of 31% (CI = 25-37%, range 0-100%, Fig. 3.4) and 46 m from a stream (CI = 39-53 m, range 0-178 m, Fig. 3.5) Independent of all other ecological variables, the odds of juvenile occurrence approximately doubled (98.4%, CI = 37.8 - 185.7%; GLIMMIX, $t_{188} = 3.71$, $p < 0.001$) for every 50 meters closer to the stream and for every 25% increase in mid-story cover (72.9%, CI = 39.7 - 113.9%; GLIMMIX, $t_{188} = 5.07$, $p < 0.0001$).

Post-hoc, I tested whether the effect of deciduous mid-story cover increased in importance with increasing proximity to streams, but I did not find support for this interaction (GLIMMIX; $F_{187} = 0.52$, $P = 0.5$). Though I found no statistical support for a

recorder bias in deciduous mid-story cover estimates between juvenile and available locations, this relationship approached significance (GLIMMIX; $F_{140}=1.78$, $p=0.07$). Thus, occasionally some observers may have been more likely to estimate greater amounts of mid-story cover at juvenile than available locations.

Juveniles also appeared to select sites with greater amounts of coarse down wood; for every doubling of coarse down wood volume, the odds of juvenile occurrence significantly increased by 41.5% (CI = 0.5%-99.2%; GLIMMIX, $t_{188} = 2$, $p = 0.04$, Table 3.2). Juveniles selected areas with a mean coarse down wood volume of 2.25 m³/ha (CI = 1.95-2.60 m³/ha), approximately 0.83 m³/ha (CI = 0.68 - 1.01 m³/ha) greater than available locations ($\bar{x} = 1.86$ m³/ha, CI = 1.61 – 2.16 m³/ha; MIXED, $t_{36} = -1.93$, $p = 0.06$, Fig.3.6).

The mean shrub cover for juvenile locations was 49 % (CI = 46-53 %), which was approximately 8% (CI = 37-44%), greater than available locations ($\bar{x} = 41\%$, CI = 37 – 44 %; MIXED, $t_{36} = -3.54$, $p = 0.001$, Fig.3.7). However, evidence that percent shrub cover was associated with juvenile occurrence was somewhat ambiguous; confidence intervals for odds ratios included zero (ROR = 31.8%, CI = -2.4% – 77.9%; GLIMMIX, $t_{188} = 1.81$, $p = 0.07$, $n=37$). Overall, excluding the juveniles with only one location did not influence my results; effects of deciduous mid-story, distance to stream and coarse down wood volume on the relative odds of juvenile occurrence changed little (the change in ROR < 0.01 % between $n=37$ and $n=35$).

Discussion

I found that juvenile Swainson's thrushes in the Oregon Coast Range tend to select locations with large amounts of deciduous mid-story cover in close proximity to headwater streams. Despite fairly weak gradients in vegetation composition and structure from riparian to upslope sites, headwater streams appear to strongly influence the distribution of this species during the post-fledging period.

The relationship between stream proximity and juvenile occurrence could be driven partly by the abundance of arthropod prey in riparian areas. During fall migration, 87% of juvenile Swainson's thrushes fecal samples included arthropods

along the northern California coast (Tietz and Johnson 2007). These arthropods have been shown to replenish protein stores more quickly than a diet of fruit (Schwilch et al. 2002). Indeed, fecal samples from Swainson's thrushes in my study area indicate that beetles, ants and, to a lesser extent, spiders, were the primary components of thrush diets. Arthropod prey abundance of both terrestrial and aquatic origin was higher adjacent to streams than in uplands (Hagar et al. 2010 unpublished data).

Though insectivorous and omnivorous birds may acquire energy directly or indirectly from aquatic insects emerging from streams (Nakano and Murakami 2001), my fecal sample data of Swainson's thrushes and samples of aquatic and terrestrial insect abundance indicate that Swainson's thrushes consume aquatic insect prey rarely, and less than expected based on availability (Hagar et al. 2010 unpublished data). Airflow patterns may also draw terrestrial insects downslope towards riparian areas (Pypker et al. 2007, Iwata et al. 2010), however, this effect appears to be stronger at night rather than during the day when I tracked my individuals as air patterns become more turbulent (Pypker et al. 2007).

Juveniles may also occur in riparian areas during the post breeding period because they are prospecting for future breeding sites (Betts et al. 2008). Anecdotally, in early August of 2009 I recaptured one second-year male Swainson's thrush that I tracked as a juvenile in 2008 within 10 meters of its initial capture location. Previous work has demonstrated higher abundance of Swainson's thrush breeding territories in headwater riparian areas (McGarigal and McComb 1992), so these locations should be most frequented by juveniles during dispersal movements. Interestingly, the congruency between breeding and post-breeding habitat selection by Swainson's thrushes in my study contrasts with several other studies on migrant birds which reveals differential habitat use between these life-history stages (Anders et al. 1998, Vega Rivera 1998, White et al. 2005). It is unlikely that juveniles were pushed out of areas dominated by conspecific adults, thereby congregating in juvenile groups in lower quality habitat (Christian 1970) because I captured conspecific adults in the same nets during the same time period as juveniles (Chapter II). The decrease in relative odds of juvenile occurrence as distance from stream increases generally mirrors the higher number of captures of adult Swainson's

thrushes near streams (Chapter II) (Fig. 3.3) and I suspect that juvenile and adult Swainson's thrushes use these areas because they offer valuable resources prior to long distance migration. Lastly, although some have suggested that riparian areas may provide movement corridors for passerines to prospect for future breeding habitat (Mitchell et al. 2010) or to search for food resources in unfamiliar terrain (Whitaker and Warkentin 2010), juvenile Swainson's thrushes did not appear to use riparian areas as movement corridors in my study area. This result coincides with similar numbers of captures between mist-nets oriented parallel and perpendicular to headwater streams in my study area (Chapter II) and does not indicate that birds were using riparian areas as movement corridors.

