



Habitat selection by juvenile Swainson's thrushes (*Catharus ustulatus*) in headwater riparian areas, Northwestern Oregon, USA



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ABSTRACT

Lower order, non-fish-bearing streams, often termed “headwater streams”, have received minimal research effort and protection priority, especially in mesic forests where distinction between riparian and upland vegetation can be subtle. Though it is generally thought that breeding bird abundance is higher in riparian zones, little is known about species distributions when birds are in their juvenile stage – a critical period in terms of population viability. Using radio telemetry, we examined factors affecting habitat selection by juvenile Swainson's thrushes during the post-breeding period in headwater basins in the Coast Range of Oregon, USA. We tested models containing variables expected to influence the amount of food and cover (i.e., deciduous cover, coarse wood volume, and proximity to stream) as well as models containing variables that are frequently measured and manipulated in forest management (i.e., deciduous and coniferous trees separated into size classes). Juvenile Swainson's thrushes were more likely to select locations with at least 25% cover of deciduous, mid-story vegetation and more than 2.0 m³/ha of coarse wood within 40 m of headwater streams. We conclude that despite their small and intermittent nature, headwater streams and adjacent riparian areas are selected over upland areas by Swainson's thrush during the postfledging period in the Oregon Coast Range.

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1. Introduction

Riparian forests profoundly influence the ecological functioning of stream food webs (Wallace et al., 1997), and also often support diverse and abundant communities of birds (Allen et al., 2006; Knopf and Samson, 1994; Stauffer and Best, 1980), 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). Riparian areas in many jurisdictions therefore receive special management consideration to protect these resources (Osborne and Kovacic, 1993). However, to date, attention has focused primarily on large, perennial, fish-bearing streams (Forest Ecosystem Management Assessment Team, 1993; Adams, 2007). Lower order, headwater streams, especially those without fish, have received less research effort and priority for protection from anthropogenic disturbances such as timber harvest (Oregon Department of Forestry, 2010).

Although much of the interest in headwater riparian areas has been related to their influence on aquatic biota and downstream

processes (Gomi et al., 2002; Spies, 2002; Wipfli et al., 2007), headwater riparian areas are themselves habitat for terrestrial vertebrates. Investigations into the function of headwater stream habitat for terrestrial animals are uncommon, but existing studies for birds suggest that during the breeding period, the abundances of some species (e.g., Pacific wren (*Troglodytes pacificus*), Swainson's thrush (*Catharus ustulatus*)) are higher in headwater riparian habitat than in adjacent uplands (McGarigal and McComb, 1992; Bub et al., 2004). Functional mechanisms underlying these differences have not been well studied, but may include greater food availability (Hagar et al., 2012; Nakano and Murakami, 2001; Iwata et al., 2003) and greater cover from predation (White et al., 2005) in riparian areas relative to uplands. However, little is known about the factors that influence habitat use by riparian-associated species along intermittent streams in headwater areas.

Singing surveys of breeding birds have provided evidence that adults of some species are associated with headwater riparian habitats (McGarigal and McComb, 1992), but non-singing juvenile songbirds are often missed using this method. As a result, far less is known about habitat selection by juvenile birds (Faaborg et al., 2010). The few studies published on habitat selection of juvenile songbirds suggest that juveniles in the postfledging period may select different habitat than that used by adults during the breeding season (Anders et al., 1998; Vega Rivera et al., 1998; White et al., 2005; Cohen et al., 2009). In particular, evidence from other

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regions indicates that riparian forests are important habitat for passerines during the period following fledging, even for species that are not strongly associated with riparian habitat as breeding adults (Anders et al., 1998). Juveniles typically experience 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. During a 2–3 month period, directly after independence from parents and before migration, individuals must acquire sufficient energy for molt and long-distance migration (Whitaker and Warkentin, 2010). It is becoming increasingly clear that the demography of migratory species is determined by events occurring throughout the entire annual cycle (e.g., beyond the breeding season) (Martin et al., 2007). Thus, determining if juvenile songbirds select, and survive, in headwater riparian zones during the postfledging period is important for informing conservation efforts.

The Swainson's thrush is a neotropical migrant and abundant breeder in the Pacific Northwest. It is associated with riparian areas during the breeding season (McGarigal and McComb, 1992) where it has shown exceptionally high return rates and site fidelity (Johnson and Geupel, 1996). This species is of conservation interest because populations have been declining over the last 40 years in the Pacific Northwest (1.78%/year, $p = 0.006$) (Sauer et al., 2008). These declines may be due to decreasing habitat availability during the breeding and post-breeding periods (Betts et al., 2010). Identifying and describing features that characterize post-breeding habitat for the Swainson's thrush could inform conservation strategies for this species. Our goal was to identify habitat features selected by juvenile Swainson's thrushes and determine if they differentiate between riparian and upland vegetation types during the postfledging period. We hypothesized that juveniles may select headwater riparian areas out of proportion to the surrounding available upland habitat because deciduous vegetation cover and proximity to water are expected to provide greater amounts of food and cover (Stauffer and Best, 1980; Naiman and Decamps, 1997; Iwata et al., 2003, 2010; Christie and Reimchen, 2008). From a forest management standpoint, understanding how proximity to stream influences habitat selection could inform riparian buffer guidelines. Therefore, in comparison to the above ecological variables, we tested the usefulness of variables measured and manipulated in forest management (i.e., the presence of deciduous or coniferous trees separated into harvestable and non-harvestable size classes) (Oregon Department of Forestry, 2010) in addition to proximity to stream for explaining habitat selection of juvenile Swainson's thrushes.

