

AN ABSTRACT OF THE THESIS OF

Lorelle Sherman for the degree of Master of Science in Forest Ecosystems & Society presented on June 3, 2019.

Title: Habitat Associations and Diet Composition of Western Purple Martins in Western Oregon.

Abstract approved: _____

Joan Hagar

The western purple martin (*Progne subis arboricola*) is a species of conservation concern throughout the Pacific Northwest. In western Oregon, the purple martin nests in three major ecosystem types: inland open-water, coastal, and upland forest. The availability of suitable breeding habitat is a major limiting factor for western purple martin populations and has likely decreased as a result of timber harvest reductions under the Northwest Forest Plan. As a cavity-nesting species that forages on airborne insects, purple martins require nesting structures in open habitat with high insect productivity. From anecdotal observations, it is assumed that dragonflies are a major prey item of purple martins. Prey limitations are unknown, as studies on the diet of western purple martin have not yet been done. An understanding of how availability of both suitable nesting cavities and prey resources limit populations is critical for developing a conservation strategy for this species.

The goal of my first study was to provide an assessment of the current status and distribution of the purple martin population nesting in upland forest in western Oregon. The objective of my habitat study was to determine the probability of occupation of purple martins at potentially suitable nesting sites in western Oregon, and to develop a prediction model of habitat suitability based on a comparison of habitat attributes at multiple spatial scales measured at used and unused sites. Each of

the variables that we used to characterize purple martin habitat were significantly different between used and unused nest sites except for snag DBH. We found strong statistical evidence that the odds of purple martins occupying a snag are affected by the area of early seral habitat within a stand. Despite the major limitation of lacking contiguous snag-level data for the study area, our prediction model of habitat suitability scores an AUC fit index of 0.8134. We intend this model to be useful in estimating the amount of suitable habitat available to support purple martin colonies both currently and under future timber harvest regimes.

The goal of my second study was to provide the foundational information on diet that will be necessary for further studies on nest site and prey limitations. The objective of my diet study was to illuminate diet composition and differences in diet composition between ecosystem types. I sampled prey composition at each ecosystem type to provide an index for prey availability. I utilized the noninvasive and innovative method of metabarcoding to produce a list of insect prey for purple martins in western Oregon. The abundance of dragonfly prey was higher at inland open-water sites compared with coastal and upland forest sites. Small insect biomass did not significantly differ between ecosystem types, though a trend of large insect hatches appeared only in open-water ecosystems.

My study fills important information gaps about suitable nesting habitat for the western purple martin and how nest site influences diet. I intend the predictive model of habitat suitability to be useful in estimating the amount of suitable habitat available to support purple martin colonies both currently and under future timber harvest regimes. I identified major limitations in statewide data availability for purple martin nesting habitat. It is recommended that further research aims to improve the continuity of snag data in western Oregon. Now that we understand the differences in diet among ecosystem types, we can target important prey taxa in sampling efforts to determine if and where prey limitations may exist. This study will guide wildlife managers as to where their efforts to protect or bolster existing populations will be most effective.

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Habitat Associations and Diet Composition of Western Purple Martins in Western
Oregon

by
Lorelle Sherman

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Lorelle Sherman, Author

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CONTRIBUTION OF AUTHORS

Dr. Joan Hagar acquired funding, assisted with study design, data analysis and interpretation of results, and provided editorial comments for all chapters. Dr. Taal Levi assisted with study design, data analysis, and interpretation of results for Chapter 3.

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CHAPTER 1. GENERAL INTRODUCTION

Lorelle Sherman

Avian aerial insectivores are a guild of birds that exclusively feed on insects in the air column. According to the North American Breeding Bird Survey (BBS) and the North American Bird Conservation Initiative (NABCI 2012), aerial insectivores in the United States and Canada are the most rapidly declining guild of birds in North America. Declines of many aerial insectivores are attributed to reduced insect populations, in addition to habitat loss and degradation (Nebel et al. 2010). Shockingly, Hallman et al. (2017) found a 76% reduction in airborne insect biomass in 27 years for protected natural areas in Germany. Global scale environmental changes, such as climate change, invasive species introductions, habitat loss and degradation, aquatic acidification, and pesticide use are likely contributing to insect population declines. The extent to which insect populations are declining globally is unknown, but ~40% of the insect species studied are listed as threatened by the IUCN (IUCN 2013). More insect species are declining than increasing on a global scale (Dirzo et al. 2014). The global decline of insect populations poses a serious threat to all aerial insectivore species.

The western sub-species of the purple martin is designated as a “critical” sensitive species in the state of Oregon because of concern that the population may decline to the point of qualifying for threatened or endangered status if conservation actions are not taken (ODFW 2017). The purple martin is also a candidate for Threatened status under the B.C. Wildlife Act in British Columbia and is a Candidate Species for listing as Threatened or Endangered in Washington State. For conservation purposes, it is critically important to recognize the distinction between the relatively abundant eastern purple martin subspecies (*Progne subis subis*), with ~10-12 million birds in eastern North America, and the at-risk western purple martin subspecies (*Progne subis arboricola*), with an estimated <5,000 pairs distributed between southwestern BC and southern CA (Western Purple Martin Working Group 2018). BBS data suggests the species as a whole is stable, but the Pacific Coast population is imperilled (Wiggins 2005) and anecdotal observations cite a population decline in the Pacific Northwest (Rockwell 2018). The eastern subspecies has become dependent on human-provided habitat, and virtually all individuals nest in artificial

housing (Tarof and Brown 2013). In contrast, the western subspecies still nests in natural cavities in the wild (Bettinger 2003, Horvath 1999). Compared to the well-studied eastern subspecies, we know very little about the life history and biology of the western subspecies. The geographic, genetic, and behavioral disparities between the subspecies warrant additional research on the western subspecies.

Availability of suitable breeding habitat is a major limiting factor for western purple martin populations. As aerial insectivores, purple martins require open habitat with high insect productivity for foraging. Suitable habitat includes open, post-disturbance forest, such as burns or clear-cuts, where legacy trees and snags provide nesting substrate (Tarof and Brown 2013). Declines in populations have been attributed to nest site competition and the reduction of natural nesting habitat from human activities (e.g., removal of snags during timber harvest) (Rockwell 2018). Competition for nest sites from invasive species such as the English sparrow (*Passer domesticus*) and European starling (*Sturnus vulgaris*) occurs near human habitations. This threat is likely reduced for birds that nest in forest lands that are remote from agricultural and urban development (Horvath 1999). Furthermore, availability of suitable early seral habitat on federal forest lands in the Coast Range and Cascade ecoregions of western Oregon has been reduced as a result of forest management practices that promote early establishment and prolonged dominance of dense conifer forest, and curtailment of timber harvesting under the Northwest Forest Plan (Phalan et al. 2019, Swanson et al. 2011, Kennedy and Spies 2004).

The snag-nesting population of purple martins in western Oregon may represent an opportunity to maintain self-sustaining populations in the Pacific Northwest. However, there is a lack of data on the processes driving the population dynamics (survival and reproduction) or western purple martin colonies. Both nest site availability and prey availability may limit colonies. From anecdotal observations, it is assumed that purple martins are limited by nest site availability in all habitat types. In sites with existing colonies, new artificial housing units installed in suitable habitat are quickly occupied by purple martins (Vesely unpublished data; Metzler unpublished data). Horvath (1999) surveyed purple martins throughout

Oregon and concluded that the breeding range had contracted based on absence from previously occupied sites. There is no information on how prey availability affects martin colonies in different habitat types. If a colony is subject to prey and nest site limitations, it may function as a population sink, in which mortality outweighs reproduction (Pulliam 1988). Colonies only subject to nest site limitations may function as source populations, especially if additional artificial housing units are installed. A source population is one where reproduction outweighs mortality and that may be supplying a surplus of individuals that disperse to less productive habitats (Pulliam 1988). Understanding what limits colonies in different habitat types will help guide management decisions about where to focus efforts in efficiently bolstering populations.

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CHAPTER 2. HABITAT SUITABILITY MODELING FOR THE WESTERN
PURPLE MARTIN IN WESTERN OREGON

Lorelle Sherman, Dr. Joan Hagar

ABSTRACT

The Western Purple Martin (*Progne subis arboricola*) is a species of conservation concern throughout the Pacific Northwest. Unlike the eastern subspecies that is almost entirely dependent on artificial housing, many pairs of the western subspecies still nest in natural cavities in the wild. Although large colonies nest in artificial housing located at lowland, wetland sites, smaller colonies nesting in natural snags are scattered throughout upland forest habitat in western Oregon. The snag-nesting population of purple martins in western Oregon may represent an opportunity to maintain self-sustaining populations in the Pacific Northwest. Our goal was to reliably predict where suitable habitat exists for snag-nesting purple martins using measured forest stand and landscape characteristics. Our specific objectives were to determine the probability of occupancy of purple martins at potentially suitable nesting sites in western Oregon, and to develop a prediction model of habitat suitability based on a comparison of habitat attributes at multiple spatial scales measured at used and unused sites. Each of the variables that we used to characterize purple martin habitat were significantly different between used and unused nest sites except for snag DBH. We found strong statistical evidence that the odds of purple martins occupying a snag are affected by the area of early seral habitat within a 0.48km radius circular plot of the snag. Despite the major limitation of lacking contiguous snag distribution data for the study area, our prediction model of habitat suitability scores an AUC fit index of 0.8134 and an optimism score of 0.01. We intend this model to be useful in estimating the amount of suitable habitat available to support purple martin colonies both currently and under future timber harvest regimes.

INTRODUCTION

The western sub-species of the purple martin is designated as a “critical” sensitive species in the state of Oregon because of concern that the population may decline to the point of qualifying for threatened or endangered status if conservation actions are not taken (ODFW 2017). The purple martin is also a candidate for Threatened status under the B.C. Wildlife Act in British Columbia and is a Candidate Species for listing as Threatened or Endangered in Washington State. For conservation purposes, it is critically important to recognize the distinction between the relatively abundant eastern purple martin subspecies (*Progne subis subis*), with ~10-12 million birds in eastern North America, and the at-risk western purple martin subspecies (*Progne subis arboricola*), with an estimated <5,000 pairs distributed between southwestern BC and southern CA (Western Purple Martin Working Group 2018). BBS data suggests the species as a whole is stable, but the Pacific Coast population is imperiled (Wiggins 2005) and anecdotal observations cite a population decline in the Pacific Northwest (Rockwell 2018). The eastern subspecies has become dependent on human-provided habitat, and virtually all individuals nest in artificial housing (Tarof and Brown 2013). In contrast, the western subspecies still nests in natural cavities in the wild (Bettinger 2003, Horvath 1999). Compared to the well-studied eastern subspecies, we know very little about the life history and biology of the western subspecies. The geographic, genetic, and behavioral disparities between the subspecies warrant additional research on the western subspecies.

Availability of suitable breeding habitat is believed to be a major limiting factor for western purple martin populations. As aerial insectivores, purple martins require open habitat with high insect productivity for foraging. Suitable habitat includes open, post-disturbance forest, such as burns or clear-cuts, where legacy trees and snags provide nesting substrate (Tarof and Brown 2013). Declines in populations have been attributed to nest site competition and the reduction of natural nesting habitat from human activities (e.g., removal of snags during timber harvest) (Rockwell 2018). Competition for nest sites from invasive species such as the English sparrow (*Passer domesticus*) and European starling (*Sturnus vulgaris*) occurs near

human habitations. This threat is likely reduced for birds that nest in forest lands that are remote from agricultural and urban development (Horvath 1999). Furthermore, availability of suitable early seral habitat on federal forest lands in the Coast Range and Cascades ecoregions of western Oregon has been reduced as a result of forest management practices that promote early establishment and prolonged dominance of dense conifer forest, and curtailment of timber harvesting under the Northwest Forest Plan (Phalan et al. 2019, Swanson et al. 2011, Kennedy and Spies 2004). The severity of forest fire continues to increase on federal lands, potentially creating new early seral habitat. However, federal land managers routinely suppress fire (Phalan et al. 2019).

The snag-nesting population of purple martins in western Oregon may represent an opportunity to maintain self-sustaining populations in the Pacific Northwest. However, there is a lack of population survey data to provide a reliable estimate of current population size and distribution of purple martins breeding in natural cavities. Horvath (1999) surveyed purple martins throughout Oregon and concluded that the breeding range had contracted based on absence from previously occupied sites. In that survey, 5% of 784 pairs of martins were found nesting in snags with the rest nesting in artificial nesting substrate; snags used were typically far from open water, in remote forested uplands that lacked European starlings. Bettinger (2003) surveyed young stands in western Oregon for snag-nesting purple martins in 2002. Six counties, including Douglas, Coos, and Curry had occupied sites. The majority of clear-cut sites occupied by purple martins were less than 6 years old. The extent of use of natural cavities by purple martins had not been quantified since Bettinger's survey in 2002.

I conducted an expanded survey of snag-nesting purple martins on BLM and USFS lands similar to surveys conducted in 2002 (Bettinger 2003). My goal was to reliably predict where suitable purple martin habitat exists using measured forest stand and landscape characteristics. My specific objectives were to determine the probability of occupancy by purple martins at potentially suitable nesting sites in

upland forest (i.e., early seral with snags) in western Oregon, and to develop a model of habitat suitability based on a comparison of habitat attributes at multiple spatial scales measured at used and unused sites. I hypothesized that snag-level characteristics (i.e. diameter at breast height and decay class) and the amount of early seral forest surrounding the nest snag are most important in determining the probability of snag occupancy. I intend this model to be useful in estimating the amount of suitable habitat available to support purple martin colonies both currently and under future timber harvest regimes.

METHODS

Study Area

The study area is located within the Willamette Valley of Oregon. The climate of the Willamette Valley is similar to Mediterranean climates with warm, dry summers and cool, wet winters (Taylor and Bartlett 1993). The coast range experiences heavy precipitation with generally mild temperatures year-round (Taylor and Bartlett 1993). The western foothills of the Cascades experience high levels of precipitation and snowfall in the winter, both increasing with elevation increase (Taylor and Bartlett 1993).

Study sites were located in western Oregon west of the Cascade Mountain Range and below 4,000 ft in elevation (Bettinger 2003). This included the western foothills of the Cascade Mountain Range, the Willamette Valley, and the Coast Range (Fig. 2.1). In 2016, the areas I surveyed for snag-nesting western purple martins included Douglas County, Coos County, and Curry County. In 2017, I added survey sites in Lane, Benton, Linn, Polk, Marion, Columbia, and Washington Counties. I also re-surveyed sites determined to be active in 2016 to verify occupancy status. The major stand-replacing disturbance events in the study area are timber management and fire that occurred within 15 years of the survey. The vegetation of purple martin survey sites was dominated by Douglas-fir (*Pseudotsuga menziesii*), with varying components of bigleaf maple (*Acer macrophyllum*), Oregon white oak (*Quercus garryana*), red alder (*Alnus rubra*), and Pacific madrone (*Arbutus menziesii*).

Sampling Design

The BLM produced a list of forest stands on public lands in Oregon west of the Cascade Mountains that had been disturbed (e.g. burned or clear-cut) within the last 10 years, had failed to regenerate to expected stocking densities, or had recent incidental detection of purple martins. I surveyed 74 stands randomly selected from this list of potential stands on BLM land in 2016. Stands with no potential nest snags were dropped after the first survey and replaced by stands randomly selected from the list of potential stands. I found that many of the identified stands on BLM land in 2016 were no longer in early seral condition, so I narrowed the criteria, resulting in a smaller pool of potential survey stands on public lands in 2017.

While crossing private timberlands to access BLM sites, I encountered numerous sites that met the criteria for stand age and had potentially suitable nest snags. I sought permission to survey private land where these conditions were opportunistically encountered, and where incidental purple martin sightings were posted to the online database, eBird (Sullivan et al. 2009). Therefore, a large portion of our survey sites in 2017 were not randomly selected, but they are representative of purple martin habitat in western Oregon, given the patchy distribution and special habitat requirements of this species. I surveyed a total of 97 unique sites on public land over both years of the study; 7 BLM sites were surveyed in both years (for 104 total surveys on public land sites, Table 2.1). I surveyed a total of 77 upland forest sites (including gourd racks and nest boxes) under private ownership over both years of the project (Table 2.1). Six sites on private land were surveyed in both years.

At each survey site, potentially suitable snags were identified as having cavities large enough to fit a purple martin. A total of 160 snags were surveyed: 36 remnant snags within suitable early seral habitat on public lands and 124 snags on privately owned timberland. Snag cavities were surveyed for occupancy by nesting purple martins. I followed a standardized protocol to determine occupancy status (Cousens and Airola 2006; Table 2.1). At active and occupied sites, I tallied birds observed at each visit by age and gender: After Second Year Males (ASYM), Second

Year Males (SYM), After Second Year Females (ASYF), Second Year Females (SYF), Hatch Year (HY) or Unknown (UNKN).