My results also indicate that vegetation structure influences habitat selection by juveniles in the post-fledging period. Juveniles were more likely to select sites that had high proportions of mid-story cover, large volumes of coarse down wood, and to a certain extent, high shrub abundance. Mid-story and shrub cover may serve as proximate cues for food resources and/or an ultimate cue for cover from predators. Deciduous tree and shrub species are known to support a diversity of both fruit and arthropods (Hagar 2007). Specifically, Lepidoptera are key prey for many songbirds and are more diverse and abundant on deciduous than coniferous foliage (Hammond and Miller 1998, Hagar 2007). In the Cascades of Washington, insect herbivory was substantially greater on deciduous than coniferous foliage (Shaw et al. 2006). Foliage density was highly predictive of Lepidoptera density in West Virginia (Marshall and Cooper 2004). As in the case of mid-story cover, arthropod abundance may explain the relationship between coarse down wood volume and juvenile habitat selection. Fecal samples from Swainson's thrushes in my study area indicate that beetles and ants are primary insect prey (Hagar et al. 2010 unpublished data). Ants often maintain colonies in coarse down wood (Stevens 1997).

Demonstrating habitat selection requires evidence of disproportionate use of particular sites in relation to those that are available, and an indication that this use is adaptive (Jones and Robertson 2001). My study reveals that juvenile Swainson's thrushes were capable of moving long distances (>500 m) around or through upland sites, but still tended to settle in headwater riparian areas with large proportions of

mid-story cover. Though challenging to test whether a choice is adaptive, it is important to note that mortality occurred in only 1 of 37 juveniles in my study. This mortality rate is substantially lower than previously reported for independent juvenile passerines (Anders et al. 1997, Kershner et al. 2004, Berkeley et al. 2007, Cohen et al. 2009), (Whittaker and Marzluff 2009). Thus, it seems quite possible that headwater streams contribute positively to the demography of the Swainson's thrush in the Pacific Northwest.

Limitations

Juveniles selected habitat within similar proximity to stream as their initial capture (Fig. 3.8). Because I eventually focused my capture efforts in riparian areas where I had the greatest capture success, I found juvenile proximity to stream is strongly related to capture location ($F_{169} = 6.75$, $p < 0.001$). Possibly, juveniles selected habitat near streams because they bias their selection toward their natal habitat (Stamps 2006). However, our interpretation is that habitat selection by juveniles was based on more than just a preference for natal habitat since individuals captured in upland areas moved across these areas to access riparian areas. Additionally, my initial captures relate to independent juveniles during or after natal dispersal which is not necessarily the location where these juveniles fledged.

Additionally, I measured vegetation cover estimates coarsely in 25% increments, therefore, mean differences between juvenile and available locations of $\leq 25\%$ (e.g., shrub cover) should be reviewed with caution.

Management Implications

Riparian areas on small headwater streams receive minimal to no protection in the Coast Range of Oregon which appears to be pervasive in policies throughout North America (Blinn and Kilgore 2001, Lee et al. 2004, ManitobaConservation 2008.). This absence of protection likely reflects a strong focus on the role of riparian vegetation in fish conservation (headwater streams do not contain fish), the high opportunity cost associated with not harvesting timber in headwater riparian areas, and the dearth of information on the ecological role of these sites. My study is one of the first to test the ecological importance of headwater streams for a migratory bird

species during the post-fledging period. Though correlative, my results demonstrate that, despite the absence of a strong gradient in vegetation composition across the riparian-upland interface, headwater streams serve an important ecological role as post-breeding habitat. The juvenile Swainson's thrushes that I observed selected these sites out of proportion to their availability. Further, the relatively strong effect of vegetation structure on habitat selection by thrushes suggests that maintaining deciduous vegetation cover in headwater streams may be particularly important. To strengthen inference, it will be critical for future studies to independently manipulate vegetation structure in riparian areas to determine to what extent juveniles select particular vegetation variables versus proximity to a stream.

Juvenile songbird habitat use and selection during the post-breeding period has often been overlooked; however, my results indicate that information gathered during the post-breeding period is important when interpreting habitat selection to inform songbird conservation. High survival of juvenile Swainson's thrushes in my study area suggests that selection for headwater riparian areas may maximize individual fitness. Knowledge of survival and habitat selection of juvenile Swainson's thrushes in headwater riparian areas provides quantitative data that can aid in species conservation.

Table 3.1. Variables and descriptions for habitat selection by juvenile Swainson's thrushes, headwaters of the Trask River Watershed, Oregon, 2008-2009.

Variable	Abbrev.	Description
Proximity to Stream	Stream	Represents a unit change of proximity to the stream (m) , unit = 50 m
Deciduous Mid-story Cover	Mid-story	Percent cover of deciduous foliage 1.5- to 15-m above the ground, unit = 25%
Shrub Cover	Shrub	Percent cover of deciduous shrubs < 1.5m in height, unit = 25%
Coarse Wood Volume	CW	Coarse wood volume, log-transformed; represents the effect of a doubling of CW (m ³ /ha)
Deciduous Large Trees	DL	Presence of stem(s) > 25.4 cm (10 in) DBH (harvestable)
Deciduous Small Trees	DS	Presence of stem(s) < 25.4 (10 in) DBH (non-harvestable)
Coniferous Large Trees	CL	Presence of stem(s) > 17.8 (7 in) DBH (harvestable)
Coniferous Small Trees	CS	Presence and absence of stem(s) < 17.8 (7 in) DBH (non-harvestable)