2. Materials and methods

2.1. Study sites

We conducted this study within the framework of the Trask Cooperative Watershed Study (<http://watershedsresearch.org/Trask/>). The Trask Watershed Study Area (25 km²) is in the headwaters of the Trask River in the northern Coast Range of Oregon (Johnson and Bilby, 2008). This area is dominated by small, seasonally intermittent and perennial streams (orders 1–2). Elevation ranges from 275 to 1100 m. The region has a maritime climate, with mild temperatures and annual rainfall of 180–300 cm.

We collected data along 6 non-fish-bearing, 2nd order streams representing the range of management plans of the ownerships in the study area. Streams were selected as part of a larger collaborative research project designed to address the ecological function of headwater riparian areas (Johnson and Bilby, 2008). During the sampling season, the six headwater study streams had an average wetted width of 1.23 m (range among sites: 0.32–3.39 m) and an

average depth of 7 cm (range among sites: 2–32 cm). The study area was owned primarily by Weyerhaeuser Company, a private timber company, and the Oregon Department of Forestry (ODF) with a small portion managed by the Bureau of Land Management. Riparian management areas as defined by Oregon Department of Forestry Administrative Rules are no more than 20 feet (6 m) in width along such small streams. Because birds easily move > 20 m within their territories, for our purposes we extended the “riparian” categorization to areas within 50 m of streams.

The Tillamook Burn (three large, consecutive wildfires that occurred between 1933 and 1945) and subsequent timber harvest removed most of the original, old-growth conifer overstory by the 1950s, resulting in a vast acreage of young, even-aged forest. This history of disturbance also may have resulted in a reduction in recruitment of woody debris to streams and riparian areas (May and Gresswell, 2003). During the 1990s, ODF conducted light to moderate thinning to a basal area target ranging from 4.13 to 6.02 m²/ha (110–160 ft²/ac) in the northwest portion of the study area, adjacent to three of the six study streams (Johnson and Bilby, 2008).

The study area is in the Douglas-fir/oceanspray (*Psuedotsuga/Holodiscus*) plant association of the Western Hemlock (*Tsuga heterophylla*) forest zone (Franklin and Dyrness, 1988). The dominant overstory was 40–70 year old conifers, primarily Douglas-fir (*Psuedotsuga menziesii*), with western redcedar (*Thuja plicata*), western hemlock (*T. heterophylla*) and noble fir (*Abies procera*). As is typical for the region (Pabst and Spies, 1998), headwater riparian areas were characterized by mixed conifers and red alder (*Alnus rubra*). Pockets of tall shrubs, mainly vine maple (*Acer circinatum*), with small amounts of beaked hazel (*Corylus cornuta*) and Pacific dogwood (*Cornus nuttallii*) were scattered throughout the study area. Other species present in the understory included trailing blackberry (*Rubus ursinus*), salmonberry (*Rubus spectabilis*), oceanspray (*Holodiscus discolor*), stink currant (*Ribes bracteosum*), Oregon-grape (*Mahonia aquifolium*), huckleberry spp. (*Vaccinium* spp.), devil's club (*Oplopanax horridum*) and sword fern (*Polystichum munitum*).

2.2. Juvenile capture and radio attachment

We captured and tracked juvenile Swainson's thrushes (hereafter referred to as juveniles) in two consecutive postfledging seasons from July 1 to September 17, 2008 and June 15 to September 4, 2009. We 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 we sampled each riparian and upland location every 2 weeks using an array of 12 mist-nets (Jenkins, 2010). We located all riparian mist-nets within 50 m of either side of streams and positioned upland mist-net arrays in a similar pattern to riparian arrays, at least 50 m from the outermost riparian mist-net. Upland mist-net arrays were outside of riparian buffers designated in future harvest plans. All mist-net arrays were purposefully set in areas with camouflage of shrub cover. In addition to captures in riparian ($n = 4/31$ captures, total mistnet hours (Hrs) = 1591) and upland net grids ($n = 3/31$ captures, Hrs = 1621), we also captured juveniles opportunistically in dense vine maple within 100 m of riparian net grids ($n = 18/31$, Hrs = 523), along logging roads ($n = 1/31$, Hrs = 67) and from nests of radio-tagged females ($n = 5/31$). We distinguished juveniles from adults using skull pneumatization and/or juvenile plumage characteristics (Pyle, 2001) and fitted them with a USGS aluminum leg band.