Occupancy Surveys

Throughout the nest establishment and fledgling production stages, from May 15 through 15 August of 2016 and 2017, each site was surveyed from one to five times (Fig. 2.2). The first survey was conducted during the nest establishment period between early May and mid-June; I did not make more than one visit to sites that did not have any snags. At all sites with at least one snag present, the first survey was conducted for at least 20 minutes between 1 hour before and two hours after sunrise. Purple martins are territorial and respond vocally to other martins entering their territory, so at sites where no purple martins were detected on the first visit, I played recordings of purple martin dawnsong at subsequent visits. Call playback of conspecifics increases detection probability in many songbird species (Grinde et al. 2018). The combination of at least three visits at dawn and call playback increased detection probability to 83.5%. Once an active cavity was confirmed (Table 2.1), sites could be surveyed later in the day because high levels of feeding activity were continuous throughout the day.

I marked the locations of all accessible snags with appropriately sized cavities at survey sites that met forest age criteria (burned or clear-cut within previous 10 years) with GPS. For each snag, regardless of use by purple martins, I measured and recorded height, diameter-at-breast-height (DBH), cavity height, decay class, species, cavity origin, and number of cavities. Some snags could not be measured because of lack of accessibility due to cliffs, yellow jackets nests, or impenetrable poison oak. In total, I measured habitat characteristics at 201 snags. However, because we were unable to measure some variables for 41 snags, I had a total of 160 snags available to develop the habitat model. Of these, 36 snags were on public lands and 124 snags were on privately owned timberland.

I also estimated the distance from each snag to the nearest edge of closed canopy forest using Google Earth and validated the estimates using Gradient Nearest

Neighbor (GNN) tree size classes 5 and 6 to define "mature" forest (Ohmann and Gregory 2002). For the purposes of this study, early seral forest was defined as conifer or broadleaf forest having an average quadratic mean diameter (QMD) of <10cm (Betts et al. 2010). I classified pasture and other non-forest vegetation types separately from early seral. I used a 120 acre (95 ha) circular plot around each snag to represent stand-level characteristics, based on the maximum allowable clearcut size under the Oregon Forest Practices Act. I used a 1-km radius circular plot (314 ha (776 acre)) centered on each snag to represent landscape level characteristics within foraging range for adult purple martins. I based this plot size on conversations with Dr. Jason Fischer, Conservation Program Manager for Disney's Animals, Science and Environment, who found that the majority (>95%) of feeding flights of eastern purple martins were less than 1 km (unpublished data). For each site, I averaged the early seral area for all overlapping plots centered on snags within the site. The GNN model predicts forest structural characteristics at a 30-meter pixel resolution by utilizing Forest Inventory Analysis (FIA) plots, mapped environmental data, and Landsat Thematic Mapper Imagery (Betts et al. 2010). At larger spatial scales, GNN predictions more closely match observed values for vegetation characteristics, including QMD (Ohmann and Gregory 2002). The GNN variables I used all have higher accuracy (correlation coefficients and R-square values) in conifer forests than hardwood forests (Bell et al. 2017). The GNN data from 2016 is the most recent, contiguous data available for all of western Oregon (Ohmann and Gregory 2002).

Statistical Analysis

Inference Model

I developed a set of candidate inference models to describe how the probability of occupancy of purple martins is a function of the habitat variable data I collected. Inferential statistical analysis informs the optimal coefficients of habitat variables needed to maximize the likelihood of snag- or site-level occupancy by nesting purple martin. This style of model output is sought after by land managers with objectives to improve or create wildlife habitat.

I used candidate inference models to characterize purple martin habitat using variables representing multiple spatial scales: snag level (DBH, cavity height, decay class), stand level (area of early seral within 95 ha, distance to closed-canopy forest), and landscape level (area of early seral within 314 ha plot centered on snags, elevation). I standardized all explanatory variables to account for their different scales of measurement using the training data mean and standard deviation. To maximize prediction model parsimony, I checked the usefulness of all predictor variables by conducting univariate tests to compare the medians of variables between used and unused groups. We used a two-sided Mann-Whitney Test for these comparisons because variables did not meet the assumptions of normal distribution. All variables except snag DBH showed significant differences between used and unused groups, so I excluded the DBH variable from the set of candidate models. I used smoothed histograms (Peck and Devore 2011) to provide a visualization of the differences between groups that could be provided by a single measure of central tendency, such as the median. Smoothed histograms, or probability density functions, more accurately reflect distribution of the underlying variable because they reduce distortion from randomness that can be accentuated in box histograms, especially with small datasets. All statistical analyses were done in RStudio Version 1.1.383 (2009-2017).

To quantify the relationship between area of early seral habitat and snag characteristics and probability of occupancy of a snag for nesting by purple martins, I used a generalized linear mixed effects model using a binomial distribution and a logit link. My response variable was the binary occupancy status (0 for non-occupancy and 1 for occupancy). I used a base model that tested the explanatory power of area of early seral habitat at two nested spatial scales (i.e. stand-scale nested within landscape-scale). Due to my hypothesis of the importance of snag characteristics in determining snag occupancy, I created candidate models by adding variables starting from the snag-level and working up to the landscape-level spatial scale (Table 2.3). The snag scale sites were nested within the stand scale sites and the stand scale sites were nested within the landscape scale sites. Every candidate model

contained a random effect representing variation among stands and a random effect representing variation among landscapes. I used the ANOVA function in RStudio to calculate AIC and BIC values and chose the best candidate model based on the lowest AIC and BIC values.

The following statistical model describes the Bernoulli generalized linear mixed effects model with a logit link fit to the data:

$$Y_t \sim \text{Bernoulli}(m_t, p_t)$$

$$\text{Mean} = \mu_t = mp_t$$

$$\text{Var}(Y_t) = (mp_t(1-p_t))$$

$$\text{Log}(p_t/1-p_t) = \beta_0 + \beta_1 \text{esland}_t + \beta_2 \text{esstand}_t + (v_i)_t + (b_j)_t$$

where:

Y_t is the observed occupancy status of the t^{th} snag where $Y = 0$ if unoccupied by purple martins, or $Y = 1$ if occupied by purple martins, $t = 1, 2, \dots, 155$

p_t is the logit link, the unobserved true probability of occupancy by purple martins

m_t is the observed number of probabilities of occupancy

β_0 is the log odds of a snag being occupied by a purple martin when there is no early seral forest

β_1 is the change in log odds of occupancy per 1 acre increase in early seral forest

β_2 is the change in log odds of occupancy per 1 acre increase in early seral forest

esland_t is the observed acreage of early seral habitat within 314 ha for the t^{th} snag

esstand_t is the observed acreage of early seral habitat within 95 ha for the t^{th} snag

- (v_i)_t is the random effect term for stand for the t^{th} snag, where v_i and v_i' are independent, $i = 1, 2, \dots, 75$
- (b_j)_t is the random effect term for landscape for the t^{th} snag where b_i and b_i' are independent, $j = 1, 2, \dots, 60$

I checked the model graphically for unusual patterns in the residuals of the fitted model and explanatory variable (Figs. 2.3 and 2.4). In these residual plots, uniformity in the y direction is expected. However, some deviation is to be expected by chance, especially with a small sample size. Due to the small sample size of this study, the deviations shown are not alarming. I checked the fitted model for lack of uniformity (not significant) and zero inflation (not significant) using the DHARMA package (Hartig 2018).

Prediction Model

I developed a prediction model for the probability of occupancy of purple martins based on the habitat variable data I collected in the field. Prediction modeling uses an existing dataset to make predictions about future observations. When utilizing prediction models, one seeks to maximize the accuracy of predictions by including variables deemed important by the literature or expert knowledge in explaining the observations or mechanisms at hand. In this study, model predictions are sought after by land managers with the objective of identifying what sites purple martins may be nesting in across a landscape. Depending on the calculated accuracy of the predictions, predictive modeling can greatly reduce effort in identifying suitable habitat for species.

I used the binary response variable occupancy status at the snag-scale (0 for non-occupancy and 1 for occupancy) in a hierarchical modelling process used to predict the probability of occupancy based on habitat variables at three spatial scales: snag level (cavity height, decay class), stand level (area of early seral within 95 ha, distance to closed-canopy forest), and landscape level (area of early seral within 314 ha plot centered on snags, elevation). I tested all variables of interest for correlation in

a pairwise matrix before including them in the model. No high correlation (>0.6) existed between any two variables, so all variables were included. We developed a set of models for each relevant spatial scale because of uncertainty about which spatial scale is most important in determining probability of occupancy. The weighted binomial generalized linear mixed model set modeled the probability of occupancy (π_i) as

$$\text{Snag-scale} \quad \ln\left(\frac{\pi_i}{1-\pi_i}\right) = \beta_0 + \beta_1\chi_{i_1}$$

$$\text{Stand-scale} \quad \ln\left(\frac{\pi_i}{1-\pi_i}\right) = \beta_0 + \beta_2\chi_{i_2} + \beta_3\chi_{i_3}$$

$$\text{Landscape-scale} \quad \ln\left(\frac{\pi_i}{1-\pi_i}\right) = \beta_0 + \beta_4\chi_{i_4} + \beta_5\chi_{i_5}$$

where values χ_{i_1} through χ_{i_5} were measured habitat characteristics and β_0 through β_5 were unknown coefficients.

I standardized all explanatory variables to account for different scales of measurement using the training data mean and standard deviation. Citing numerous concerns with stepwise model selection, Burnham et al. (2009) proposed including all models that fall within an *a priori* decided Delta AICc range in a weighted model set. Each model in the model set was tested for fit using the AICc criteria outlined in Burnham et al. (2009). I calculated AICc weights and model averaged predictions with the training dataset using the MuMIn package (Barton 2017). The model-averaged predictions are made on the scale of the model and then inverse-linked after averaging. I calculated the AUC fit index for the model averages using the pROC package (Robin et al. 2011). I internally validated the model by calculating the optimism of the fit statistic. To do this, I resampled and bootstrapped clustered data with 100 replications, then subtracted the training data AUC from the resampled data AUC.

ArcGIS Mapping

I obtained the raster layers for the explanatory variables area of early seral within 95 ha and area of early seral within 314 ha plot centered on snags by creating a mask of the GNN quadratic mean diameter raster layer. Pixels with QMD values $\geq 10\text{cm}$ were excluded as non-early seral forest. I further masked this single early seral factor raster layer to include the following Ecological Systems Landcover Classes (Grossmann et al. 2008, ESLF) in addition to early seral: Cultivated Cropland, North Pacific Herbaceous Bald and Bluff, Northern and Central California Dry-Mesic Chaparral, Open Water (Brackish/Salt), Open Water (Fresh), Pasture/Hay, Willamette Valley Upland Prairie and Savanna, Willamette Valley Wet Prairie. These landcover classes were included due to their ability to serve as suitable foraging and nesting habitat. All other landcover classes were not included in the model. Elevation data was obtained using an Oregon digital elevation model (DEM) raster layer and masked to include only the range of values represented in the training dataset. The raster layer for the explanatory variable, distance to closed-canopy forest, was created by calculating the Euclidean distance of each pixel to forest categorized as size class 5 or 6 according to the GNN data.

I standardized each of the explanatory variables using the training dataset mean and standard deviation in the ESRI ArcGIS raster calculator. I then input the model-averaged and weighted coefficients of the model set into the raster calculator. The output of this raster calculation was converted from log odds of occupancy to probability of occupancy.

RESULTS

Occupancy Surveys

I found snag-nesting purple martins widely distributed throughout the study area in western Oregon (Fig. 2.1). Out of a total of 96 sites surveyed on public lands in both years (104 unique sites plus 7 BLM site surveyed both years), I found 17 nests at 16 occupied sites (occupancy rate = 15%). The occupancy rate on BLM land alone was 14% (11 sites used for nesting out of 78 sites surveyed). I found 58% of the sites

we surveyed on private lands to have at least one pair of nesting martins (45 sites used for nesting out of 78 site surveys), but this is not a reliable estimate of occupancy rates on private lands across western Oregon because survey sites were non-randomly selected based on having a component of early seral forest.

Inference Model

Each of the variables that I used to characterize purple martin habitat had strong evidence for a difference in means between used and unused nest sites except for snag DBH (Fig. 2.5G). The median cavity height was lower for unused snags (Fig. 2.5A). The median elevation at used snags was lower than at unused snags (Fig. 2.5F). The snag decay class, median distance to closed canopy, and median area of early seral at the stand (95 ha) and landscape (314 ha) spatial scales were all greater at used than unused nest sites (Figs. 2.5B-E).

The best candidate model based on the lowest AIC and BIC values was the model (Model 1) containing the variables: area of early seral within 95 ha plot and surrounding 314 ha landscape (Table 2.3).

I found strong statistical evidence that the odds of purple martins occupying a snag are affected by the area of early seral habitat within a stand ($F_{1,70} = 25.29$, $p < 0.0001$). The odds of a purple martin occupying a snag increases multiplicatively by 1.05-fold (95% CI 1.02 to 1.08-fold) for every 1 acre increase in early seral forest habitat in a stand. The estimated positive relationship of early seral forest acreage and the probability of occupancy is shown in Figure 2.6.

Prediction Model

I tested each model in the model set for fit using the AICc criteria outlined in Burnham et al. (2009, Table 2.4). Due to the high Delta AICc value and lack of contiguous data at the snag spatial scale in Oregon, the snag scale model was

removed from the model set for further analyses. The landscape scale model was included, but had minimal influence with a weight of 0.01.

The AUC fit index for the model set was 0.813. The optimism (bias) score for validation of fit was 0.001 (Fig. 2.7). This is a “B” on the traditional academic point system, a rough guide for interpreting AUC suggested by Thomas G. Tape at the University of Nebraska Medical Center (<http://gim.unmc.edu/dxtests/Default.htm>).

I developed a raster layer visualizing probability of occupancy values for each 30m pixel using a stretched color scale (Figs. 2.8 and 2.9). Values were only assigned to pixels that matched our early seral definition or pixels classified to one of the ESLF codes we selected.

Five out of 22 snag sites with a predicted probability of occupancy greater than 0.75 were not occupied by purple martins. Out of 104 snag sites with a predicted probability of occupancy less than 0.25, 11 were occupied by purple martins. There were more snags with high predicted probability of occupancy values not being used by purple martins than snags with low probability of occupancy values being used by purple martins (Fig. 2.10).

DISCUSSION

I found that breeding purple martins were widely distributed throughout western Oregon, but our results confirm that there is a positive association between probability of occupancy and amount of early seral at both spatial scales. The strong positive association of purple martin occupancy with recently disturbed forests likely explains why purple martins were relatively rare on public forest lands managed under the Northwest Forest Plan. Reductions in timber harvest over the last two decades have decreased the availability of early post-disturbance forest on public lands (Kennedy and Spies 20014, Swanson et al. 2011). I observed that forest regrowth at many sites on BLM land that had been previously clearcut apparently rendered the sites no longer suitable for nesting, even when regeneration was poor,

and despite of the presence of large snags. Instead, purple martins were more common on private lands where continuous cycles of regeneration harvesting maintain sufficiently large areas of early seral habitat.

The significantly larger distance to closed canopy forest for nest snags compared to unused snags, combined with the positive association with early seral condition, highlights the importance of snags in the open as nesting substrates for this species. As the largest swallow in North America, purple martins are morphologically and behaviorally suited to flight in open spaces (Tarof and Brown 2013). They may also prefer to nest away from forest edges to decrease risk of predation from forest-dwelling predators, such as squirrels and owls. The data suggest that snags < 100 m from closed-canopy forest were infrequently used for nesting (Fig. 2.5C).

The lower height of used cavities compared to unused cavities (Fig. 2.5A) was not expected because lower cavities are likely to be more vulnerable to predation. This result is likely explained by variables we did not measure, such as cavity size, cavity shape, or decay properties. I suspect that snag diameter explains the generally lower height of occupied cavities compared with unoccupied cavities. Anecdotally, snags that are intentionally left during timber operations in modern times are noticeably smaller in diameter than those that were historically left. Higher cavities on residual snags with small diameters (30-60cm diameter at breast height) may not have the internal volume or structure to accommodate 4-6 purple martin nestlings. Decay properties may also explain this result. All occupied cavities in snags of decay class 4 were under 25.5 meters, while cavities in snags of decay class 2 and 3 were measured at 48 and 50 meters, respectively.

This first version of a prediction model for suitable purple martin habitat throughout western Oregon is a valuable tool for identifying sites for future occupancy surveys. Users can decide on a suitable threshold of probability of occupancy and extract all locations above this threshold for on the ground occupancy and reproduction surveys. Locations with moderate probability of occupancy values

can be further examined for habitat enhancement opportunities, such as the creation of snags.