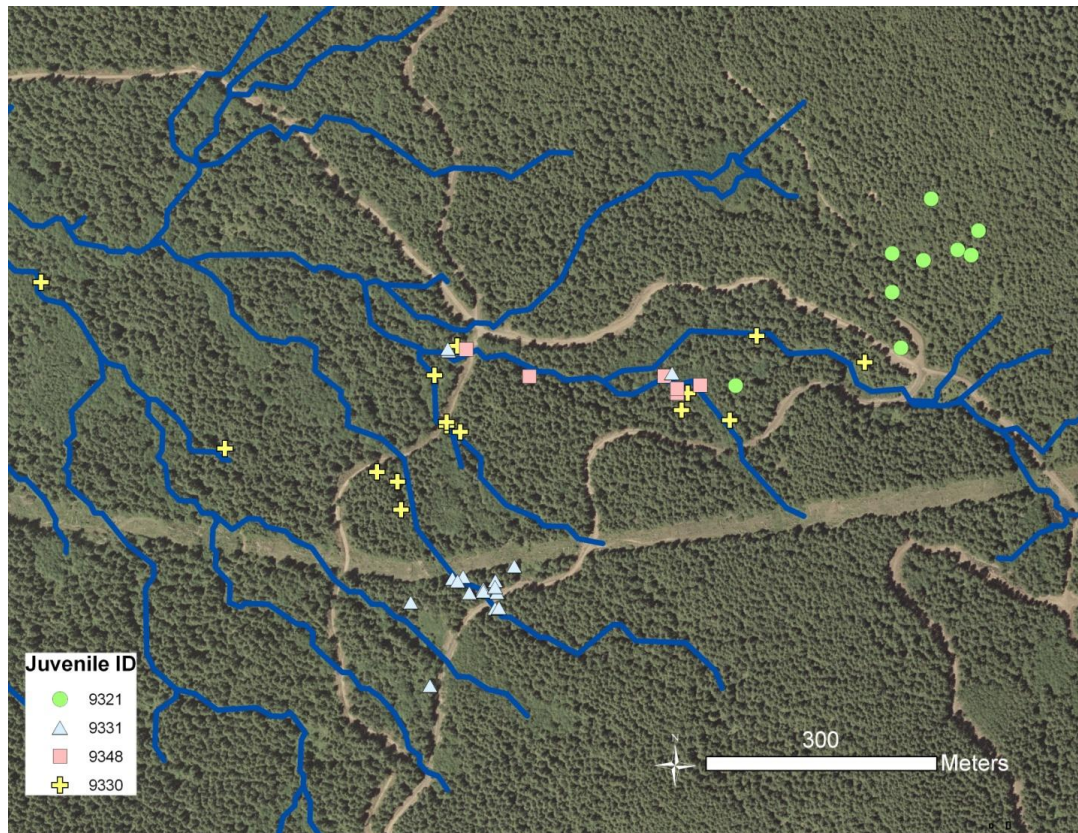


Figure 3.1. Locations of juvenile Swainson's thrushes in the headwaters of the Trask River Watershed, Oregon, 2008-2009. For clarity, only four individuals (total $n = 37$) are shown. Each symbol denotes an individual. Locations are separated by 1-2 days.

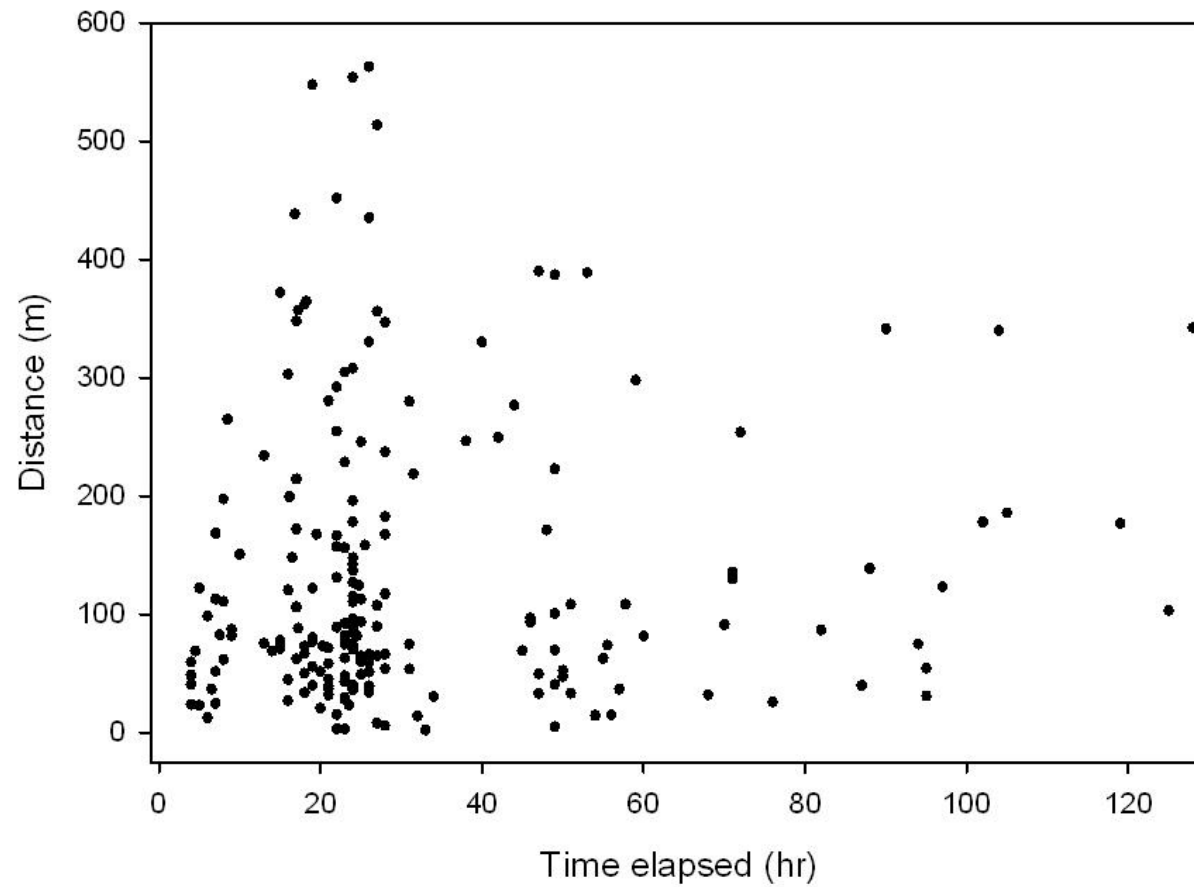


Figure 3.2. Distance (m) between subsequent locations for all juvenile Swainson's thrushes ($n = 37$) as a function of time (hr) elapsed between subsequent locations in headwaters of the Trask River Watershed, Oregon, 2008-2009.