In 2008 we attached 1.1 g transmitters (battery life 8 weeks, Advanced Telemetry Systems, Isanti MN) using a combination of eye-lash adhesive (Ardell Lash Grip Adhesive, copyrighted) and

epoxy. Glue-on transmitters generally fell off the juveniles before the end of the battery life, therefore, in 2009 we extended retention time by attaching transmitters (0.9 g; battery life 12 weeks; Blackburn Transmitters, Nacogdoches TX) with thin elastic using a modified leg harness method (Rappole and Tipton, 1991). Transmitters were fabricated with an additional hole drilled near the bottom of the transmitter to facilitate quick harness assembly. In order to ensure timely processing of juveniles, we fastened craft crimping beads (Michaels Stores, Inc.) onto each appropriately fitted harness near the transmitter rather than using time-consuming knots and glue.

We attached transmitters to nestlings when they were 10–11 d old. Nestlings were returned immediately to the nest, where they fledged within 1–2 d. 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 we did not observe any adverse effects of transmitters on daily activities of birds or when we had the opportunity to re-examine them upon recapture.

2.3. Data collection

We tracked juveniles on foot with a 3-element Yagi antenna and 3000 (2008) or TRX100 (2009) receivers (Wildlife Materials, Carbondale, Illinois). To reduce observer bias, we avoided assigning the same bird to an individual observer for more than two consecutive days. We assumed juveniles were independent when parent-offspring interactions were no longer observed; for example, they were no longer being fed by their parents or emitting begging calls, and neither parent was detected in the area. After attaching transmitters, we followed each juvenile for 30 min to assess dependency status (dependent or independent) (Rivera et al., 2000). Once independence was confirmed, we recorded UTM coordinates of the location of each juvenile every 1–2 days, alternating between morning and late afternoon or evening so each juvenile was monitored during different diurnal periods. On rare occasions ($N = 7/200$ locations), the time between consecutive locations of an individual spanned 4–5 days when signals were temporarily lost or when transmitters fell off but were reattached upon recapture. Topographical features and restricted access to locations useful for acquiring radio signals limited our ability to effectively detect radio signals to within a 6–9 km radius of previous locations. We checked each lost radio frequency daily for 5 days and then approximately every 3 days thereafter to verify loss of transmission.

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, we defined availability according to typical daily movement distances for juvenile Swainson's thrushes, documented from pilot data in the same study area. Based on this ecological definition, we considered distances < 300 m from each previous location to be available. We collected habitat data at each juvenile location as well as at a paired random location (termed 'random'), obtained from a random bearing and distance from the juvenile's previous location (30–300 m, uniform distribution). We omitted from analysis each juvenile's first location because it was not possible to pair it with a random location based from a previous location. Independent juveniles are likely to be physiologically capable of movement greater than 300 m over 1–2 day periods (maximum distance in our study = 714 m); thus, our results are conservative given the inherent spatial autocorrelation in vegetation composition and

structure of consecutive locations of juveniles (Schwartz et al., 2003).

We sampled habitat characteristics at every juvenile and random location using 2 subplots (5-m radius) per location. One subplot was centered at the juvenile location or random plot center with the other subplot centered 20 m away in a random direction. At each subplot we ocularly estimated percent cover for shrubs (0–1.5 m tall) and deciduous mid-story (from 1.5 to 15 m above ground in vertical strata) in 25% resolution categories (i.e., 0, <25, 26–50, 51–75, 76–100%). Within each subplot we recorded presence/absence of live deciduous and coniferous trees > 10 cm diameter at breast height (DBH) for 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. We estimated volume of coarse downed wood (hereafter coarse wood) along a 20-m linear transect between the two subplots at each location using protocols adapted from De Vries (1974) and Waddell (2002). Coarse wood was defined as dead tree boles and other large wood pieces either lying on the ground or elevated off the ground up to 45°, but no longer supported by roots. Coarse wood did not include live material and was measured if it was (1) >10 cm in diameter where it crossed the linear transect and (2) >1 m in length. Mean volume per hectare was calculated by totaling volume per hectare for each plot by first summing the volume per hectare of all individual pieces tallied on the plot. Volume per hectare of each piece was calculated using the formula:

$$\text{Volume} = \frac{\pi}{2L} \frac{(\pi/4)d_i^2 l_i}{l_i} f$$

where L is the total length (m) of the transect, d_i is the diameter (cm) and l_i is the length (m) of each piece and f is 10,000 m² ha⁻¹ (Waddell, 2002).

To estimate percent overstory cover, we used an ocular tube (PVC pipe fitted with cross hairs, 5 cm in length and diameter). We recorded the occurrence of deciduous, coniferous, and open canopy that intersected the cross hairs (Emlen, 1967) at equal intervals along a 20-m linear transect between the two subplots at each location. We took four ocular tube readings per location in 2008, and 11 per location in 2009.

We measured distance to nearest stream from the center of the subplot at which we located the juvenile and from the first subplot of the corresponding random location using the "NEAR" feature of Hawth's tools (Beyer, 2004) in ArcMap 9.3 (ESRI, 2009).