A major limitation of the model is the lack of landscape-level data on snag distribution. With no contiguous snag data available for western Oregon, sites identified as having high probability of occupancy values based on area of early seral must be visited to check for the presence of cavities in leave trees or snags. The “good” AUC value infers that there will be some false positives in the model output. In this situation, the model would identify a site lacking available nest snags as having a high probability of occupancy by nesting martins due to favorable measures of other habitat variables. This may account for the disparity between occupancy status from occupancy surveys and probability of occupancy scores in this study. However, four snags occupied by nesting purple martins in the training data were in areas with very little early seral habitat at the stand-scale. These anomalous sites may also contribute to the lower AUC value. Two of the four snags also had very little early seral at the landscape-scale. Of these two, one snag sits within 4km of large tracts of agricultural land, which may supplement feeding opportunities. The second snag is likely a historic nesting spot for purple martins, where nesting pairs continue to return even as the surrounding understory matures. Recent wildfires sweeping through this area may renew early seral habitat. Without data on reproductive output for these snags, it’s difficult to know why nesting pairs still return.

I recommend the development of a snag data component for inclusion in future model versions. Reliable and continuous snag data is challenging to collect due to their highly variable spatial distribution, which requires complex and intensive sampling methods (Wing et al. 2015). There have been attempts to create an algorithm to extract snag presence from LiDAR (Wing et al. 2015) and Landsat (Frescino et al. 2001) data. However, these studies are plagued by variable detection rates and several methodological limitations. For example, Bater et al. (2009) successfully retrieved live and dead tree data from the use of LiDAR based on the assumption that the presence of standing dead trees and vertical stand structure are

strongly related. This may be true for naturally regenerating forest and may not be true for snags retained during clearcut harvesting. Martinuzzi et al. (2009) found higher accuracy of snag detection in mature multistory and old growth forest than in young multistory and understory reinitiation forests. I suggest that improvements in snag-detection algorithms for early seral forest are needed for use in purple martin habitat models. The estimates of snag densities and heights in harvest units and recent burns would substantially improve the model. Snag density data may allow for estimates of current population size and of the current total amount of suitable purple martin habitat in western Oregon.

The scope of this study is limited to future studies that define early seral forest as having <10cm quadratic mean diameter, model quadratic mean diameter estimates using 2016 GNN data, and identify stand- and landscape-level sites as 95 ha and 314 ha circular plots centered around potential nest snags, respectively. Detection of purple martins is increased by using the call playback system, so future similar studies must use the call playback system. Wildlife and forest managers in Oregon should be cautioned in using these results outside of the region encompassed by the study area, because forest management practices vary widely regionally and with different land owners.

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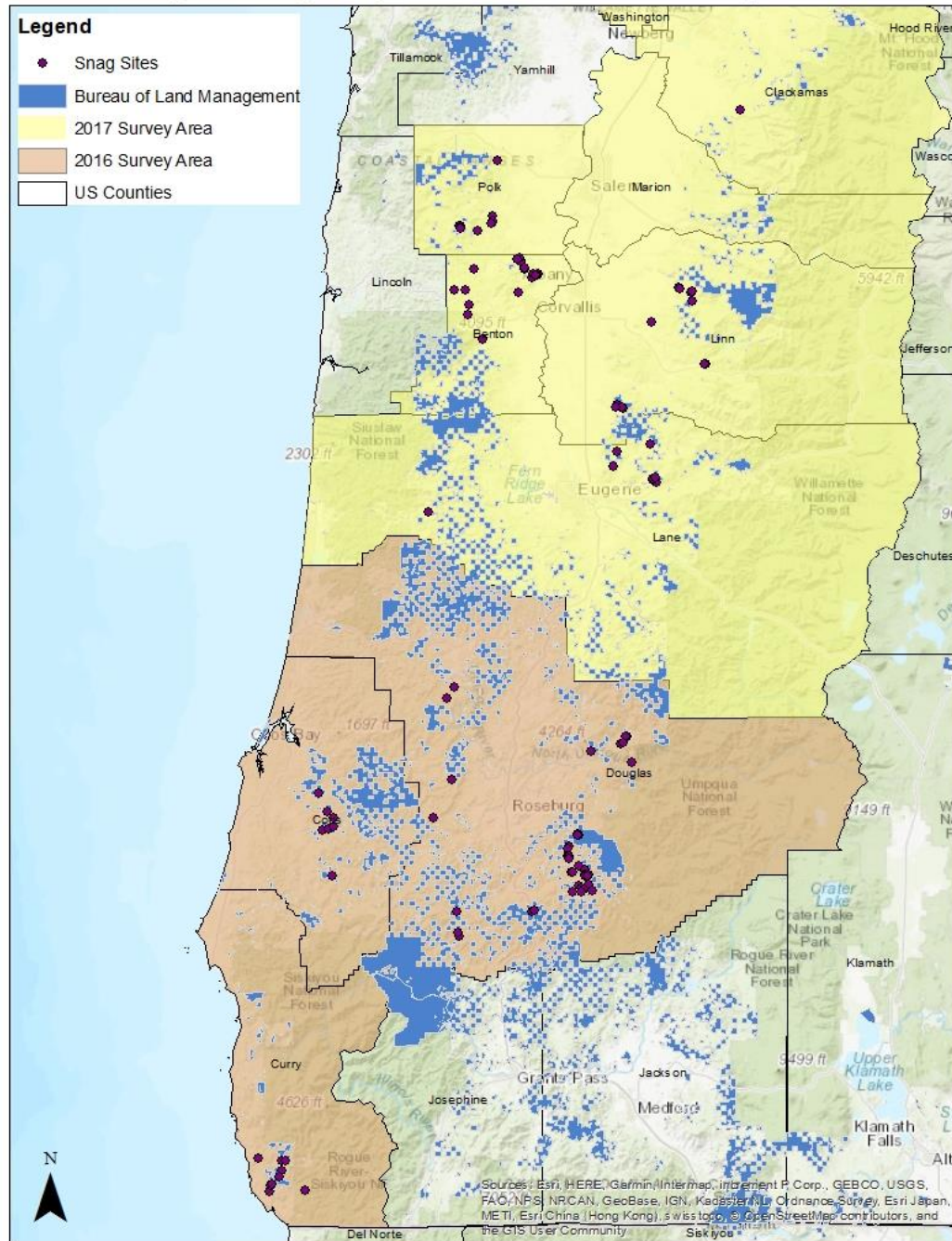


Figure 2.1. The study area for surveys of snag-nesting purple martin habitat characteristics. The area surveyed in 2016 is in orange by county and the area surveyed in 2017 is in yellow by county. Sites with measured snag and habitat characteristics that were included in the habitat suitability model are shown as red dots. Bureau of Land Management public lands is shown as blue polygons.

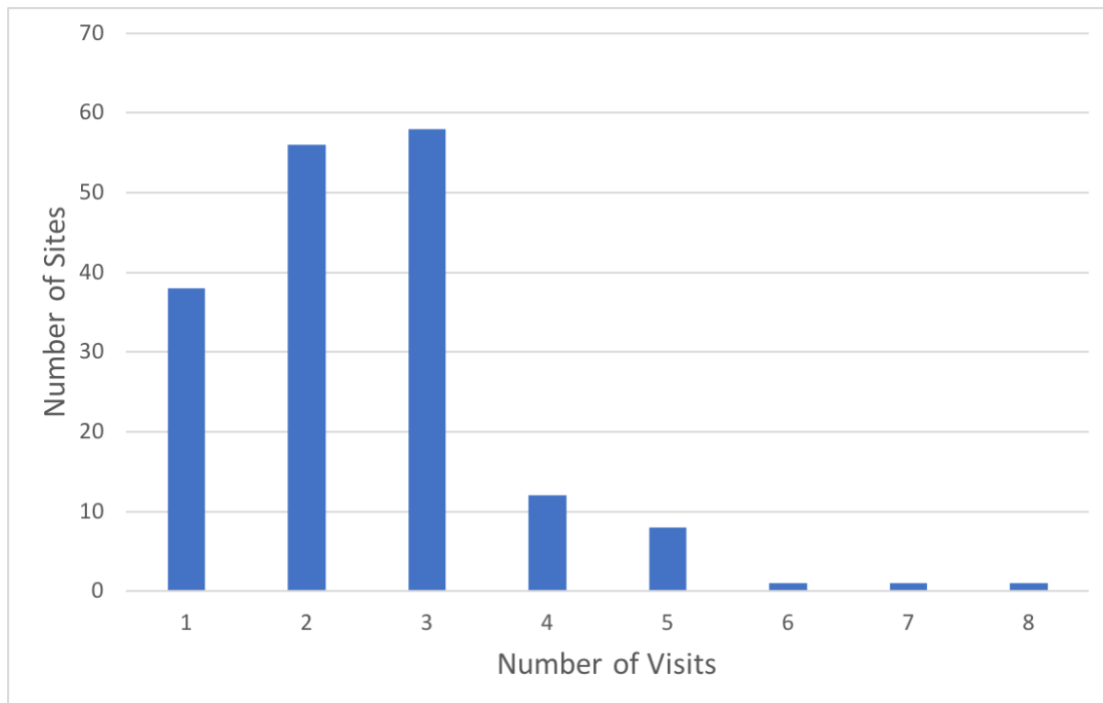


Figure 2.2. During purple martin occupancy surveys, the number of visits per site required to determine occupancy status. Sites were visited between two hours before and after dawn and call playback was used to increase the detection probability.

DHARMA scaled residual plots

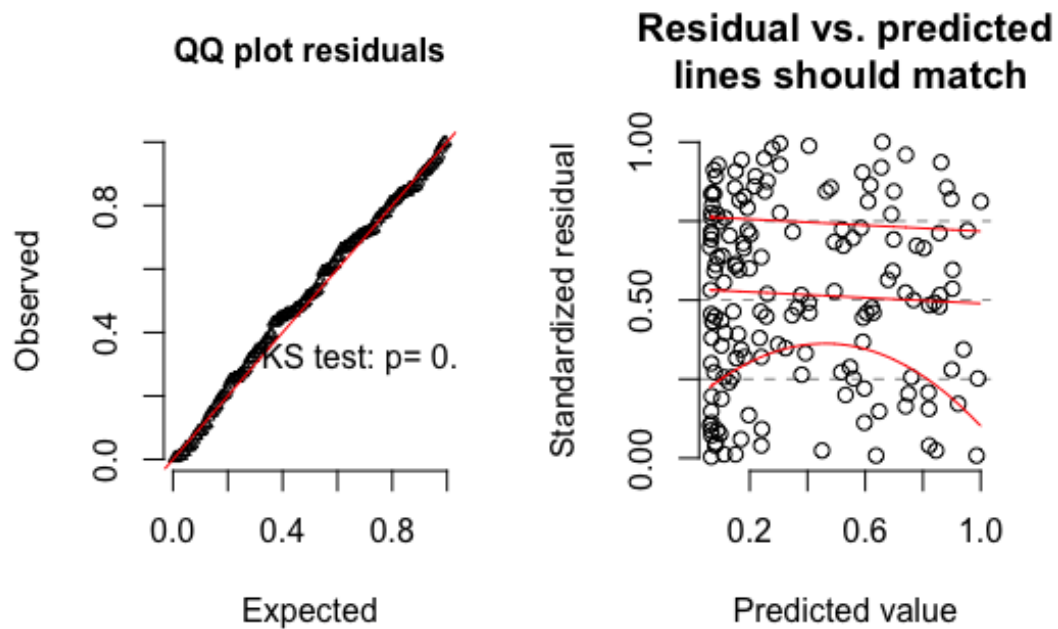


Figure 2.3. The DHARMA package (Hartig 2018) scaled residual plots showing the observed fitted model residual values as a function of the expected residual values. Ideally, residual points shown as black points in the QQ plot should align exactly with the red line. In the residuals vs. predicted plot, red lines should align horizontally with black dotted lines. However, due to small sample size, the deviation seen in both plots is expected.

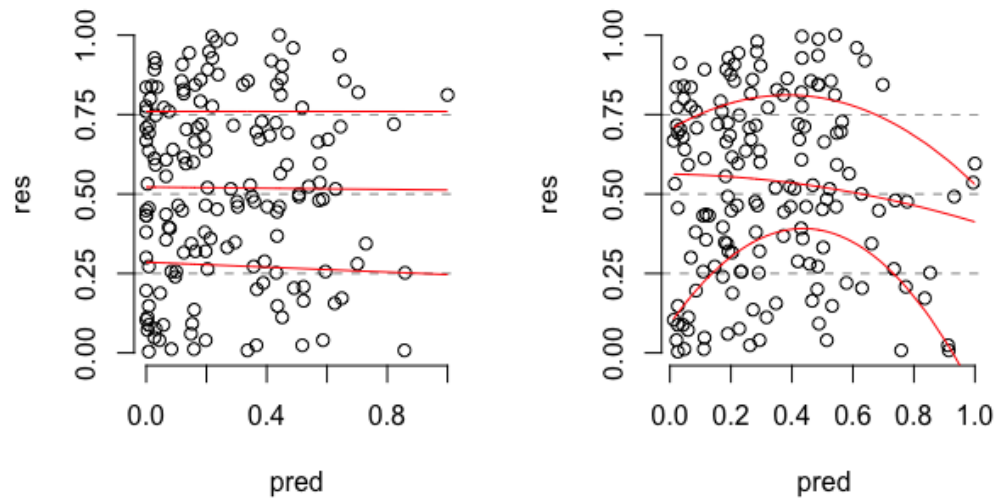


Figure 2.4. The DHARMa package (Hartig 2018) scaled residual plots showing the fitted residual values as a function of the predicted residual values for the explanatory variables, Early Seral Acreage Within 95 ha (left) and Early Seral Acreage Within 314 ha (right). The red lines should align horizontally with black dotted lines. However, due to small sample size, the deviation seen in both plots is expected.

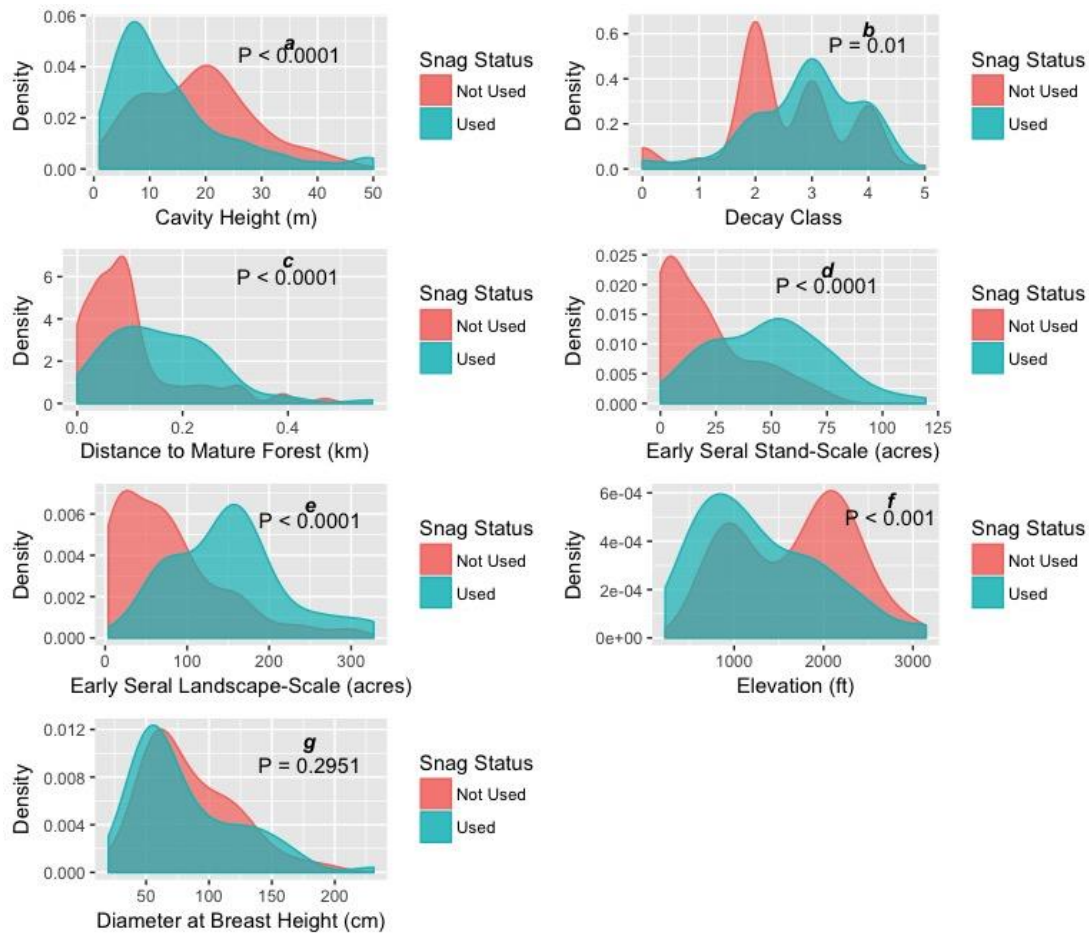


Figure 2.5. Smoothed histograms comparing habitat predictor variables at upland forest sites used for nesting by western purple martins with unused sites in western Oregon, 2016-2017. The distribution of data shown in red represents snags that were not used for nesting by purple martins. The distribution of data shown in blue represents snags that were used for nesting by purple martins. The vertical axis is frequency density – the number of cases per unit of the variable on the horizontal axis. The P-value is the probability associated with the null hypothesis of no difference between used and unused groups (two-sided Mann-Whitney Test).