Table 3.2. Relative odds ratios (ROR) of juvenile Swainson's thrushes occurrence for each parameter included in the ecological model in headwaters of the Trask River Watershed, Oregon, 2008-2009. ROR LCL denotes lower confidence limits and ROR UCL denotes upper confidence limits.

Variable	DF	<i>P</i>	ROR	ROR LCL	ROR UCL
Intercept	36	0.0022			
Stream	188	0.0003	1.984	1.378	2.857
Mid-story	188	<0.0001	1.729	1.397	2.139
Shrub	188	0.0714	1.318	0.976	1.779
CWD	188	0.0465	1.415	1.005	1.992

Table 3.3. Relative odds ratios (ROR) of juvenile Swainson's thrushes occurrence for each parameter included in the management model in headwaters of the Trask River Watershed, Oregon, 2008-2009. ROR LCL denotes lower confidence limits and ROR UCL denotes upper confidence limits.

Variable	DF	<i>P</i>	ROR	ROR LCL	ROR UCL
Intercept	36	0.0295			
Stream	187	0.0001	2.008	1.420	2.839
DL	187	0.4610	1.197	0.741	1.933
DS	187	0.6743	1.119	0.661	1.896
CL	187	0.3090	0.788	0.497	1.249
CS	187	0.5710	1.190	0.650	2.178

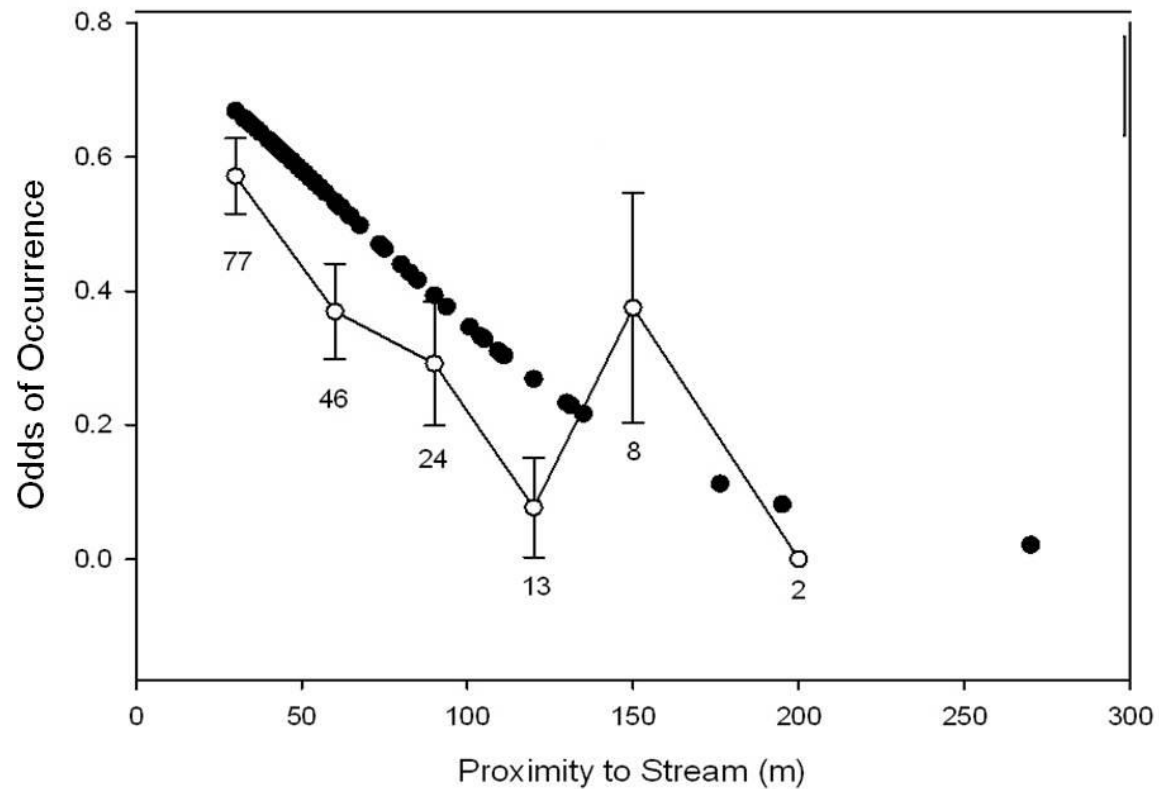


Figure 3.3. The relative odds of juvenile occurrence (black circles) compared to the proportion (\pm SE) of adult Swainson's thrushes (open circles) captured in relation to proximity to stream in headwaters of the Trask River Watershed, Oregon, 2008-2009. Time periods overlapped [June 15 –Aug 13 (adults) and July 15 – Sept15 (juveniles)]. Numbers under standard error bars denote sample size. For graphical purposes, proportions were calculated from a ratio of presences to absences within 6 categories of distance to stream (0-29m, 30-59m, 60-89m, 90-119m, 120-149m, >150m). Standard error was calculated as the square root of $((p*q)/N)$ where p is the proportion of presences and q is the proportion of absences