2.4. Statistical analysis

2.4.1. Vegetation characteristics

We compared vegetation characteristics (Table 1) at juvenile locations to those at paired, random locations. We averaged each vegetation variable across subplots for each location, except for overstory, which we summarized by using the overstory category (i.e., deciduous, coniferous, open) with the greatest frequency of occurrence for each location. We combined both years of data because vegetation remained relatively stable (i.e., no major windstorms, wildfire, or timber harvest). We excluded deciduous overstory cover because it was highly correlated with deciduous mid-story and shrub cover ($r > 0.60$), and because Swainson's thrushes nest close to the ground and generally forage low in the vertical strata (Mack and Yong, 2000). All variables were correlated with $r < 0.12$, except shrub and mid-story, which had a correlation coefficient of 0.40. We compared means of each habitat variable between juvenile and random locations by fitting a mixed effects model in SAS PROC MIXED (SAS, 2000), with individual bird as a random effect and paired plots as replicate samples of juvenile and random locations. In the event that juveniles moved greater

Table 1
Independent variables used to model habitat selection by juvenile Swainson's thrushes in headwater riparian areas, Northwestern Oregon, USA, 2008–2009.

| Variable | Abbrev. | Description |
|---------------------------|-----------|--|
| Proximity to stream | Stream | Represents a unit change of proximity to the stream, unit = 10 m |
| Deciduous mid-story cover | Mid-story | Percent cover of deciduous foliage 1.5–15-m above the ground, unit = 25% Categorical labels of 0, 1, 2, 3, 4 refer to 0%, 1–25%, 26–50%, 51–75%, and 76–100% respectively |
| Shrub cover | Shrub | Percent cover of deciduous shrubs < 1.5 m in height, unit = 25% Categorical labels of 0, 1, 2, 3, 4 refer to 0%, 1–25%, 26–50%, 51–75%, and 76–100% respectively |
| 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 cm (10 in.) DBH (non-harvestable) |
| Coniferous large trees | CL | Presence of stem(s) > 17.8 cm (7 in.) DBH (harvestable) |
| Coniferous small trees | CS | Presence and absence of stem(s) < 17.8 cm (7 in.) DBH (non-harvestable) |

distances as time elapsed, we used a mixed effect model in SAS PROC MIXED (SAS, 2000) with individual bird as the random effect to test if the distance between consecutive locations depended on the time elapsed between consecutive locations.

2.4.2. Juvenile habitat selection

Data were collected using a matched case-control design with matching occurring at the level of the bird. The number of relocations associated with each juvenile varied because we could not control when they died or migrated out of the study area, resulting in M:N matching. We used a stratified, M:N matching, conditional, logistic regression (Hosmer and Lemeshow, 1989) in SAS PROC PHREG (SAS, 2000) and SAS Macro mcstrat.sas (Vierkant et al., 1999; Vierkant and Kosanke, 2009) to test the relative odds (ROR) of occurrence at juvenile locations relative to random locations based on habitat variables (percent cover of shrubs, percent cover of deciduous mid-story, coarse wood, distance to stream, and presence/absence and type of trees (coniferous or deciduous)). We accounted for temporal and spatial autocorrelation among multiple locations for a juvenile by treating each juvenile as a sampling unit (Otis and White, 1999; Mitchell et al., 2010).

We developed two a priori models for juvenile habitat selection. Our primary hypothesis was that proximity to stream would influence habitat selection, and therefore this variable is included in both models. One model, based on ecological criteria postulated to be important to juveniles, included deciduous mid-story cover, shrub cover, coarse wood and proximity to stream (Stauffer and Best, 1980; Naiman et al., 1993; White et al., 2005). The second model focused on current forest management priorities, incorporating variables that are measured and manipulated in forest management (i.e., the presence of deciduous or coniferous trees separated into harvestable and non-harvestable size classes (see Table 1), as well as proximity to stream.

We had two pairs of siblings in our study. There is no evidence to suggest that one sibling may select habitat based upon the location of another sibling (Lang et al., 2002; White et al., 2005). We tested for spatial correlation between siblings by randomly removing 1 sibling from each family from analysis, 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, we retained all siblings as independent samples.

We report relative odds ratios (i.e., the ratio of the odds of occurrence under one condition relative to another). We report the exponentiated mean and confidence interval of the logarithmically transformed variable (i.e., coarse wood). We used alpha = 0.05 when reporting confidence intervals.

3. Results

3.1. Juvenile daily location and movements

We tracked 31 juveniles confirmed to be independent of their parents for 2 to 22 d (mean number of locations per juvenile 6.5 ± 0.7 (SE), range 2–16). We tracked juveniles, on average, for 7.9 ± 4.7 d (SD) (median date of all observations = August 19). We captured the majority (90%) of juveniles < 40 m from the stream. Overall, we documented one mortality of an independent juvenile. The remaining 30 juveniles survived to move outside of the study area.