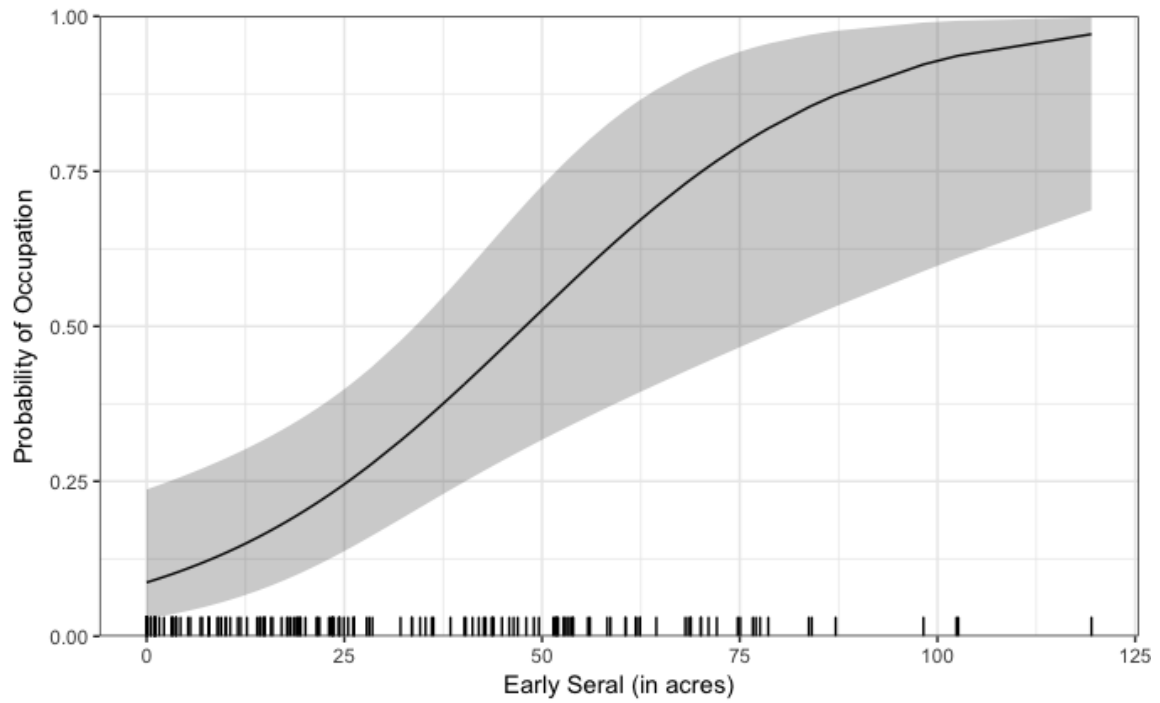


Figure 2.6. The estimated relationship between the probability of occupancy of a snag for nesting by purple martins and the acreage of early seral habitat within a 0.48 km circular radius of the snag. The gray ribbon is the 95% confidence interval and the solid line indicates the estimated values. Black tick marks represent raw data values.

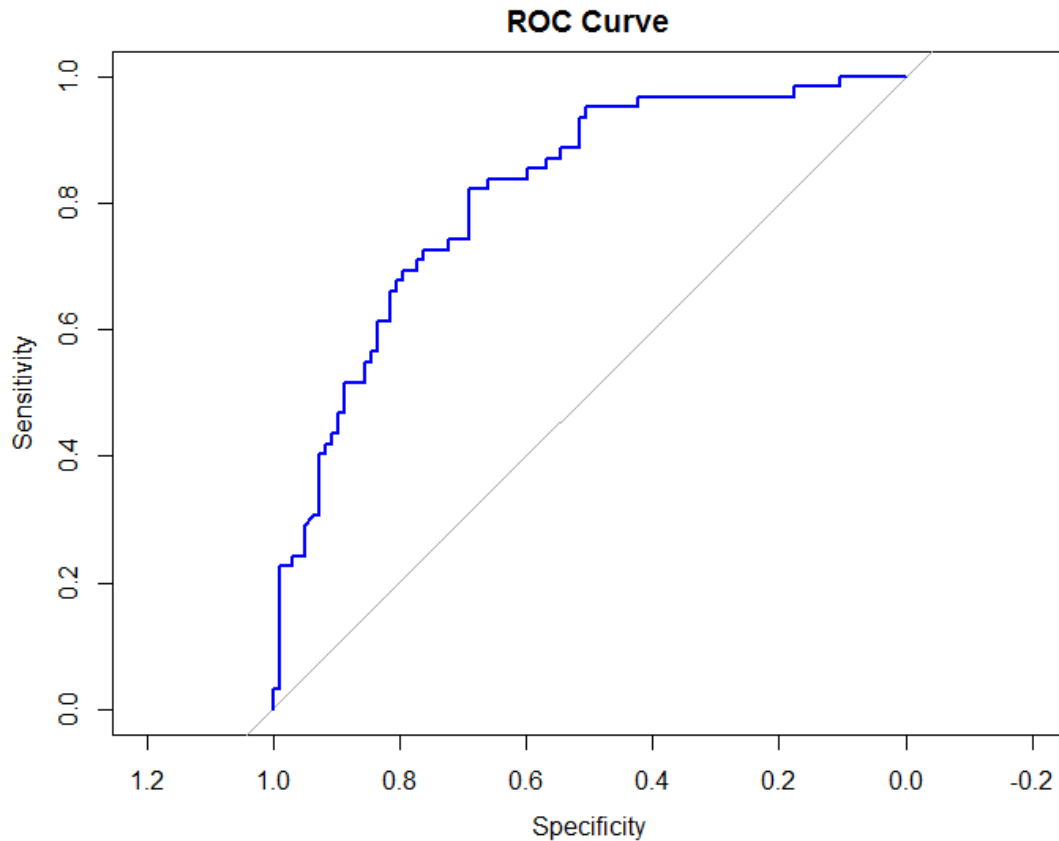


Figure 2.7. The ROC Curve for weighted model averages of the model set modeling the probability of occupancy of a snag by purple martins in western Oregon. The AUC fit index is 0.8134 with an optimism score of 0.01. The blue line represents the ability of the model set to classify used snags as used and unused snags as unused, where a curve displaying perfect classification would reach a sensitivity and specificity of 1.0.

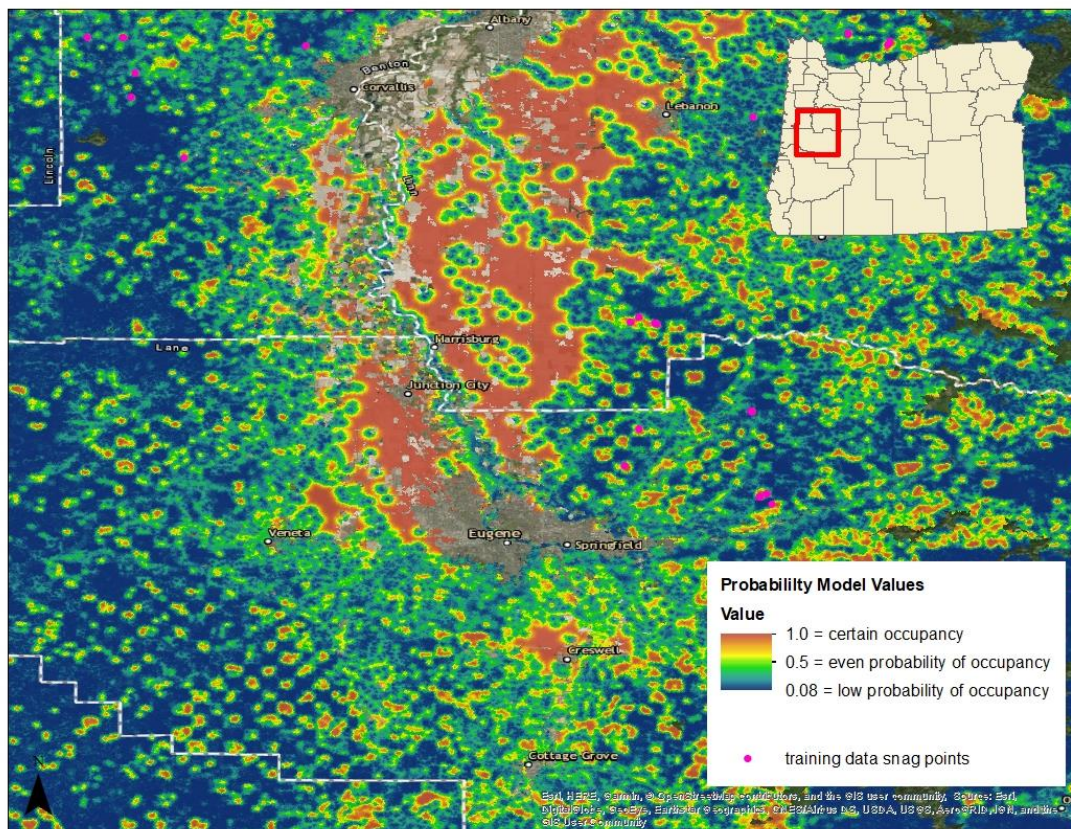


Figure 2.8. A stretched color scale visualization of the probability of occupancy of snags by purple martins assigned to the central Willamette Valley, Coast Range, and Cascade Range using the probability model set. Pink points represent the snag sites where data was collected for use as the training dataset. Red represents high probabilities of occupancy and blue represents low probabilities of occupancy. Forest with quadratic mean diameter values of $\geq 10\text{cm}$ were excluded as non-early seral forest. I further masked this single early seral factor raster layer to include the following Ecological Systems Landcover Classes (Grossmann et al. 2008, ESLF) in addition to early seral: Cultivated Cropland, North Pacific Herbaceous Bald and Bluff, Northern and Central California Dry-Mesic Chaparral, Open Water (Brackish/Salt), Open Water (Fresh), Pasture/Hay, Willamette Valley Upland Prairie and Savanna, Willamette Valley Wet Prairie.

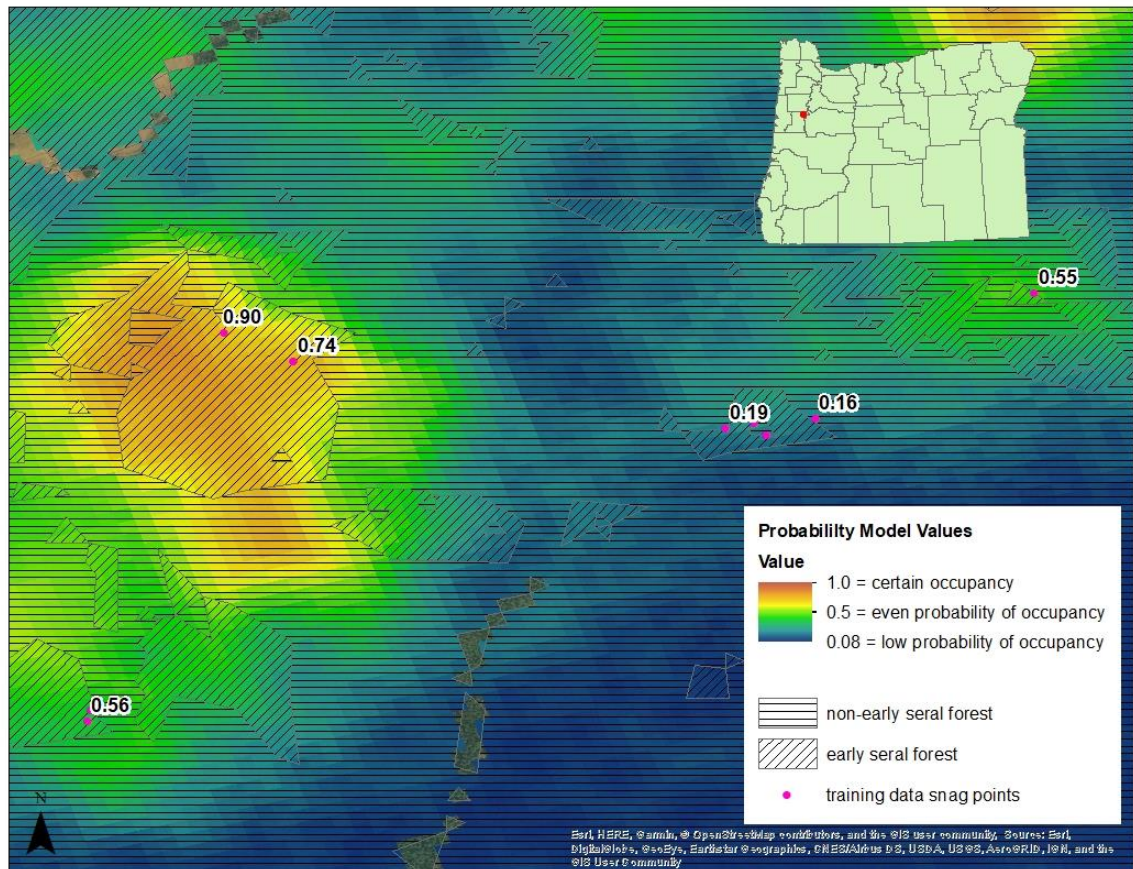


Figure 2.9. An excerpt from the probability of occupancy model set output with values assigned to each 30m² pixel. Pink points represent the probability of occupancy values predicted for each snag in the training data set. Diagonal hash marks represent area defined as early seral forest where QMD, where horizontal hash marks represent area not defined as early seral forest. Forest with quadratic mean diameter values of ≥ 10 cm were excluded as non-early seral forest. I further masked this single early seral factor raster layer to include the following Ecological Systems Landcover Classes (Grossmann et al. 2008, ESLF) in addition to early seral: Cultivated Cropland, North Pacific Herbaceous Bald and Bluff, Northern and Central California Dry-Mesic Chaparral, Open Water (Brackish/Salt), Open Water (Fresh), Pasture/Hay, Willamette Valley Upland Prairie and Savanna, Willamette Valley Wet Prairie.

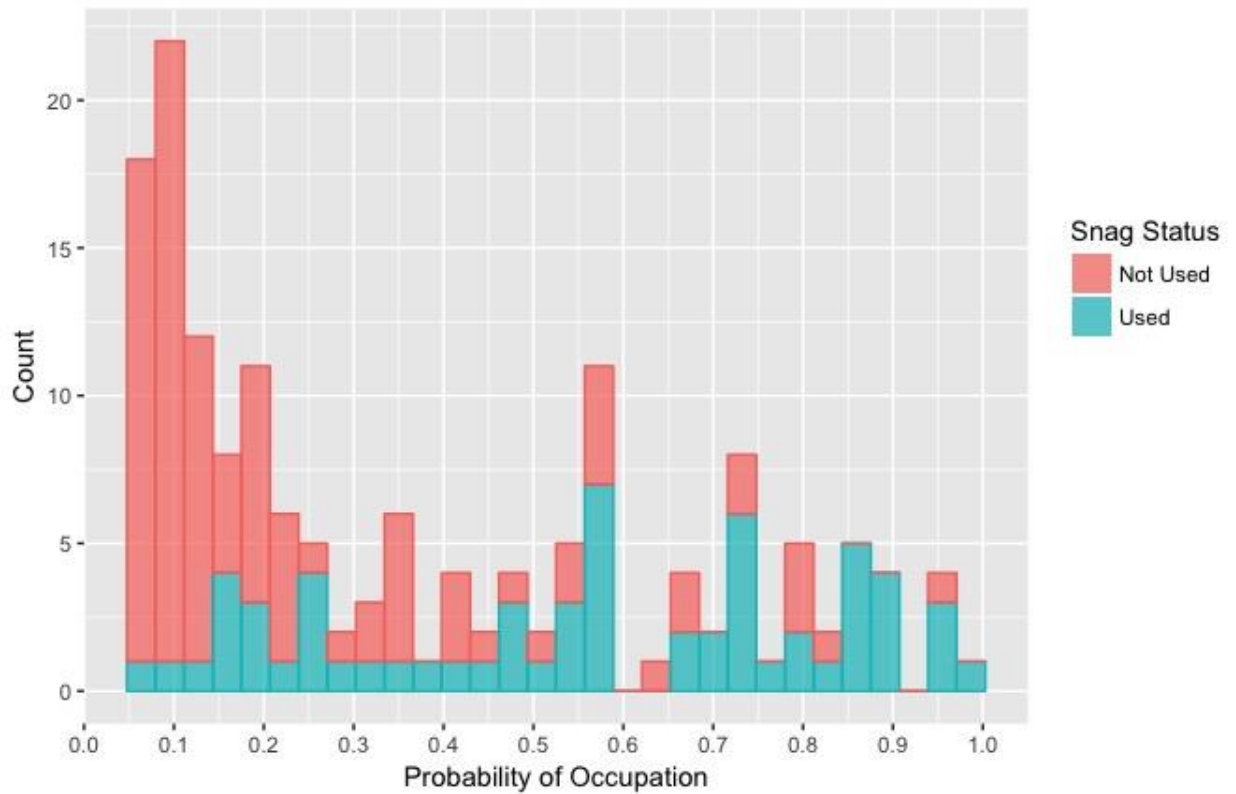


Figure 2.10. A stacked histogram showing the distribution of weighted model set predicted probabilities of occupancy of a snag by purple martins. Blue bars represent snags that were used by purple martins and red bars represent snags that were not used by purple martins in western Oregon.