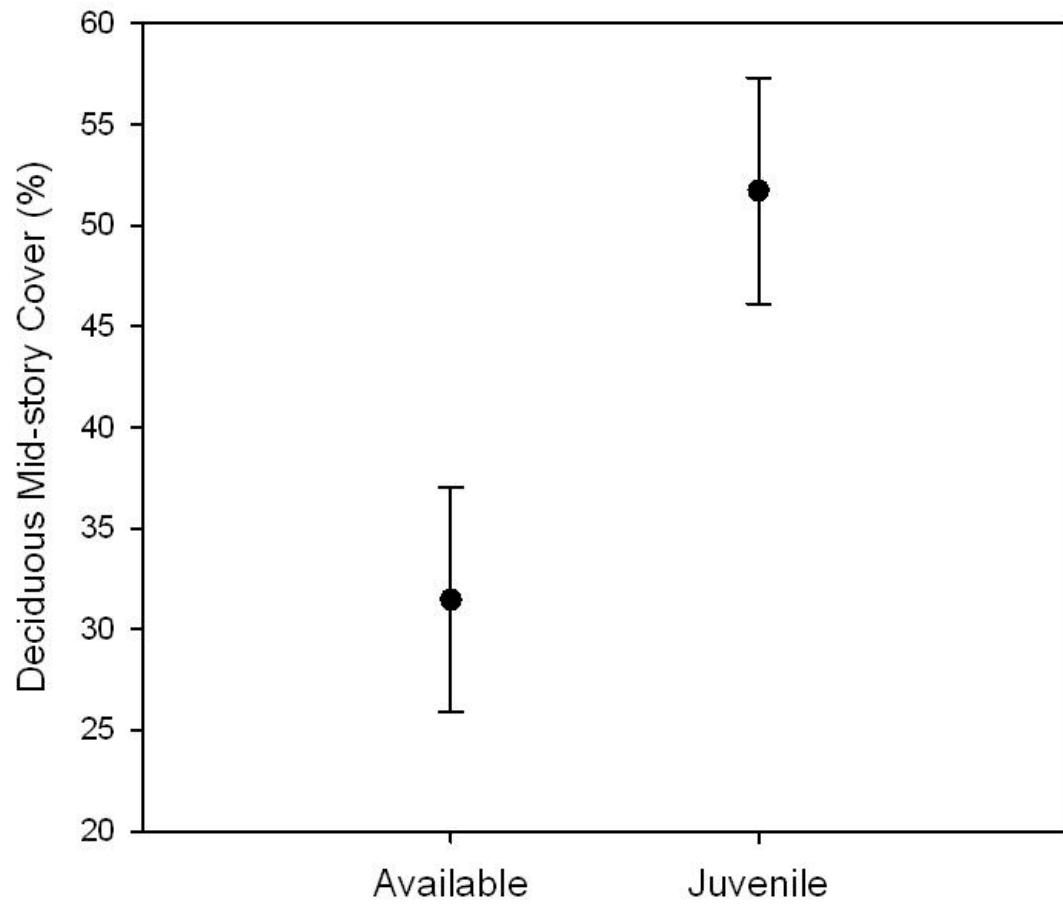


Figure 3.4. Percent mid-story cover ($\bar{x} \pm 95\%$ CI) in available and juvenile Swainson's thrushes locations in headwaters of the Trask River Watershed, Oregon, 2008-2009.

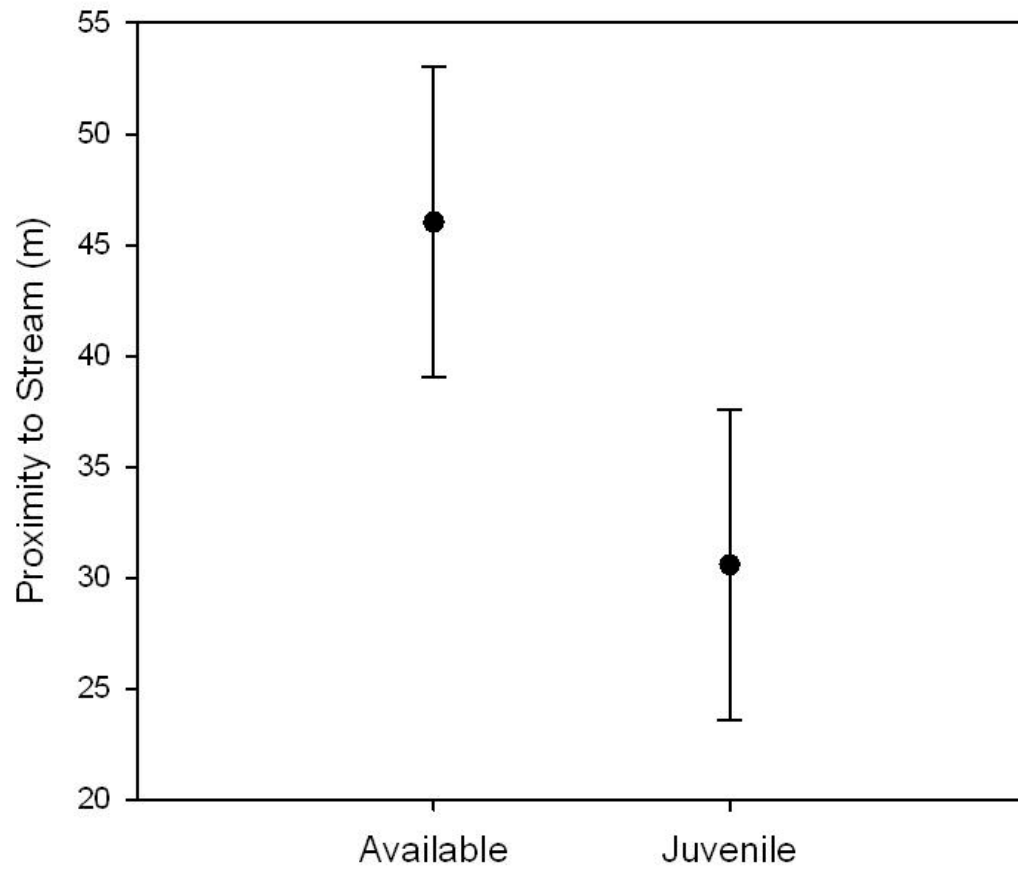


Figure 3.5. Percent mid-story cover ($\bar{x} \pm 95\%$ CI) in available and juvenile Swainson's thrushes locations in headwaters of the Trask River Watershed, Oregon, 2008-2009.