The distance between consecutive locations of each juvenile averaged 133 ± 81 (SD) m (range 2–714 m, median 87 m) and there was little relationship of distance to elapsed time ($\beta = 0.6$ m/h CI = -0.1–1.2, $p = 0.1$). The mean amount of time between consecutive locations of individuals was 32.1 ± 1.7 (SE) h (range 4–128 h, median 24.0 ± 1.7 (SE) h). Greater than 60 h elapsed between consecutive juvenile locations in 11% of our sample (22/200 locations) due to the loss and subsequent reattachment of a transmitter onto a juvenile, and to limited personnel on 2 weekends (see Fig. 1).

3.2. Habitat selection

Overall, the ecological model (Table 2) was more useful in explaining juvenile habitat selection than the management model (Table 3). This model contained proximity to stream, deciduous mid-story cover, shrub cover and coarse wood volume. Juveniles selected locations that were closer to streams and had greater amounts of deciduous mid-story cover and coarse wood than random locations (Table 2). Juvenile locations were on average 16 m closer to streams (CI = 7–25 m, $p < 0.001$, Fig. 2A) than random locations. Independent of all other ecological variables, the odds of juvenile occurrence increased by 20% (CI = 10–31%, $p < 0.001$) for every 10 m closer to the stream and were five times greater (CI = 3.1–10.6, $p < 0.001$) in areas with more than 25% mid-story cover than in areas with less than 25% mid-story cover.

Juveniles tended to select locations with greater amounts of coarse wood (Fig. 2B). For every doubling of coarse wood volume, the odds of juvenile occurrence increased by 44% (CI = -1, 110%, $p = 0.054$). Juveniles selected locations with 23% greater coarse wood volume (CI = 1–51%, $p = 0.04$, Fig. 2B) than random locations.

We did not detect a difference in mean shrub cover between juvenile and random locations ($F_{1, 29} = 0.02$, $p = 0.88$) nor did we have any evidence that relative odds of occurrence were related to percent shrub cover, after accounting for distance to stream and volume of coarse wood ($\chi^2_4 = 0.60$, $p = 0.43$).

We were not able to discriminate juvenile from random locations using management-oriented variables (i.e., the presence of deciduous or coniferous trees separated into harvestable and non-harvestable size classes) (Table 3).

4. Discussion

Our finding that juvenile Swainson's thrushes selected habitat in close proximity to headwater streams indicates that headwater riparian areas are disproportionately important as habitat during the postfledging period, even despite fairly weak gradients in vegetation composition and structure between riparian areas and

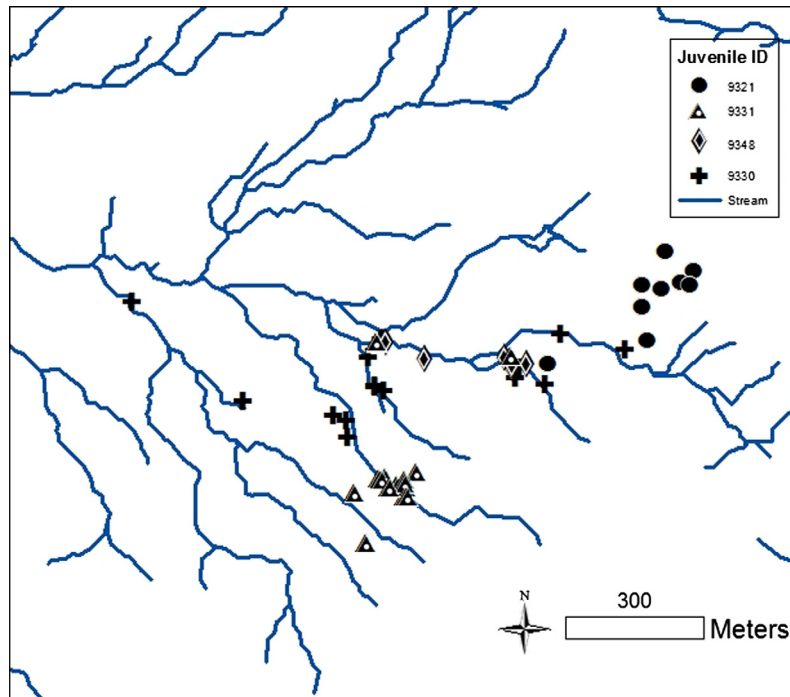


Fig. 1. Locations of juvenile Swainson's thrushes in the headwaters of the Trask River Watershed, Oregon, USA, 2008–2009. For clarity, only four individuals are shown (total $n = 31$). Each symbol denotes an individual. Locations are separated by 1–3 days. Juvenile 9321 remained 50–175 m from mapped streams, in habitat dominated by deciduous vegetation and near fully-vegetated linear depressions in topography that suggested this area may have intermittent water flow.