Table 2.1. The number of unique sites in western Oregon surveyed for purple martin occupancy status in 2016 and 2017, by ownership. Seven BLM sites and six private sites were surveyed in both years; totals in parentheses include re-surveyed sites.

Ownership	2016	2017
Public Ownership		
BLM	74	4 (+7)
Elliott SF	12	0
USACE	0	5
USFWS	0	1
Total Public	86	10(18)
Private Ownership		
Campbell-Global	1	1 (+1)
Coquille Tribe	1	0
Hampton	0	2
OSU	0	22
Port Blakely	0	5
Portland Audubon	0	1
Starker	0	9
Weyerhaeuser	4	10 (+3)
Other Private	12	10 (+2)
Total Private	18	60 (65)
Grand Total	104	70 (83)

Table 2.2. The criteria for determining occupancy status of potential nesting sites by purple martins. All sites were surveyed between two hours before dawn and two hours after dawn. Sites were visited at least three times, or until an active cavity was confirmed. Call playback was used to increase the probability of detection. Reprinted from Cousens and Airola (2006) with permission.

Colony/Site Status codes

U = Unoccupied: No PUMA observed nearby in **20 min** observation period during usual time of peak activity. Monitor <2 hr after sunrise or <2 hr before sunset, esp. prior to nestling feeding activity locally. Monitoring observations should coincide with the nestling feeding period in the area to be conclusive (nesting timing can be highly variable over relatively short distances due to local climate variables).

P = Present: Bird(s) observed near or high above potential nest site, feeding, etc., NOT using nesting structures

OC = Occupied: Pair(s) of birds perched near or entering cavities or flying about potential nesting structures. Bird(s) seen entering, defending or guarding cavity, or adding nest material.

AC = Active Cavity Confirmed: Egg(s) or nestling(s) in nest cavity; evidence includes: young observed at entrance, dead nestlings, nestling begging calls heard from within nest cavity/structure, adults observed delivering food, adults carrying fecal sacks out of cavity.

Table 2.3. Candidate inference models for characterizing purple martin nesting habitat in upland forest sites in western Oregon shown with BIC, AIC, chi-square P-values, and $R^2_{\text{GLMM(c)}}$ (Nakagawa and Schielzeth 2012) for each model. Early seral predictor variables were decided to be included *a priori*. Snag predictor variables were *a priori* decided to be added first due to their likely importance for purple martins in choosing nest sites. Predictor variables were then added at an increasing scale with stand-scale variables first followed by landscape scale variables.

Model ID	Model Description	BIC	AIC	P-value	$R^2_{\text{GLMM(c)}}$
Model 1	Linear mixed effects with area of early seral within 95 ha	170.31	161.18	-	0.555
Model 2	Linear mixed effects with area of early seral within 95 ha and 314 ha plots	173.49	158.27	0.03	0.633
Model 3	Model 2 + Cavity Height	176.03	159.11	0.28	0.630
Model 4	Model 2 + Cavity Height, Decay Class	180.30	159.00	0.15	0.636
Model 5	Model 2 + Distance to Mature Forest Edge	183.33	160.25	1.00	0.630
Model 6	Model 2 + Elevation	180.31	159.00	0.13	0.634

Table 2.4. Akaike's information criteria (AIC) with small sample bias adjustment, AICc, delta AICc, and the model weights for each of the three spatial scale models in the set of models developed to predict purple martin habitat occupancy in western Oregon. Due to the nested structure of spatial scales, use of a weighted model set allowed all spatial scale models to be used and each model to contain only variables from its unique spatial scale (Burnham et al. 2009).

Model	AICc	Delta	Weight
Stand-scale	167.6	0.00	0.99
Landscape-scale	176.9	9.23	0.01
Snag-scale	189.1	21.45	0.00

CHAPTER 3. DIET COMPOSITION AND PREY AVAILABILITY OF THE
WESTERN PURPLE MARTIN (*PROGNE SUBIS ARBORICOLA*) IN WESTERN
OREGON

Lorelle Sherman, Taal Levi

ABSTRACT

The western purple martin (*Progne subis arboricola*) is an aerial insectivore and a species of conservation concern throughout the Pacific Northwest. Declines of many aerial insectivores are attributed to reduced insect populations, in addition to habitat loss and degradation. Large colonies of the western subspecies nest in artificial housing located in low elevation, coastal and inland open-water ecosystems, while smaller colonies nesting in natural snags are scattered throughout upland forest in western Oregon. There is no information on western purple martin diet composition or how prey availability affects martin colonies in different ecosystem types. From anecdotal observations, Odonates are assumed to be an important prey taxon in all ecosystem types. To address the major information gap about resource limitations that may influence western purple martin population dynamics, my project addressed the following questions: do upland forest, inland open water, and coastal ecosystems differ in the composition and abundance of prey available to purple martins, and what are the main prey items fed to purple martin nestlings in each ecosystem type? My objectives were to compare the composition (species make-up) and abundance of prey available to purple martins and other aerial insectivores among ecosystem types and to utilize noninvasive metabarcoding methods to compare nestling diet composition between ecosystem types. I also tested the use of game cameras to determine nestling provisioning rates. I found strong evidence that dragonfly abundance differed among ecosystem types, but little to no evidence that abundance of other arthropod taxa differed between ecosystem types. Diptera was the main prey order in nestling diet for all ecosystem types. Purple martins in the open water ecosystem utilize a wider range of Dipteran genera than martins in the coastal and upland forest ecosystems. Therefore, nestlings in the open water ecosystem are likely more resistant to changes in prey composition and abundance due to anthropogenic or natural disturbance. Dipterans were detected in the nestling diet more frequently than expected based on availability in all ecosystems, suggesting preferential use of Diptera over other more abundant arthropod orders. Game camera photos led to the discovery that extreme heat events may be detrimental to nestling

success through lowered provisioning rates. The results of this study serve as a foundation that can be used to determine if purple martins are limited by prey availability, nest site availability, or both. Ecological studies like this are necessary for demystifying the decline of all aerial insectivores.

INTRODUCTION

Avian aerial insectivores are a guild of birds that exclusively feed on insects in the air column. According to the North American Breeding Bird Survey (BBS) and the North American Bird Conservation Initiative (NABCI 2012), aerial insectivores in the United States and Canada are the most rapidly declining guild of birds in North America. Declines of many aerial insectivores are attributed to reduced insect populations, in addition to habitat loss and degradation (Nebel et al. 2010). Shockingly, Hallman et al. (2017) found a 76% reduction in airborne insect biomass in 27 years for protected natural areas in Germany. Global scale environmental changes, such as climate change, invasive species introductions, habitat loss and degradation, aquatic acidification, and pesticide use are likely contributing to insect population declines. The extent to which insect populations are declining globally is unknown, but ~40% of the insect species studied are listed as threatened by the IUCN (IUCN 2013). More insect species are declining than increasing on a global scale (Dirzo et al. 2014). If insect populations are declining at a global scale, a serious threat is posed to all aerial insectivore species.

The western purple martin (*Progne subis arboricola*) is an aerial insectivore and a species of conservation concern throughout the Pacific Northwest. Unlike the eastern subspecies that has been widely studied, there is little known about the western subspecies. While the eastern subspecies is entirely dependent on artificial housing, the western subspecies still uses natural cavities in snags (standing dead trees) for nesting in the wild (Bettinger 2003). Large colonies of the western subspecies nest in artificial housing located at low elevation, coastal and inland open-water sites, while smaller colonies nesting in natural snags are scattered throughout upland forest ecosystems in western Oregon. Horvath (1999) found only 5% of 784

pairs of martins in western Oregon to be nesting in snags; snags used were typically far from open water, in remote forested uplands. Purple martins historically nested exclusively in natural cavities (Tarof and Brown 2013), often far from water.

To sustain self-sufficient purple martin colonies, managers must gain an understanding of the processes driving their population dynamics (survival and reproduction). Both nest site availability and prey availability may limit colonies. From anecdotal observations, it is assumed that purple martins are limited by nest site availability in all ecosystem types. In sites with existing colonies, new artificial housing units installed in suitable habitat are quickly occupied by purple martins (Vesely unpublished data; Metzler unpublished data). However, there is no information on how prey availability affects martin colonies in different ecosystem types. If a colony is subject to both limitations, it may function as a population sink, in which mortality outweighs reproduction (Pulliam 1988). Colonies only subject to nest site limitations may function as source populations, especially if additional artificial housing units are installed. A source population is one where reproduction outweighs mortality and that may be supplying a surplus of individuals that disperse to less productive ecosystems (Pulliam 1988). Understanding what colonies in different ecosystem types are limited by will help guide management decisions about where to focus efforts in efficiently bolstering populations.

To address the major information gap about resource limitations that may influence western purple martin population dynamics, I addressed the following questions: (1) do upland forest, inland open water, and coastal ecosystems differ in the composition and abundance of prey available to purple martins, and (2) what are the main prey items fed to purple martin nestlings in each ecosystem type (upland forest, inland open-water, and coastal)? My objectives were to compare the composition and abundance of prey available to purple martins among ecosystem types, and utilize noninvasive metabarcoding methods to compare nestling diet composition between ecosystem types. Metabarcoding is a combination of DNA taxonomy and high throughput DNA sequencing that has been verified against

traditional morphological taxonomic assignment (Yu et al. 2012). Metabarcoding has only recently been successfully applied to avian diet studies (Jedlicka et al. 2016; Trevelline et al. 2016; Moran et al. 2019) and only very recently to aerial insectivores (McClenaghan et al. 2019). To my knowledge, there have been no diet studies of the western purple martin.

The relevance of this work extends beyond a single species because purple martins represent a guild of broader conservation concern: aerial insectivores. Surveys have measured substantial declines in many aerial insectivore species, but there is little indication of reasons underlying declines. It can be reasonably assumed that declines are due to a combination of reduced insect populations and habitat loss and degradation. However, the extent to which either of these factors influences aerial insectivore decline is unknown. This is due in part to the lack of studies on aerial insect populations. Other than a couple studies (Chapman et al. 2004, Greenstone et al. 1991), there has been especially little effort to measure high altitude insect populations. My project addressed these information gaps by studying the relationship between prey availability and nestling diet of an aerial insectivore. It serves as a foundational study that can be used to determine if purple martins are limited by prey availability, nest site availability, or both. Ecological studies like this are necessary for demystifying the decline of all aerial insectivores.

METHODS

Study Area

Study sites were located in western Oregon west of the Cascade Mountain Range and below 4,000 ft in elevation (Bettinger 2003). This included the western foothills of the Cascade Mountain Range, the Willamette Valley, the Coast Range, and the southern Oregon Coast (Fig. 3.1). Due to a small number of total available nesting sites on a mosaic of land ownerships, sites were non-randomly chosen based on where I was able to obtain access permits. I chose fifteen total sites with five each equally representing the three ecosystem types martins nest in. Each site consisted of a 1km radius around the nest cavity and all sites were at least 5km from each other.

Purple martins are capable of flights much farther than this. However, I assumed that martins are primarily feeding within 1km of the nest site, because the energetic demands of longer feeding flights likely begin to outweigh energy input of prey at farther distances. Other aerial insectivores remain close to their nest site during the nestling period for increased provisioning rates and protection against predators (McCarty 1995). Tree swallows forage mostly within 100-200m of their nest site during the nestling period (McCarty and Winkler 1999). Because purple martins are ~3 times the mass and ~1.3 times wingspan as tree swallows (Tarof and Brown 2013, Robertson et al. 2011), I assumed the average feeding flights of martins are much farther.

Martins at the inland, open-water ecosystem nested in artificial housing installed by the U.S. Army Core of Engineers (USACE). Martins in the coastal ecosystem types nested in artificial housing installed through the Coos Bay BLM District's Purple Martin Nest Box Project. In the upland forest ecosystem, martins nested in artificial housing and in both natural and created snags in the McDonald-Dunn Research Forest.

Four of the five upland forest sites were clearcut units that were identified as having active purple martin nests by ongoing surveys for snag-nesting martins in upland forest habitats (Hagar and Sherman 2018). Land ownership types for upland forest ecosystem sites include: the McDonald-Dunn OSU Research Forests located north of Corvallis, a private timber unit owned by South Coast Lumber Co. in the Coos Bay BLM District, and a private landowner's property near Stayton, Oregon

The Willamette Valley has three major reservoirs with existing martin colonies that make up the open water ecosystem type. All three reservoirs are owned and operated by USACE. Fern Ridge Reservoir, west of Eugene, is the largest of the three reservoirs and has three sites that are all at least 5km from each other. One additional site is located at Cottage Grove Lake and one at Dorena Lake, both located southeast of Cottage Grove.

Several colonies of martins nest in artificial housing on tidally-influenced, coastal waterways. A monitoring program conducted by the Coos Bay BLM records the annual occupancy and reproductive rates of these nest boxes. Land ownership types for coastal ecosystem sites include: USACE-owned docks on the western shores of Coos Bay, BLM owned North Spit of Coos Bay, South Slough Nature Reserve east of Charleston, a private landowner's property in Charleston, and the Smith River South Side Bridge in Reedsport.

Sampling Design

Sample Collection

Fecal samples - I collected fecal samples from nestlings in all ecosystem types in July of 2017 and 2018. Immediately upon removal from the nest cavity, individual nestlings were held over a fresh piece of wax paper until they excreted fecal material. Sterilized tweezers or sterile Q-Tips were used to remove fecal samples from the wax paper for direct placement into labelled Eppendorf tubes. Any fecal material that slid off the wax paper was considered contaminated and discarded. Fecal samples were put on ice in a cooler for preservation throughout the day and later transferred for long-term storage at -20°C on Oregon State University campus. Nestlings were banded, weighed, measured, and aged. Fecal sample nest numbers were recorded next to individual nestling data. All fecal samples from individuals in one nest were pooled and homogenized to account for variation between individuals within a nest (Adams et al. 2016).

Prey abundance - To quantify prey availability in each ecosystem, I installed Malaise traps to passively collect flying arthropods at three sites in each ecosystem. I was only able to sample at one coastal site due to extreme winds during the sampling period. At each site, I set up one Malaise trap at ground level and one trap raised 20ft off the ground suspended from either osprey nesting poles or residual trees. Prey sampling occurred for 24 hours at each site and within the fecal sample collection time period. Sample collections were stored in the killing agent (biodegradable antifreeze) until processing. Each sample was sorted into two categories of body

length: <13mm (small) or >13mm (large). Large arthropods were considered potential prey for purple martins based on my personal observations of the size of prey being brought to the nest. I identified and counted large arthropod individuals to family when possible. Small arthropods were considered potential prey items for predatory arthropods, such as dragonflies and damselflies. I measured dry biomass of the entire small arthropod sample for each ecosystem. Dry biomass of large arthropods samples was not measured, because this method destroys the integrity of the sample and these large insects may need to be used for creating a local reference DNA sequence database.