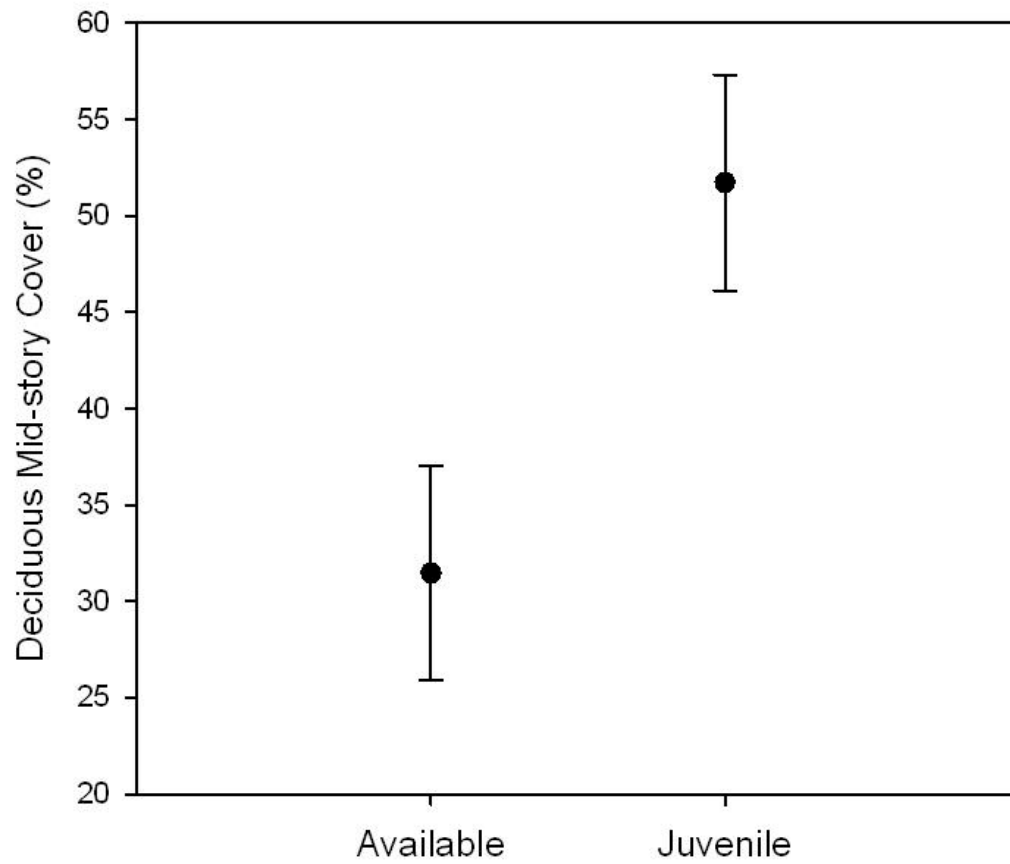


Figure 3.6. Coarse wood volume ($\bar{x} \pm 95\%$ CI m^3/ha) in available and juvenile. Swainson's thrushes locations in headwaters of the Trask River Watershed, Oregon, 2008-2009.