Table 2
The relative odds ratio (ROR) in an ecologically-based model (see text) of juvenile Swainson's thrushes occurrence in the Trask River Watershed, Oregon, USA, 2008–2009, given a one unit change for each independent variable. LCL and UCL denote lower and upper 95% confidence limits. Independent variables are defined in Table 1.

| | shbcat | middcat | Estimate | SE | Chi-square | P | DF | ROR | UCL | LCL |
|---------|-------------------|---------|----------|--------------------|------------|-------|-------------------|--------------------|-------|-------|
| stream | | | 0.18 | 0.04 | 18.14 | <.001 | 1 | 1.20 ^a | 1.10 | 1.31 |
| cw | | | 0.37 | 0.19 | 3.71 | 0.054 | 1 | 1.44 ^b | 0.99 | 2.10 |
| middcat | | 1 | 0.74 | 0.46 | 2.62 | 0.105 | 1 | 2.10 ^c | 0.86 | 5.13 |
| middcat | | 2 | 1.79 | 0.46 | 15.09 | <.001 | 1 | 6.01 ^c | 2.43 | 14.85 |
| middcat | | 3 | 2.13 | 0.52 | 17.04 | <.001 | 1 | 8.43 ^c | 3.06 | 23.21 |
| middcat | | 4 | 2.43 | 0.55 | 19.61 | <.001 | 1 | 11.38 ^c | 3.88 | 33.41 |
| middcat | cat(234): cat(01) | 1.75 | 1.87 | 31.54 ^g | <.001 | 1 | 5.75 ^d | 3.12 | 10.59 | |
| shbcat | 1 | | -0.11 | 1.39 | 0.01 | 0.935 | 1 | 0.89 ^e | 0.06 | 13.57 |
| shbcat | 2 | | 0.03 | 1.38 | 0.00 | 0.983 | 1 | 1.03 ^e | 0.07 | 15.43 |
| shbcat | 3 | | 0.43 | 1.38 | 0.10 | 0.758 | 1 | 1.53 ^e | 0.10 | 22.97 |
| shbcat | 4 | | 1.06 | 1.47 | 0.52 | 0.470 | 1 | 2.89 ^e | 0.16 | 51.54 |
| shbcat | cat(234): cat(01) | 3.37 | 4.34 | 0.60 ^g | 0.437 | 1 | 1.75 ^f | 0.42 | 7.24 | |

^a Change in odds of juvenile occurrence as approach 10 m closer to the stream.

^b Change in odds of juvenile occurrence with each doubling of coarse wood volume.

^c Change in odds of juvenile occurrence in listed mid-story cover category relative to no cover.

^d Change in odds of juvenile occurrence in greater than 25% mid-story cover relative to less than or equal to 25%.

^e Change in odds of juvenile occurrence in listed shrub cover category relative to no cover.

^f Change in odds of juvenile occurrence in greater than 25% shrub cover relative to less than or equal to 25%.

^g Wald chi-square.

Table 3
Relative odds ratios (ROR) in a management-based model (see text) of juvenile Swainson's thrushes occurrence in the Trask River Watershed, Oregon, USA, 2008–2009, given a one unit change for each independent variable. LCL and UCL denote lower and upper 95% confidence limits. Independent variables are defined in Table 1.

| | Estimate | SE | Chi-square | P | DF | ROR | LCL | UCL |
|--------|----------|------|------------|-------|----|------|------|------|
| Stream | 0.17 | 0.04 | 18.72 | <.001 | 1 | 1.18 | 1.10 | 1.28 |
| DL | 0.18 | 0.25 | 0.51 | 0.475 | 1 | 1.19 | 0.73 | 1.94 |
| DS | 0.23 | 0.29 | 0.66 | 0.416 | 1 | 1.26 | 0.72 | 2.21 |
| CL | -0.23 | 0.25 | 0.90 | 0.342 | 1 | 0.79 | 0.49 | 1.28 |
| CS | 0.08 | 0.33 | 0.06 | 0.810 | 1 | 1.08 | 0.57 | 2.06 |

adjacent upland (Pabst and Spies, 1998). While subtle, the pattern of increasing deciduous cover with proximity to headwater

streams (Pabst and Spies, 1998) may potentially explain the affinity of juveniles Swainson's thrushes for riparian habitats. The habitat selection patterns that we observed suggest that large amounts of deciduous mid-story cover near headwater streams may be a proximate and ultimate cue, respectively, for food and cover resources.

Juvenile Swainson's thrushes may be selecting riparian habitat due to high abundance of invertebrate prey within close proximity to stream (Nakano and Murakami, 2001; Iwata et al., 2003). Riparian areas along larger streams can support a greater diversity and abundance of terrestrial and aquatic invertebrates than adjacent upland areas (Stauffer and Best, 1980; Iwata et al., 2003, 2010; Christie and Reimchen, 2008). This pattern was also observed on