A common limitation of the Malaise trap is the potential for taxonomic bias (Matthews and Matthews 2017). Dragonflies are agile predatory insects that can readily avoid obstacles, such as a Malaise trap. From anecdotal observations, dragonflies are believed to be an important prey taxon for purple martins (Bruce Cousens, personal communication). I developed a dragonfly visual encounter survey modeled after avian point count surveys in order to measure dragonfly abundance. Each survey site consisted of a 50m radius plot surrounding each Malaise trap. Surveys were repeated four times at each site. At each plot, I surveyed for 10 minutes using binoculars, conservatively counting and identifying dragonflies to family, or genus when possible. Surveys occurred in July of 2018 between 10am – 1pm and only when temperatures were above 63°F with wind <18mph and no rain (Smallshire & Beynon 2010). Dragonflies are likely not active outside of these conditions.

DNA Extraction, Amplification, and Sequencing

The prey remains within a fecal sample can be unevenly distributed, so fecal samples were thawed and homogenized by vortexing with garnet beads for 20 minutes. I initially extracted prey DNA from fecal samples using the Qiagen Blood & Tissue Kit (Model 69504) by following the manufacturer's instructions. However, due to the difficulty of removing inhibitors with this kit, I had extremely limited success with extraction and amplification and switched to using the Qiagen PowerFecal DNA Kit (Model 12830-50). I followed the kit protocol with the

following modifications to maximize DNA yield: during the lysing step, heat the tubes at 65°C for 20 minutes; vortex post-lysing at maximum speed for 20 minutes; centrifuge tubes at maximum speed for 1.5 minutes; follow all 2-8°C incubation steps. Negative control extractions were performed using identical methods and reagents without any fecal material to enable identification of contamination during the extraction process. Extraction batches ranged from 10-18 samples and final extractions were frozen at -20°C.

I assumed that purple martins are exclusively eating arthropods. I amplified a ~180 base pair target region of the COI gene using ANML primers developed by Jusino et al. (2019). These primers were chosen based on their short amplicon length and ability to amplify a broad array of arthropods. Short amplicon lengths are preferred when the DNA source is highly degraded, as is the case with fecal material. A sequence alignment check in Geneious (version 10.1)(Kearse et al. 2012) confirmed high conservation at primer binding regions in a broad group of potential purple martin prey taxa. In order to bind to the Illumina flow cell for sequencing, the ANML primers were appended with Nextera adaptors.

I used the Polymerase Chain Reaction (PCR) reagent proportions and cycling conditions outlined by Jusino et al. (2019). PCR was done in triplicate to enable identification of sequence artifacts in the bioinformatics phase. A single negative PCR control was included on each reaction plate to aid in contamination identification during the amplification process. The PCR product was quantified using the Quant-iT PicoGreen dsDNA Assay Kit (Thermo Fisher Scientific), normalized, and pooled into four libraries. All PCR products were cleaned of PCR buffers and unamplified DNA with Solid Phase Reversible Immobilization (SPRI) beads (Aline Biosciences). Nextera forward and reverse index tags were added through an additional PCR reaction to allow for library differentiation post-sequencing. The libraries were sequenced on the Illumina HiSeq 3000 by the Center for Genome Research and Biocomputing (CGRG) at Oregon State University.

Bioinformatics and Data Analysis

The sequence output was filtered with custom code to remove sequences with <50 counts and <120 base pairs in length. Any taxonomic assignment that occurred in fewer than two out of three PCR replicates was removed due to the high risk of rare sequences being artifacts of sequencing error. Sequence output was taxonomically assigned using BLAST against all CO1 sequences publicly available in Genbank. Sequences assigned to non-arthropods were removed due to the high risk they arose from contamination during sample collection or from stomach contents of prey items.

Due to taxonomic bias in the efficiency of primer binding, the quantification of proportion of biomass of prey items in fecal samples may not always be reliable. However, Frequency of Occurrence (FOO) and Relative Read Abundance (RRA) are two relative methods of qualitatively describing diet composition. I calculated FOO and RRA for the sequence data after summarizing by ecosystem type. FOO allows the comparison of frequency of use of a prey item by calculating the proportion of samples that the sequence is in. RRA is the proportion of read counts of a certain prey sequence out of the total read counts of all prey sequences in that sample. I took the mean RRA for each taxon and standardized it by the number of samples to give equal weight to each sample. RRA gives a rough estimate of the relative proportions of biomass in dietary samples. It can be tested against samples with known proportions of prey biomass and then compared with sequence output to determine the strength of correlation between input and output, which can range from no to strong correlation depending on the species and the study (Deagle et al. 2019). I used RRA to aid in interpreting dietary differences between ecosystem types and to get a rough estimate of the importance of specific prey taxa in the diet. RRA is more useful than occurrence data for this, because occurrence data can severely inflate or deflate the importance of specific prey taxa in the diet.

In an attempt to quantify the level of bias associated with the efficiency of primer binding for each of the prey orders, I chose candidate species present in the fecal samples as representatives of the order. I assigned a bias score for each

nucleotide mismatch between the prey sequence and the primer sequence starting with 1 point given for mismatches at the 5' end and increasing by 1 point at each consecutive nucleotide. This increasing point system from the 5' to the 3' end reflects the increased costliness of degeneracy at the 3' end for primer binding efficiency than at the 5' end (King et al. 2008).

Shannon's diversity index (H) is a commonly used metric for quantifying taxonomic diversity in a community. The H index assumes that all potential community taxa have been sampled, which ignores the taxonomic bias introduced into metabarcoding data through PCR amplification. I treated ecosystem types as a community, aggregating all nest fecal samples. I calculated H at the order, family, genus, and species level for each ecosystem type. H was calculated as the proportion of frequency of occurrence for each prey type in an ecosystem multiplied by the natural log of that proportion, then summed per ecosystem and multiplied by -1.

Game Camera Nest Monitoring

Motion-activated game cameras have been successfully used to quantitatively measure the size of prey items brought to nestlings (Sinkovics et al. 2018). The frequency of large prey items brought to nestlings was found to be an indicator of nestling survival in sparrows (*Passer domesticus*) (Schwagmeyer and Mock 2008). I set up three game cameras in each ecosystem type to test their use for identifying prey taxa and size. The game cameras were positioned to face the cavity opening of active nest cavities. All cameras were standardized with the following settings: three photos per trigger and high motion sensor sensitivity. Unfortunately, two cameras in the coastal ecosystem fell, one camera in the upland forest ecosystem malfunctioned, one in the open water malfunctioned and one produced poor quality photos. This combined loss severely limited the sample size. I manually scanned for adults removing nestling fecal sacs from the nest to indicate the hatching of nestlings and the start of the nestling provisioning phase. Some prey items brought back to the nest are small enough to be enclosed within the purple martin's beak and go undetected by visual scanning. To avoid missing these feeding events, I counted every new entry to

the nest cavity by male or female as a feeding event once fecal sac removal was confirmed. I taxonomically assigned large prey items to order or family when possible. This method could be used as a quantitative measure of purple martin nestling diet by cross-referencing visible prey items with published data on prey size. I was able to cross-reference this data with the metabarcoding output to inform on potential bias from taxonomic disparity in primer binding efficiency.

RESULTS

Prey Availability

The Malaise traps collected a total of 151 arthropod specimens that were >13mm (large). Of the 151 total arthropods, 63 were collected in the open water ecosystem, 77 in the upland forest ecosystem, and 11 in the coastal ecosystem. I identified all arthropods to family except for Lepidopterans, which remained at the order level due to their difficulty in identification after wing discoloration and damage from the killing agent. A total of 5.9g of dry small arthropod biomass was collected in the Malaise traps, with 3.7g in the open water ecosystem, 1.5g in the upland forest ecosystem, and 0.7g in the coastal ecosystem. I found weak evidence for a difference in small insect biomass means between ecosystem types (Fig. 3.2)($F_{2,11} = 2.76$; p-value = 0.11). I found no evidence for a difference in large insect count means between ecosystem types (Fig. 3.3)($F_{2,11} = 0.39$; p-value = 0.69). The Shannon's H-index values for insect prey diversity at the order level for coastal, open water, and upland forest ecosystems are 1.59, 1.2, and 1.96, respectively (Fig. 3.4).

During the dragonfly visual encounter surveys, a total of 95 dragonflies were observed in the open water ecosystem and 5 in the coastal ecosystem. No dragonflies were counted during the observation period in the upland forest ecosystem. However, dragonflies were observed at upland forest sites on other occasions. There is strong evidence for a difference in dragonfly count means between ecosystem types (Fig. 3.5)($F_{2,25} = 35.4$; p-value <0.0001).

DNA Extraction, Amplification, and Sequencing

Extractions done with the Qiagen DNeasy Blood & Tissue Kit amplified at a 25.9% success rate (Table 3.1). The Qiagen PowerFecal DNA Kit far outperformed the DNeasy Blood & Tissue Kit with an amplification rate of 80.1% . The QIAamp Fast DNA Stool Kit was tested for use as a backup on a small subsample of extractions and had a 100% amplification rate.

The average sequence read count per sample for coastal, open water, and upland forest ecosystems were 95,120, 242,370, and 115,836, respectively. After the data filtering process, there were a total of 8,514 unique sequence reads assigned to 482 taxon in Genbank. The number of taxonomically assigned prey items per sample ranged from 1 to 44. Sequence reads taxonomically assigned to phylums external to Arthropoda included Porifera (sponges), Echinodermata (starfish, sea urchin, and sea cucumber), Rhodophyta (red algae), Rotifera (rotifers), Streptophyta (green algae), Nematoda (nematodes), Mollusca (molluscs), Mucoromycota (fungi), Basidiomycota (Basidiomycota fungi), Cnidaria (jellyfish and hydrozoans), and Annelida (ringed worms). I assumed that the amplification of these phyla was either due to contamination or the presence of stomach contents in prey items.

The dietary richness at the order level for nestlings in coastal, open water, and upland forest ecosystems is 13, 15, and 10, respectively. The dietary richness at the genus level for nestlings in coastal, open water, and upland forest ecosystems is 64, 139, and 72 respectively.

Ephemeroptera (mayflies), Neuroptera (lacewings), and Psocoptera (barklice) were only present in nestling diet in open-water ecosystems (Fig. 3.6). Siphonaptera (fleas) and Thysanoptera (thrips) were only present in the coastal ecosystem (Fig. 3.6). Plecoptera (stoneflies) and Trombidiformes (mites) were absent from nestling diet in upland forest ecosystems, but Blattodea (termites) was only present in the upland forest ecosystem (Fig. 3.6). All other orders are present in nestling diet in all three ecosystems (Fig. 3.6). Reads that could not be assigned to the order level are

listed as N/A. Diptera (flies) was the most frequently detected order in all ecosystem types (Table 3.2) with FOO values ranging from 0.58 to 0.69. The 5 most common prey genera in the coastal ecosystem were: Chironomus (nonbiting midge), Hybomitra (horse fly), Peckia (flesh fly), Dicranomyia (crane fly), and Hydrophoria (root-maggot fly) (Fig. 3.7). The 5 most common prey genera in the open water ecosystem were: Chironomus, Dicranomyia, Culex (mosquito), Hybomitra, and Glyptotendipes (Glyptotendipes fly) (Fig. 3.8). The 5 most common prey genera in the upland forest ecosystem were: Peckia, Hydrophoria, Hybomitra, Limonia (crane fly), and Chironomus (Fig. 3.9). All of these prey genera were present in the diet at most nestling age in days.

Diptera was the most frequent component of nestling diet across all ages and ecosystems (Figs. 3.10-3.11). No Odonata (dragonflies,damselflies) were fed to nestlings before day 6. Stoneflies were most frequent in the nestling diet at day 1. Araneae (spiders) are present in the diet from day 7 through 24. Surprisingly, Trombidiformes are present in a substantial percent of the total nest sites from day 26-28. Open water had the most coverage of all nestling ages due to the larger number of extracted samples (Fig. 3.11). While Araneae are utilized in all ecosystem types, they are more frequently fed to nestlings in open water (Fig. 3.11).

The three prey orders with the highest relative biomass as measured by RRA for the coastal ecosystem are: Diptera (18.3%), Hemiptera (true bugs) (14.0%), and Orthoptera (crickets, grasshoppers) (13.5%) (Table 3.3). The three prey orders with the highest relative biomass as measured by RRA for the open water ecosystem are: Diptera (33.1%), Coleoptera (beetles) (16.4%), and Trombidiformes (14.4%) (Table 3.3). The three prey orders with the highest relative biomass as measured by RRA for the upland forest ecosystem are: Diptera (28.5%), Hemiptera (15.3%), Hymenoptera (bees, wasps, ants) (11.3%) (Table 3.3). At the level of prey genus, no single taxa comprised of $\leq 10\%$ of the total RRA for any ecosystem type (Table 3.4).

Shannon's diversity index (H) does not provide any information on functionality or abundance of taxa, so it is not entirely useful on its own. When

coupled with abundance or frequency data, the H index becomes more informative for how species may respond to changes in prey. For example, pairing the diversity index with frequency of occurrence data gives insight into the sensitivity of purple martins to changes in prey abundance and composition. The H index values at the order level for coastal, open water, and upland forest ecosystems are 1.51, 1.24, and 1.15, respectively. Interestingly, the H index for prey availability in coastal and open water ecosystems are within .09 and .04 units of the nestling diet composition H index values. The H index for the available prey community in the upland forest ecosystem is much greater than the H index for diet composition in that ecosystem. The H index values at the family level for coastal, open water, and upland forest ecosystems are 3.35, 3.16, and 3.15, respectively. The H index values at the genus level for coastal, open water, and upland forest ecosystems are 3.88, 3.98, and 3.59, respectively.

Nestling Provisioning

Game camera photo collection at the South Coast Lumber upland forest site took place over the course of 32 days. Game camera photo collection at the Dunn Research Forest took place over 34 days. Both cameras captured the entirety of the nestling phase. The game camera in the coastal ecosystem malfunctioned after 10 days. The open water game camera captured the majority of the nestling phase at one nest site. The coastal ecosystem type had the highest nestling provisioning rate with the open water ecosystem following close behind (Table 3.5). The upland forest ecosystem had the lowest nestling provisioning rate (Table 3.5). There was a wide range of daily number of provisioning visits for all ecosystem types. It was possible to identify large prey items (e.g. dragonflies, butterflies, and wasps) to family and sometimes genus. Smaller prey items were either completely enclosed in the beak or enclosed enough to obscure taxonomic assignment. Interspecific interactions with Bewick's wren (*Thryomanes bewickii*), northern flicker (*Colaptes auratus*), tree swallows (*Tachycineta bicolor*) and Townsend's chipmunk (*Nectamias townsendii*) were also captured from the game camera photos. In the upland forest ecosystem, photos captured nestlings of approximately 16 days of age exiting the artificial

housing unit cavity to sit on the platform ledge for four consecutive days. On these days, the ambient temperature ranged from 98-104°F (Oregon Climate Service).

DISCUSSION

Prey Availability

Upland forest, open water, and coastal ecosystems were found to have a variety of arthropod prey available to purple martins. The composition of prey availability did not differ drastically between ecosystem types, however the open water ecosystem had the highest taxonomic diversity of arthropods at all levels of taxonomic assignment. Open water had the highest abundance of dragonflies and is likely the most productive ecosystem for arthropod prey. Furthermore, aquatic arthropods are higher in fatty acid content than terrestrial arthropods, making them more energetically beneficial prey items for purple martin nestlings (Twining et al. 2016). This may explain the larger colony sizes observed in open water ecosystems, but more research is needed on determining if nest site limitations in upland forest. The large components of Coleoptera and Lepidoptera found to be available in upland forest suggest this ecosystem is suitable for purple martin, though it is unclear how the energetic content of these prey items impacts nestling condition compared with aquatic prey. It is recommended that future studies focus on differences in nestling body condition between the three ecosystem types.

The open water ecosystem had more small insect biomass than other ecosystems (Fig. 3.2). Dragonflies are preying on small insects, so the greater small insect biomass may explain the significantly higher abundance of dragonflies in the open water ecosystem (Fig. 3.5). Dragonflies are tied to freshwater aquatic habitats during the nymph stage and reproductive phase of their life cycle. This may also explain their elevated abundance in open water compared to upland forest ecosystems. Dragonflies were observed hunting in upland forest stands outside of visual encounter survey periods, but at lower abundance than the open water and coastal ecosystems. The low abundance of dragonflies in the coastal ecosystem may

be explained by the low tolerance of many dragonfly genera to salinity levels in coastal tidally influenced waterways (Zinchenko and Golovatyuk 2013). The low abundance was likely exacerbated by extreme wind at survey sites during the survey period.

Hymenoptera was the most frequently captured order in Malaise traps in all ecosystem types. However, Hymenopterans comprised of a smaller proportion of the nestling diet than Dipterans, which were not as frequently caught by the Malaise traps (Figs. 3.4 & 3.10). Therefore, I hypothesize that purple martins are selecting Dipteran prey for nestlings more often than they are available in the environment. Damselflies were only captured in Malaise traps in the coastal and open water ecosystems. In all traps, damselflies were observed gripping smaller arthropods, so I infer that they were incidentally trapped while feeding on other trapped arthropods. No dragonflies were captured in Malaise traps likely because they are agile predatory insects capable of easily avoiding obstacles.