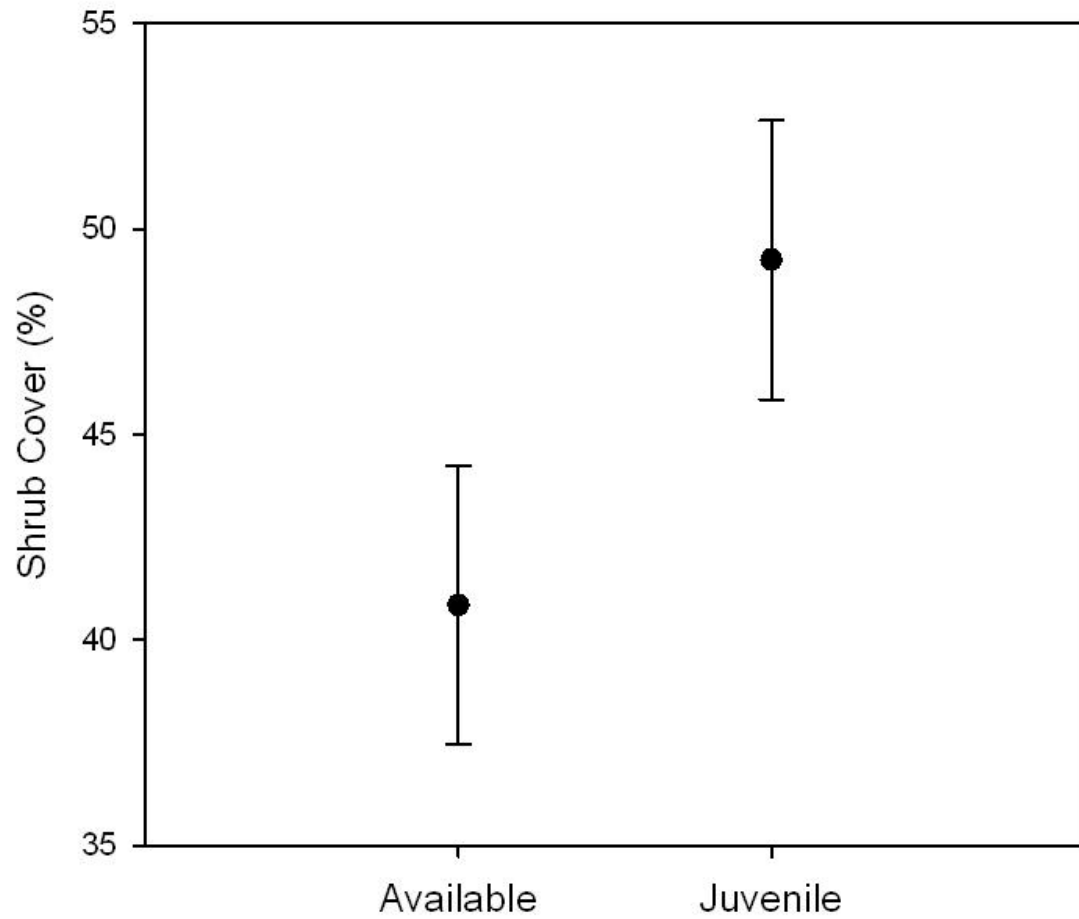


Figure 3.7. Percent shrub cover ($\bar{x} \pm 95\%$ CI) in available and juvenile Swainson's thrushes locations in headwaters of the Trask River Watershed, Oregon, 2008-2009.

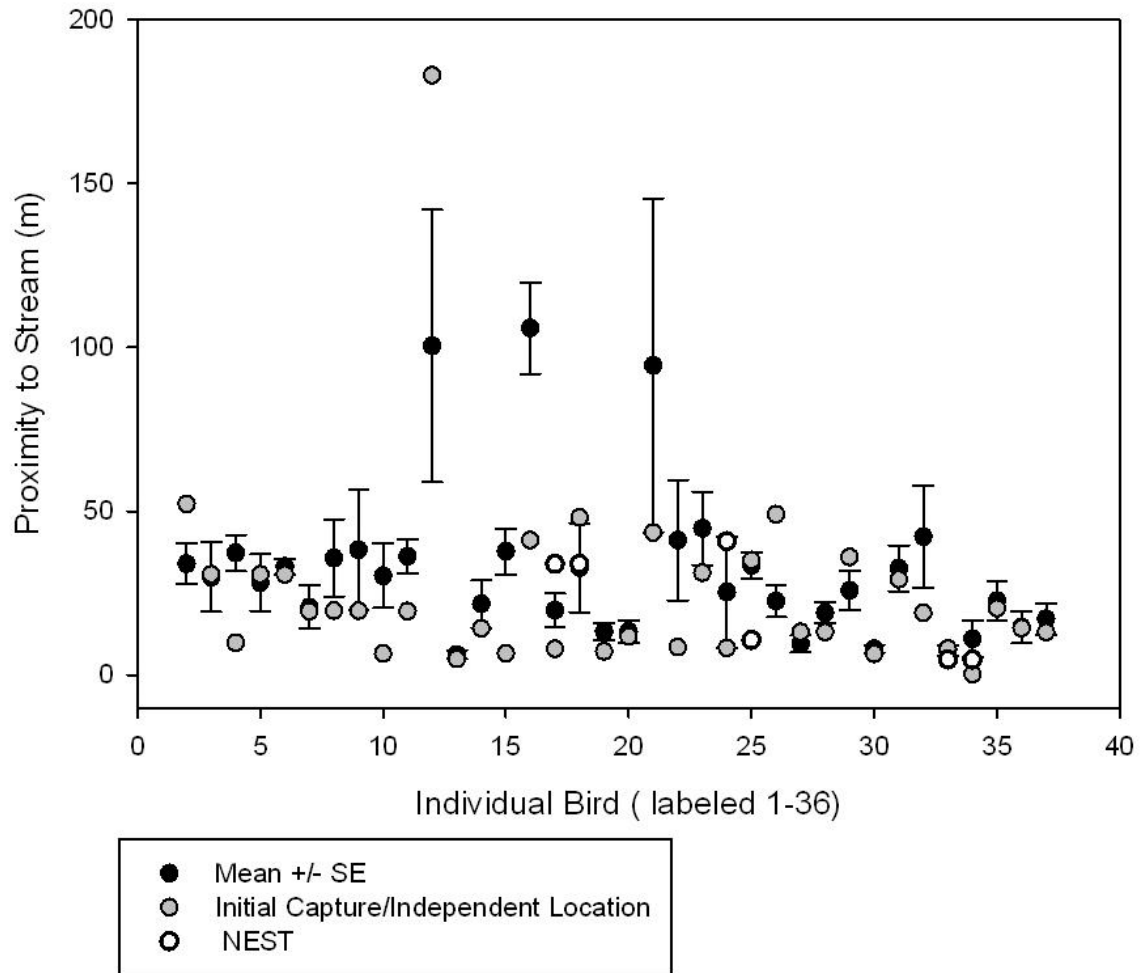


Figure 3.8. The mean proximity (\pm SE) to the nearest stream for juvenile Swainson's thrushes in the headwaters of the Trask River Watershed, Oregon, 2008-2009. Gray dots denote capture or first independent location (if tagged as a nestling), three of which are outside of the riparian area (>40 m from the stream). Open circles denote nest locations of tagged nestlings.

CHAPTER IV – SUMMARY AND RECOMMENDATIONS

This study indicates that headwater riparian areas are disproportionately important as songbird habitat during the post-breeding period. This is supported by three main findings. First, the capture rate of all species combined, as well as capture rates of Swainson's thrushes and winter wrens, were greater in riparian versus adjacent upland locations. Second, juvenile Swainson's thrushes selected habitat near streams that had high proportions of deciduous mid-story cover and large volumes of coarse down wood. Lastly, comparative to other studies, survival of juvenile Swainson's thrushes was disproportionately high in my study area (97.3%). It is possible that vegetation cover in riparian areas may afford better concealment from predators and, therefore, may explain capture rates and habitat selection of juvenile Swainson's thrushes (White et al. 2005, Mitchell et al. 2010, Whitaker and Warkentin 2010). However, in my study, vegetation cover appeared largely similar between riparian and upland locations, thus, it is more likely that higher capture rates and juvenile Swainson's thrushes' selection for headwater riparian habitat was a result of either higher amounts of food near the stream or using the stream as a movement corridor.