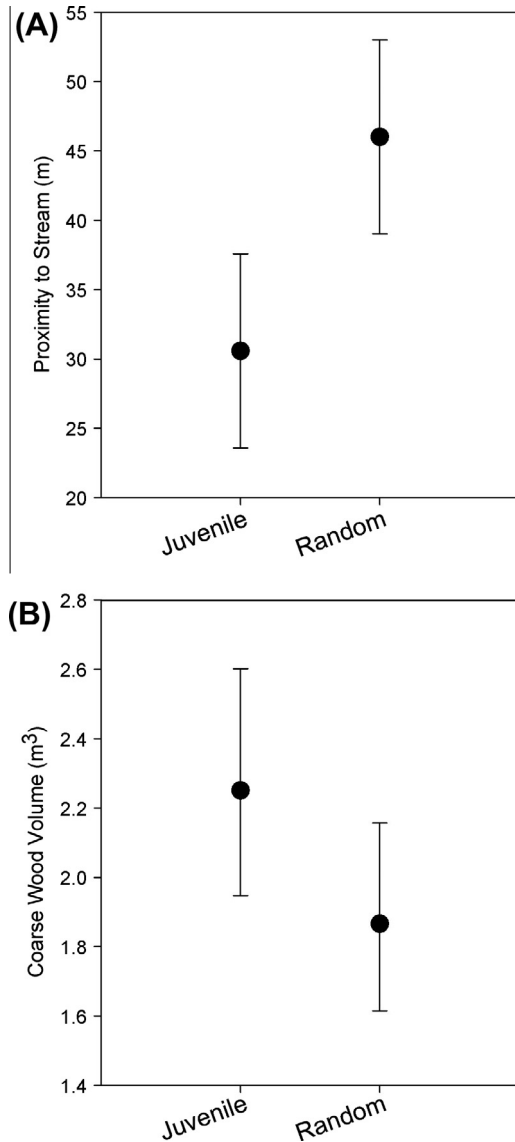


Fig. 2. Comparison of (A) proximity to stream and (B) coarse wood volume ($\bar{x} \pm 95\% \text{CI}$) between juvenile Swainson's thrush locations and paired random locations in the headwaters of the Trask River Watershed, Oregon, 2008–2009.

our study sites, where arthropod prey was more abundant in riparian areas than in adjacent uplands (Hagar et al., 2012). As a result, riparian areas may provide for greater densities of birds that eat insects, such as the Swainson's thrush.

Deciduous tree and shrub species support a diversity of mast (Hagar, 2007), so it is possible that juveniles selected large amounts of deciduous mid-story cover because of associated fruit resources. Indeed, 69% of Swainson's thrush diet samples in our study area contained fruit (Hagar et al., 2012). However, we believe it is more likely that juveniles selected habitat based on availability of arthropod prey and cover rather than fruit abundance for several reasons. First, fruiting shrub cover was similar between riparian and upland areas in our study sites (Jenkins, 2010) and fruiting vegetation was primarily located within 1.5 m from the ground, corresponding with vegetation structure that we described as shrub cover and we did not find to be important in juvenile habitat selection within the range of shrub cover represented on our study sites (Table 2). Second, principal components in the diet of Swainson's thrushes in our study area were arthropod taxa including beetles, true flies and ants (Hagar et al., 2012). Third, the mid-story

cover positively associated with habitat selection by juvenile Swainson's thrushes (Fig. 3) was dominated by vine maple and red alder, which do not bear fruit. Vine maple is known to have higher diversity of arthropod prey than some other common shrub and tree species in the Oregon Coast Range (Doolittle, 2000) such as sword fern, which is typically more abundant on hillslopes as distance to stream increases (Pabst and Spies, 1998). Due to varied tolerance of environmental factors as well as asynchronous emergence, populations of any one species of forest insect can fluctuate seasonally and among generations; therefore, diversity of arthropod prey may provide a stable prey resource throughout the post-fledging period (Jackson, 1979; Danks, 1994). Fourth, deciduous vegetation has been postulated to be important cover from predators for juvenile songbirds, including Swainson's thrushes (White et al., 2005; Mitchell et al., 2010; Whitaker and Warkentin, 2010). Juvenile survivorship is typically lower than that of adults (Blomberg and Shine, 2001; Sandercock et al., 2005; Gardali et al., 2009) and large amounts of deciduous cover near headwater streams may afford sufficient concealment to aid in juvenile survival, thereby having direct effects on population maintenance.

In addition to proximity to stream and deciduous mid-story cover, the amount of coarse wood was also associated with habitat selection by juveniles. Beetles and ants consume and nest in decaying wood (Siitonen, 2001) and, taken together, were the primary prey taken by Swainson's thrushes in our study area (Hagar et al., 2012). Therefore, abundance of arthropod prey may explain selection by juvenile Swainson's thrushes for areas with relatively high volumes of coarse wood.

Previous research suggests that riparian areas may provide movement corridors for passerines prospecting for future breeding habitat (Betts et al., 2008; Mitchell et al., 2010) or searching for food resources in unfamiliar terrain (Whitaker and Warkentin, 2010). However, we did not detect along-stream movement that would indicate juveniles were using headwater streams as movement corridors. While it is impossible to know if this process occurred on a finer temporal scale, daily movements were generally concentrated within 40 m of streams, but were not oriented directionally along streams.