Malaise traps are commonly used to monitor flying arthropod species composition and abundance. However, they are subject to taxonomic and placement bias. For example, Coleoptera are known to drop to the ground when they hit an obstacle, reducing their chance of being captured in the Malaise trap collection bottle (Matthews and Matthews 1971). Unfortunately, the Malaise trap sampling design used in this study was not robust enough to comprehensively measure prey availability.

DNA Sequencing

Dipteran prey was the most important order for purple martin nestlings in all ecosystem types. Trevelline et al. (2018) suggests that Dipterans may be preferentially chosen as nestling prey due to a combination of high digestibility and foraging efficiency. It is unclear to what extent purple martin nestling digestive systems are able to process the chitin of arthropod exoskeletons, but generally large amounts of chitin are not digestible (Bell 1990). Many Dipterans are partially soft-

bodied, while Odonates have extensive exoskeletons made of chitinous plates. Purple martin parents are potentially selecting for Dipteran prey based on their increased digestibility by nestlings. Odonates are agile flyers which increases capture effort and handling time. According to the Optimal Foraging Theory, prey is selected as a function of energy content and handling time, such that energy intake is maximized by trade-offs between prey size, nutritional content, and capture and handling time (MacArthur and Pianka 1966). Dipteran prey may outweigh other taxa in the foraging trade-off due to reduced capture and handling time.

Dipterans were found to be the most frequently occurring prey item in nestling diet of another swallow aerial insectivore, the barn swallow (*Hirundo rustica*) (McClenaghan et al. 2019). Within the Diptera order, barn swallows were selecting larger prey items out of proportion to their availability within the environment (McClenaghan et al. 2019). As a trade-off between digestibility and energy content, purple martins may be selecting the largest Dipteran prey items over Odonates. Dipterans were found to be most available in the environment in the upland forest ecosystem, though still comprising of a small component of total prey composition. While the openwater ecosystem has the highest dragonfly abundance and largest taxonomic diversity, upland forest may be comparably suitable due to its Dipteran availability.

Surprisingly, Coleoptera are a more important part of nestling diet in the open water ecosystem than in the upland forest ecosystem. Coleoptera were only present in Malaise traps at upland forest sites. However, purple martins are capable of feeding flights over 1km from the nest and individuals from open water sites may be travelling to upland forest or additional ecosystem types I did not sample from to acquire Coleoptera. The high diversity of arthropods in the diet at the genus level led to a surprisingly narrow range of RRA values.

Purple martins in open water ecosystems are utilizing a more taxonomically diverse array of arthropod prey items than coastal and upland forest ecosystems (Figs. 3.6-3.9). Interestingly, the upland forest habitat had the highest diversity of taxa

availability as measured by Malaise trap catch (Fig. 3.4) and the lowest diversity of taxa present in nestling diet (Fig. 3.6). This suggests that purple martins are preferentially selecting certain prey taxa for nestlings diet out of proportion to the overall taxonomic diversity. Consumption of a wide range of Diptera genera at high frequencies in open water (Fig. 3.8) is likely reflective of a greater taxonomic diversity and availability of Dipteran genera in this ecosystem. This suggests that nestlings in open water ecosystems may be more resistant to changes in composition and abundance of certain prey genera compared with nestlings in upland forest and coastal ecosystems (Figs. 3.6-3.8).

Dipteran prey were a frequent part of nestling diet across all nestling ages. The five most frequently utilized Dipteran prey genera in all ecosystem types are all present in the nestling diet at a wide range of nestling ages. These genera are likely reliably present in high numbers throughout the breeding season. Odonates were not present in the nestling diet until age 6. This is probably due to the size of many Odonates being prohibitively large compared with body size of nestlings until age 6 days. Interestingly, the frequency of Trombidiformes in the diet increases substantially from nestling age day 26-28. The genera of Trombidiformes present in nestling diet (*Piona sp.*, *Limnesia sp.*) are known to parasitize many of the arthropods present in the nestling diet, especially Chironomidae (Wiecek and Gabka 2013; Smith and Oliver 1976). I hypothesize that the increase in FOO of Trombidiformes at day 26-28 correlates with a buildup of parasites in large flying arthropods over the course of the nestling fecal survey period.

The overwhelming preferential use of Odonata by purple martins has been a long-standing belief based on reported observations of purple martins in artificial housing units. Artificial housing units tend to be erected near bodies of water. Based on my data, Odonata are frequently used in open water ecosystems, so support of this theory makes sense. Additionally, Dipterans are often more difficult to identify in the bill than Odonates. I observed this disparity in ease of identification between prey taxa while going through game camera photos. Odonata are less frequently utilized in the nestling diet in coastal and upland forest ecosystems. The frequency of Araneae in

open water ecosystem diet was a surprise. Araneae are commonly seen constructing webs on artificial nesting structures in the open water sites. It is unclear whether purple martins are gleaning Araneae off of web or while they aerially disperse across bodies of water. The high taxonomic diversity of open water nestling diet suggests purple martins in this ecosystem type are less sensitive to changes in prey species composition due to anthropogenic changes, such as climate change or land use changes. However, as discussed in the context of nestling provisioning, there are other implications of climate change on nestling survival.

Similar to this study, barn swallow fecal samples were found to contain mosquito and blowfly nest parasite DNA sequences (McClenaghan et al. 2019). The eastern subspecies of purple martin has been found to only rarely opportunistically consume mosquitos when they are in large numbers (Kale 1968; Johnston 1967). However, purple martins have been advertised as having the capacity to act as a control for mosquito populations. Although backed by no scientific data, companies used this theory as a marketing strategy to sell purple martin houses and a backlash by purple martin researchers ensued (Kale 1968). Interestingly, western purple martins utilize mosquitos as a prey item for nestlings in all three ecosystems, especially in the open water ecosystem. I've readily observed blowfly nest parasites on purple martin nestlings during nestling handling. It is impossible to determine through metabarcoding whether nestlings are being fed blowflies in the larval stage out of the nest or in the adult life stage captured in the air column.

Taxonomic bias due to the disparate efficiency of primer-to-amplicon binding between taxa reduces the quantitative power of metabarcoding studies. However, primer bias can be overcome by improved primer design as metabarcoding continues to progress (Yu et al. 2018). The ANML primers (Jusino et al. 2018) amplify a broader array of arthropod taxa than previously described primers, but they are subject to taxonomic bias during initial PCR and sequencing. For example, on the forward primer, Dipteran prey genera have 0-2 nucleotide mismatches, while Odonate prey genera have 2-6 nucleotide mismatches, with some occurring closer to the 3' end. This undoubtedly leads to some inflation of FOO and RRA values for Dipteran

prey species in this study. However, other metabarcoding studies of avian diet using different primers presumably with different taxonomic biases also found Dipterans to be a major component of nestling diet (Moran et al. 2019; McClenaghan et al. 2019; Trevelline et al. 2018).

Nestling Provisioning

Nestling provisioning rates can affect nestling diet quality, which can provide insight into the survival rate of nestlings after fledging. Provisioning rates are hard to interpret without information on prey size and nutritional content. High provisioning rates might suggest increased use of smaller prey items with lower nutritional quality. However, the reduction in energy expenditure during capture and handling time might outweigh the nutritional cost. The wide range of number of feeding events in a day in all ecosystem types could be reflective of the inefficiency of game cameras sensors in detecting fast entry into cavities (Table 3.5). Alternatively, it reflects the response of provisioning rates to daily changes in temperature and moisture conditions. Aerial arthropods don't usually fly in wet or very cold conditions. As aerial insectivores, purple martin activity is directly impacted by the reduction of flying arthropod activity during inclement weather.

During the game camera survey time period, foggy conditions occurred in the coastal and upland forest habitats. Rain events were not detected. Western Oregon experienced an extreme heat event lasting four days during the nestling phase in July. Temperatures displayed on game cameras during this time were 115°F in the upland forest and 121°F in the open water, however these temperatures likely differ from ambient air temperatures. The Oregon Climate Service archived temperatures ranging from 98-104°F on these days. Nestling provisioning rates dropped during the afternoons over the course of this extreme heat event. In fact, the upland forest game camera logged nestlings as being in the nest for 30 days before fledging. The typical fledging phase lasts 28 days. The upland forest nestlings were noticeably emaciated when banded at approximately age 16. I observed several underdeveloped nestlings in the water and surrounding vegetation well before the anticipated fledge date at open

water sites. As seen on the upland forest game camera, nestlings exited the artificial nest cavity to potentially find refuge on the small landing platform. On this model of artificial nest, the platform is lined with a raised lip, which prohibited the nestlings from falling off. The platform on nest boxes at open water sites do not have a lip, so it is likely that nestlings fell off while seeking refuge from high temperatures.

The increased frequency and severity of extreme heat events due to climate change is predicted to increase lethal impacts to birds (McKechnie and Wolf 2009). Physiological lethal impacts include evaporative water loss leading to dehydration even while birds are inactive in the shade (Wolf and Walsberg 1996). Purple martins remain relatively inactive in shaded cavities for the entirety of their nestling phase. Artificial housing units may not buffer internal cavity temperatures as efficiently as snag cavities do. It is recommended that future studies examine the relationship between internal cavity temperature and cavity wall material and thickness. In the context of climate change, certain styles of artificial housing units may become lethal during extreme heat events. Purple martins nesting in snag cavities in upland forest early seral forest have little refuge from extreme heat events. In fact, many aerial insectivores are early seral obligates and may be physiologically imperiled by the increased frequency and severity of extreme heat events. Declines of many aerial insectivores are attributed to reduced insect populations, in addition to habitat loss and degradation (Nebel et al. 2010). Climate change may act synergistically with these threats to accelerate the decline of aerial insectivores as a guild.

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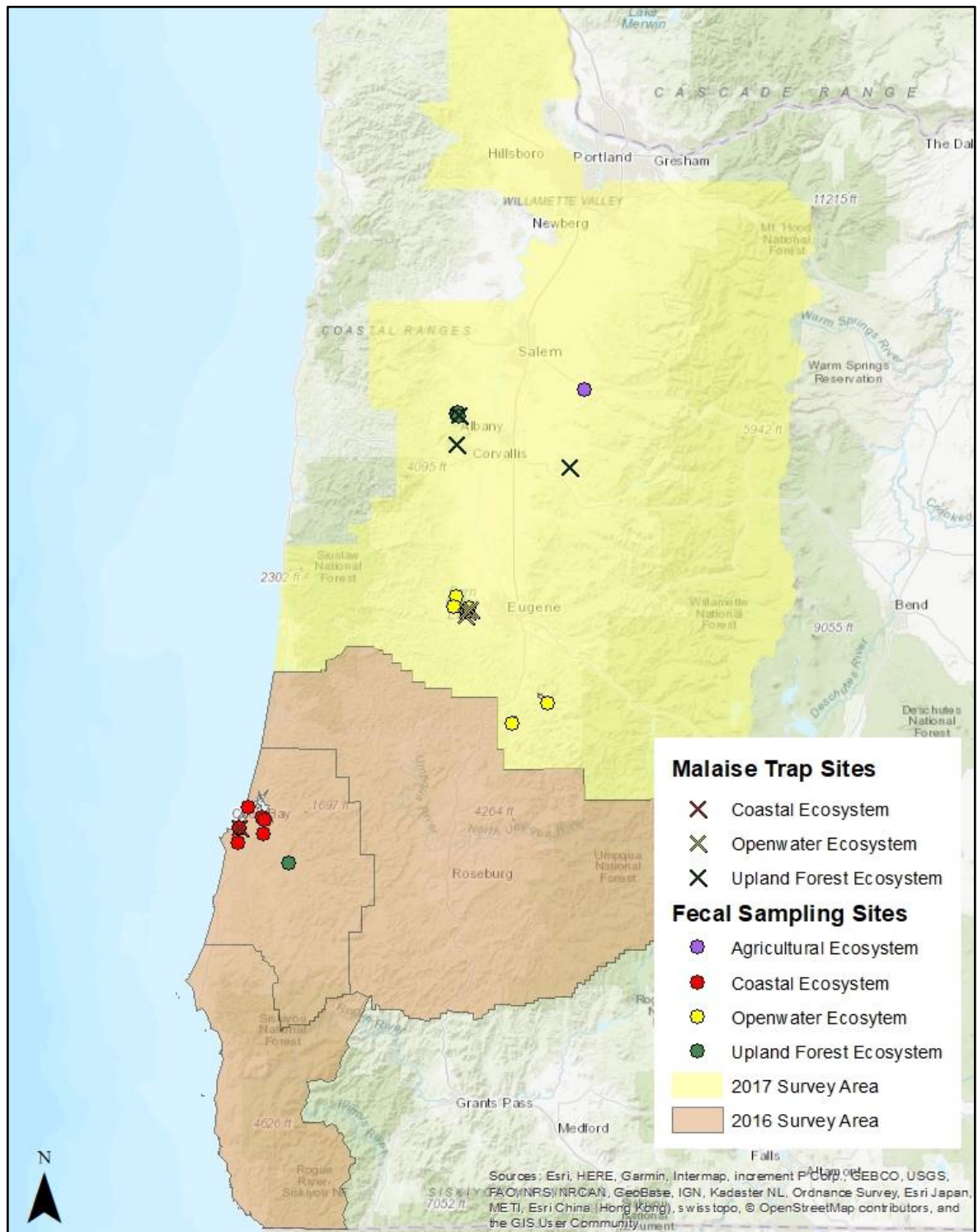


Figure 3.1. Aerial topographic imagery of the study area for prey availability sampling and nestling fecal sampling in western Oregon in 2016 and 2017. Points represent sites where nestling fecal samples were collected during the nestling color-banding program and crosses represent sites where Malaise traps were employed to measure prey availability.

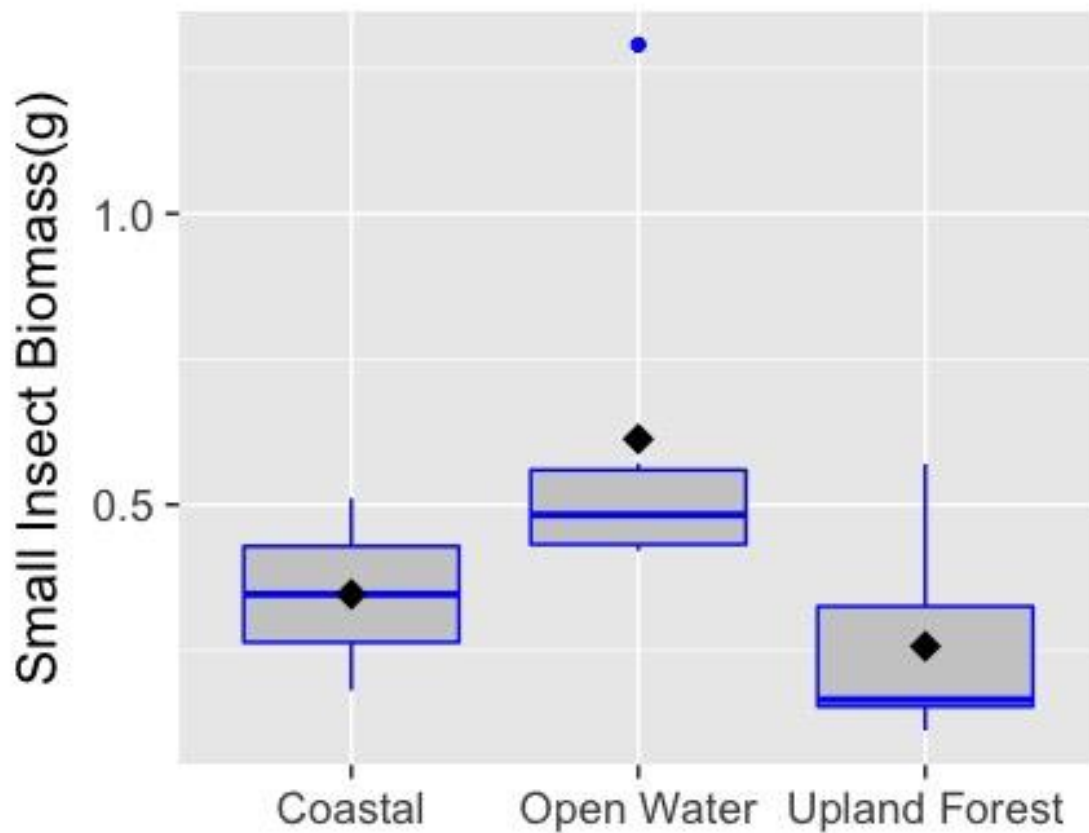


Figure 3.2. A box plot displaying the median, mean, minimum and maximum values for <13mm insect biomass for coastal, inland open-water, and upland forest ecosystems. Horizontal center blue lines represent the median. Black diamonds represent the mean. Minimum and maximum values are represented by the vertical whiskers, with maximum above the box and minimum below the box. Blue points represent outliers likely due to insect hatch events.