Furthermore, shrub species composition varied even though the amount of fruiting shrub cover was similar between riparian and upland locations. This indicates that while overall fruiting shrub cover does not explain my results, the presence of particular shrub species in riparian locations likely contributed to higher capture rates and juveniles Swainson's thrushes preference for riparian features. Specifically, salmonberry was disproportionately high in riparian locations and may have contributed to the higher capture rates in riparian locations by providing both fruit and arthropod prey (Shirley 2005). However, in my study, salmonberry ripened in mid-July, therefore fruit availability does not explain the high capture rates in riparian locations or habitat selection of juveniles Swainson's thrushes near streams after fruit production has passed. As a broad-leaved species, salmonberry may host high densities of arthropods because of easily digestible leaves (Shaw et al. 2006) and is suggestive that high capture rates in riparian locations and juvenile Swainson's thrushes preference for stream is most likely a result of the food afforded by terrestrial arthropods rather than fruit availability. This is further supported by greater abundance of terrestrial and aquatic arthropod prey near streams, the past evidence

of high arthropod abundance related to deciduous vegetation, and preference for areas with large volumes of coarse down wood. I hypothesize that juvenile Swainson's thrushes select habitat near streams with high amounts of mid-story cover because arthropods are more abundant near streams therefore potentially increasing foraging opportunities. Additionally, deciduous mid-story cover may serve a dual purpose by also providing cover from predators.

Birds may also use riparian areas as movement corridors as juveniles navigate unfamiliar terrain (Mitchell et al. 2010) or as birds in search of resources become less territorial after breeding (Whitaker and Warkentin 2010). In boreal mixed-wood forest of northeastern Ontario, more birds were captured in mist-nets oriented perpendicular to the stream than in parallel mist-nets (Mosley et al. 2006); however in my study, I found little evidence of a difference in the numbers of birds between perpendicular and parallel mist-nets. This coincides with subsequent locations of juvenile Swainson's thrushes that did not appear to follow streams, but were generally located in headwater riparian areas. Taken together, this indicates that while birds in my study area disproportionately use headwater riparian habitat relative to the upland; they do not appear to be using headwater riparian areas as movement corridors.

The only other study to document bird use of headwater riparian and upland habitat during the post-breeding period was conducted where there were distinct vegetation differences between riparian and upland areas (Akresh et al. 2009). Importantly, my study on bird assemblages in headwater areas of temperate forests indicates that birds used riparian areas disproportionately to the adjacent upland during the post-breeding period even though there were not distinct contrasts between riparian and upland vegetation cover. This indicates that birds appear to be using headwater riparian areas for reasons beyond vegetation structure.

My results contrast with previous research conducted in the Pacific Northwest during the breeding season (McGarigal and McComb 1992). We know that behavior and physiology of birds differ throughout their annual cycle (Faaborg et al. 2010), therefore, this contrast could be due to differing resource use between breeding and post-breeding periods for acquisition of energy for migration/winter survival.

Additionally, I sampled songbird communities with a different sampling methodology of using mist-nets rather than point counts. Mist-netting provides information on cryptic species and secretive individuals within the shrub-layer and, therefore, samples different components of the bird community than traditional point counts.

Whereas other mechanisms cannot be ruled out, it is interesting to speculate that headwater riparian areas provide better quality songbird habitat than adjacent upland primarily due to higher arthropod availability. We suggest that maintaining deciduous plant and shrub species known to host terrestrial invertebrates in headwater riparian areas will benefit songbirds during the post-breeding period. Adult and juvenile songbird habitat use and selection during the post-breeding period has often been overlooked; however, my results indicate that information gathered during the post-breeding period is important when interpreting habitat selection to inform songbird conservation. High survival of juvenile Swainson's thrushes in my study area suggests that selection for headwater riparian areas may maximize individual fitness. Beyond information on bird occurrence derived from mist-net captures, knowledge of survival and habitat selection of juveniles Swainson's thrushes in headwater riparian areas provides quantitative data that can aid in species conservation.

Although riparian areas cover a small proportion of western North America (Kondolf et al. 1987), these areas support high abundance and species richness, some of which only occur in riparian areas. Results of my research will help forest managers achieve goals related to maintaining biodiversity and will provide quantitative data on forest structural features essential to songbirds during the post-breeding period. Because birds are ecological indicators, it is reasonable to speculate that headwater riparian areas may also provide habitat for unique assemblages of other wildlife species. Indeed this has already been demonstrated for species of amphibians (Sheridan and Olson 2003), small mammals (Gomez and Anthony 1998), and arthropods (Progar and Moldenke 2002, Iwata et al. 2003). Despite the fact that headwater riparian areas provide habitat and contribute to biodiversity, these areas are often affected by human alterations (e.g., timber harvest).

The results of my study suggest that deciduous plant and shrub species near headwater streams are important. Future studies should seek to explicitly examine songbird response to manipulation of vegetation structure and composition in headwater forests. Specifically, future manipulative experiments could provide information on songbird habitat use and selection in response to varied riparian buffer characteristics as well as possible mechanisms for habitat selection. Additionally, future work should compare fitness consequences that result from an individual's use of riparian and upland areas. For some riparian associates (e.g., the Swainson's thrush), headwater riparian areas may be of conservation interest. Studying juvenile survival to reproductive status and habitat selection is an important step to determine how headwater riparian and upland areas differ in habitat quality.

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