Although the majority of juveniles were initially captured in headwater riparian areas, our findings are not an artifact of initial capture location. First, our study provides evidence that juvenile

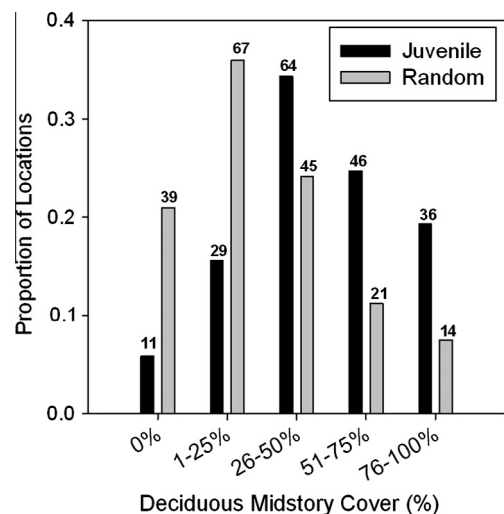


Fig. 3. The proportions of juvenile Swainson's thrush and random locations in deciduous mid-story cover categories (0%, 1–25%, 26–50%, 51–75%, 76–100%) in the headwaters of the Trask River Watershed, Oregon, 2008–2009. Number of locations in each category is noted above each bar.

Swainson's thrushes were capable of moving long distances (up to 714 m) around or through upland areas in short periods of time (<3 days), but still concentrated in headwater riparian areas with >25% mid-story cover. Second, out of the six juveniles captured in upland areas > 40 m from a stream, all subsequent locations for the majority of these juveniles ($n = 4$) were closer to streams.

Demonstrating habitat selection requires evidence of disproportionate use of particular sites in relation to those that are available (Johnson, 1980; Jones, 2001) and an indication that this use is adaptive (Jones and Robertson, 2001). Although it is challenging to test whether a choice is adaptive, it is important to note that 30 of 31 independent juveniles survived (96.8%) to the point of signal loss during our study. This survival rate is higher than previously reported for independent juvenile passerines (Anders et al., 1997; Kershner et al., 2004; but see Whittaker and Marzluff, 2009) suggesting that selection of headwater riparian habitats may be adaptive. If this is the case, headwater riparian habitats with adequate (>25%) deciduous mid-story cover may benefit population viability for Swainson's thrushes in the Oregon Coast Range.

Juveniles on our study sites selected similar habitat to that recorded for adult Swainson's thrushes. Previous work has demonstrated higher abundance of Swainson's thrushes along 2nd and 3rd order streams than in upland habitats in the Coast Range during the breeding period (McGarigal and McComb, 1992). Interestingly, the congruency between breeding and post-breeding habitat selection by Swainson's thrushes in our study contrasts with several other studies on migrant birds that reveal differential habitat use between these life stages (Anders et al., 1998; Vega Rivera et al., 1998; White et al., 2005). It is unlikely that juveniles in our study were pushed out of areas dominated by conspecific adults, thereby congregating in juvenile groups in lower quality habitat (Christian, 1970) because we captured conspecific adults in the same nets during the same time period as juveniles (Jenkins, 2010). Both juvenile and adult Swainson's thrushes used riparian areas prior to migration, which suggests abundant resource availability in headwater riparian areas.

4.1. Management implications

The high survival rate of juvenile Swainson's thrushes in our study area suggests that headwater riparian areas probably function as population sources for Swainson's thrushes. Juvenile survival is critical to overall population viability; therefore, protecting habitat for fledgling birds is an important conservation strategy (Faaborg et al., 2010). As in other regions throughout North America, riparian areas on small headwater streams in the Coast Range of Oregon generally receive less protection than larger streams, and in some cases are unprotected from anthropogenic disturbances (Blinn and Kilgore, 2001; Lee et al., 2004; Manitoba Conservation and Manitoba Water Stewardship, 2008). Reduced protection likely reflects a strong focus on the role of riparian vegetation in fish conservation (headwater streams in our study area 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 riparian areas for terrestrial wildlife. Our sample is representative of the population of Swainson's thrush in the Oregon Coast Range. Land management, enduring features, and environmental and anthropogenic factors are similar in our study area to that of the central and northern Oregon Coast Range; therefore, we expect the results of this study to transfer. Though correlative, our results provide evidence that, despite the absence of a strong gradient in vegetation composition across the riparian-upland interface, headwater riparian areas provide important post-fledging habitat for the Swainson's thrush. Thus, protection of headwater stream areas is likely to be beneficial for this species.

Since juveniles may be selecting headwater areas with large amounts of deciduous mid-story for resources such as insect prey or cover from predators, we hypothesize that conifers are not a primary factor in habitat selection by juvenile Swainson's thrushes. Our results suggest that maintaining at least 25% cover of deciduous, mid-story vegetation and more than 2.0 m³/ha of coarse wood (e.g., within 40 m of headwater streams may benefit this species. Because our study results did not establish cause and effect relationships, this combination of habitat features should be treated as a working hypothesis for future investigations, and bird response to implementation should be monitored in an adaptive management framework. Future studies on habitat selection could independently manipulate vegetation structure in riparian areas to separate the influences of proximity to stream alone versus vegetation structure.

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