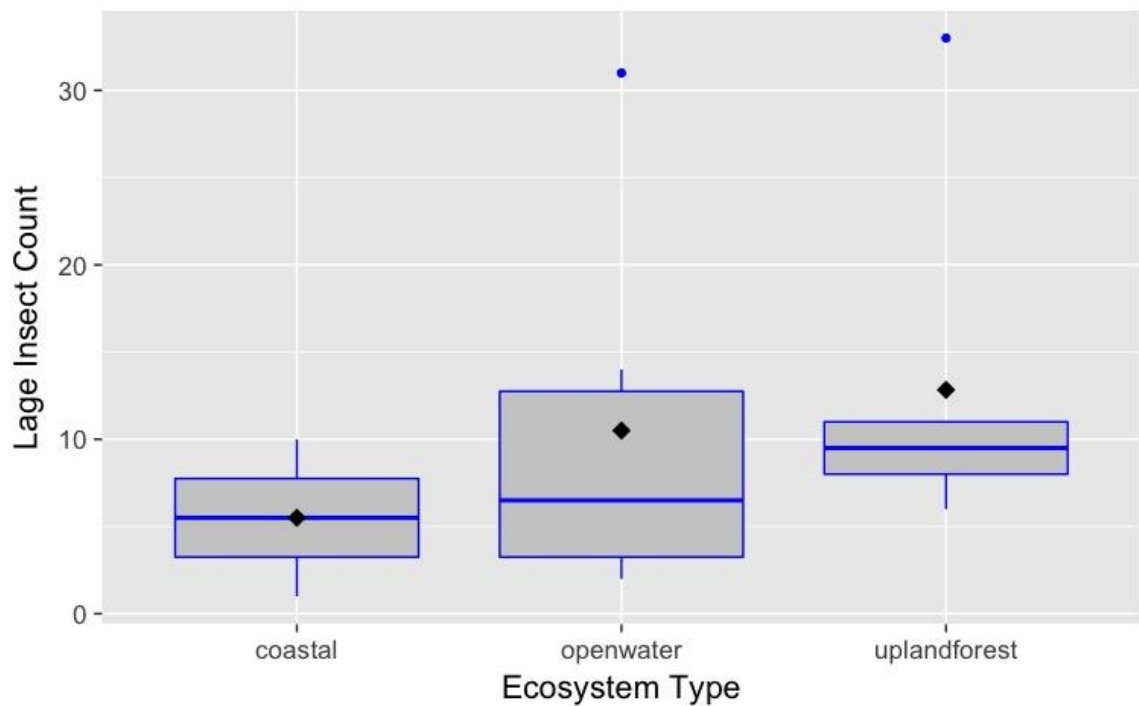


Figure 3.3. A box plot displaying the median, mean, minimum and maximum values for >13mm insect count for coastal, inland open water, and upland forest ecosystems. Horizontal center blue lines represent the median. Black diamonds represent the mean. Minimum and maximum values are represented by the vertical whiskers, with maximum above the box and minimum below the box. Blue points represent outliers likely due to insect hatch events.

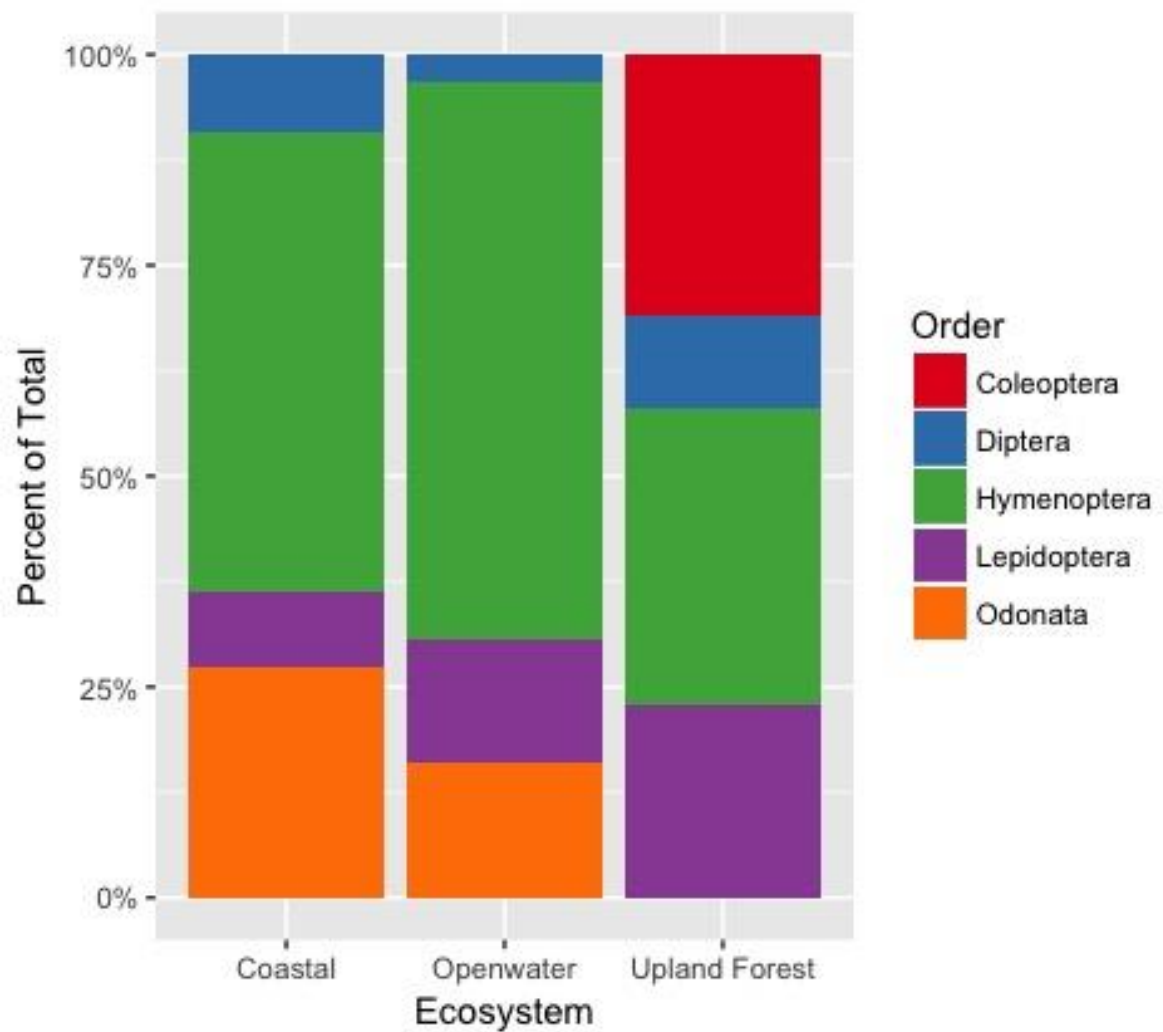


Figure 3.4. A stacked bargraph showing the composition of arthropod orders by ecosystem type (i.e. coastal, openwater, upland forest) as a percent out of total arthropods in the sample. Arthropod samples were collected passively in Malaise traps in each ecosystem type to inform prey composition and abundance. Arthropod orders are coded by color.

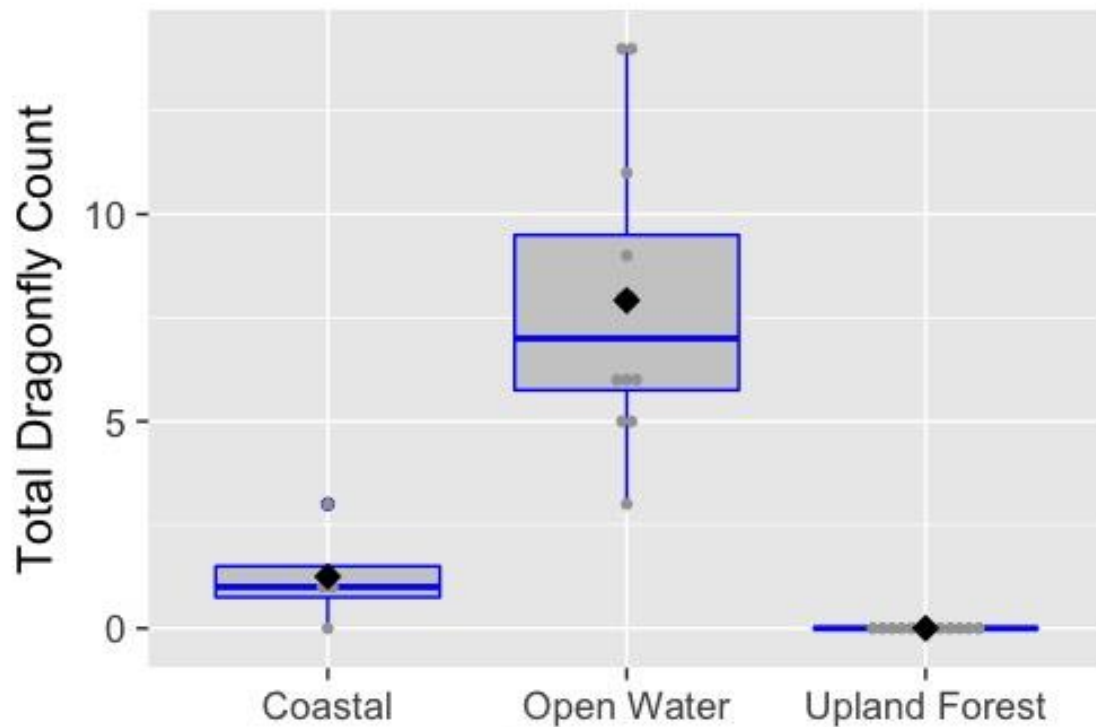


Figure 3.5. A box plot displaying the median, mean, minimum and maximum values for total dragonfly count in coastal, inland open-water, and upland forest ecosystems. Dragonfly count was determined by four 10-minute visual encounter survey periods at three sites in each ecosystem type. Horizontal center blue lines represent the median. Black diamonds represent the mean. Minimum and maximum values are represented by the vertical whiskers, with maximum above the box and minimum below the box.

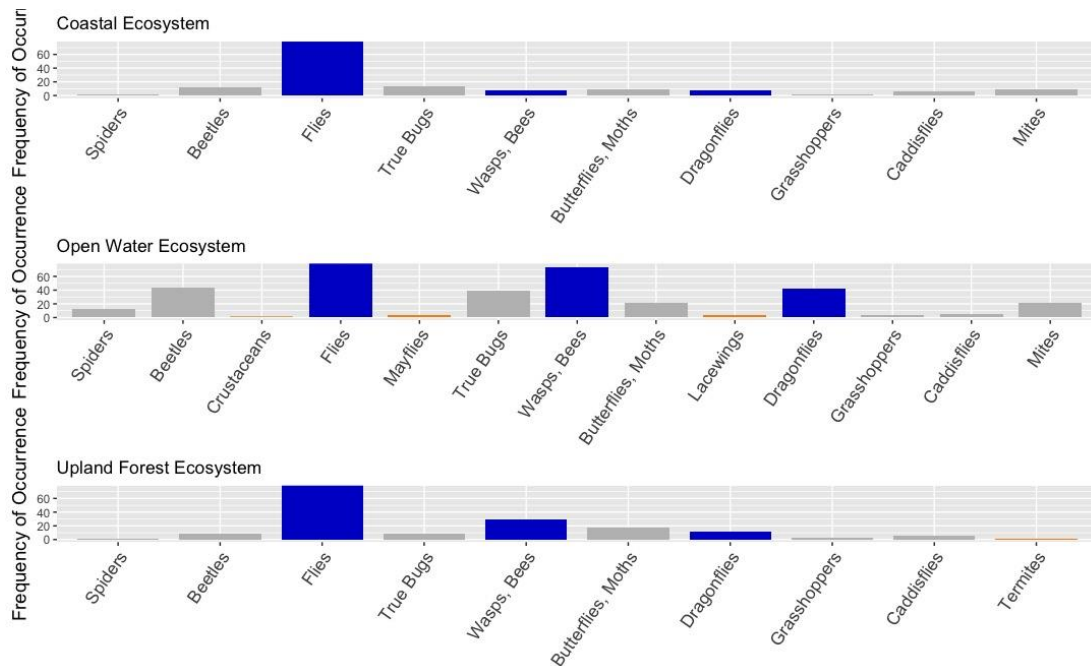


Figure 3.6. A bargraph with a y-axis break at 80 FOO displaying the composition of prey items found in nestling fecal samples by arthropod order for coastal, open-water, and upland forest ecosystems. Ecosystems were standardized by the number of samples in each. The N/A category represents reads that were not taxonomically assigned at the order level.

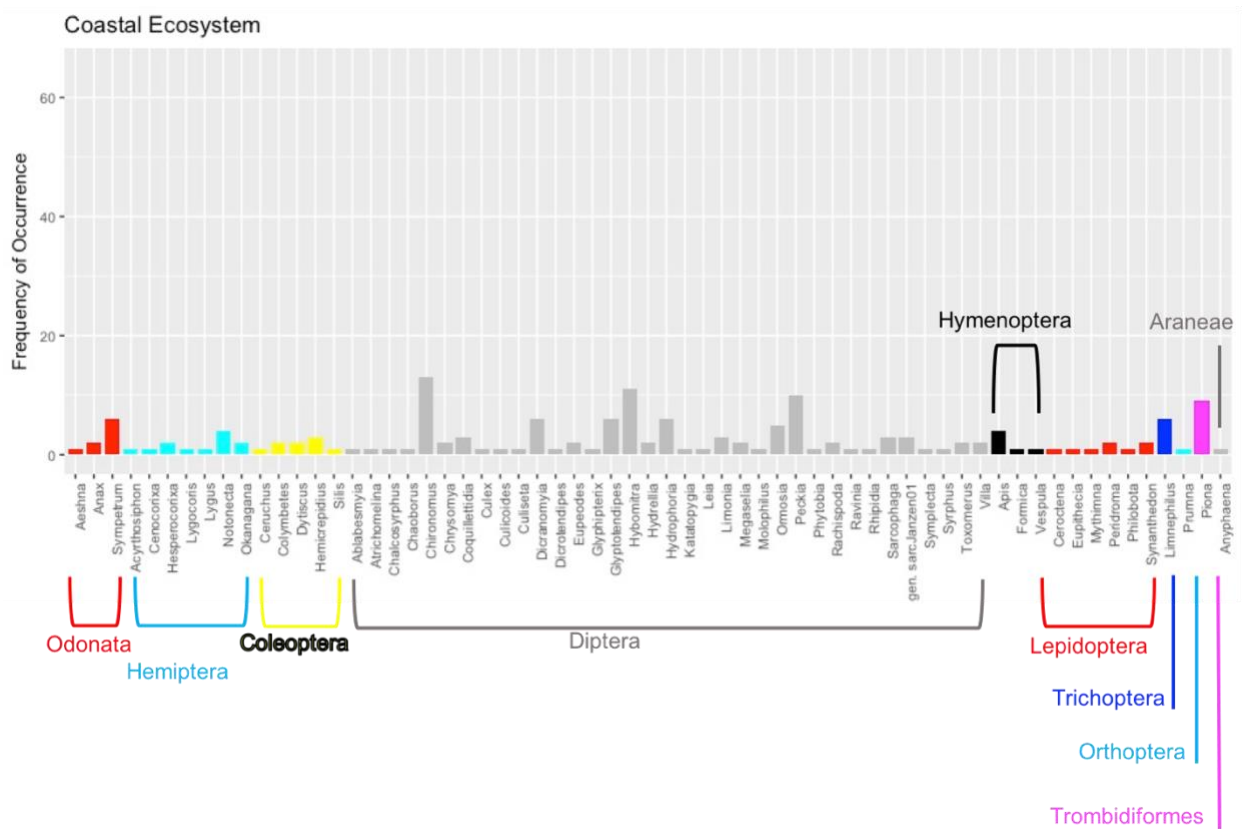


Figure 3.7. A bar graph showing the frequency of occurrence of prey taxa by arthropod genus in nestling fecal samples with a y-axis break at 65 FOO for the coastal ecosystem. Prey genera are grouped and color coded by taxonomic order.

Figure 3.8. A bar graph showing the frequency of occurrence of prey taxa by arthropod genus in nestling fecal samples with a y-axis break at 65 FOO for the open water ecosystem. Prey genera are grouped and color coded by taxonomic order.

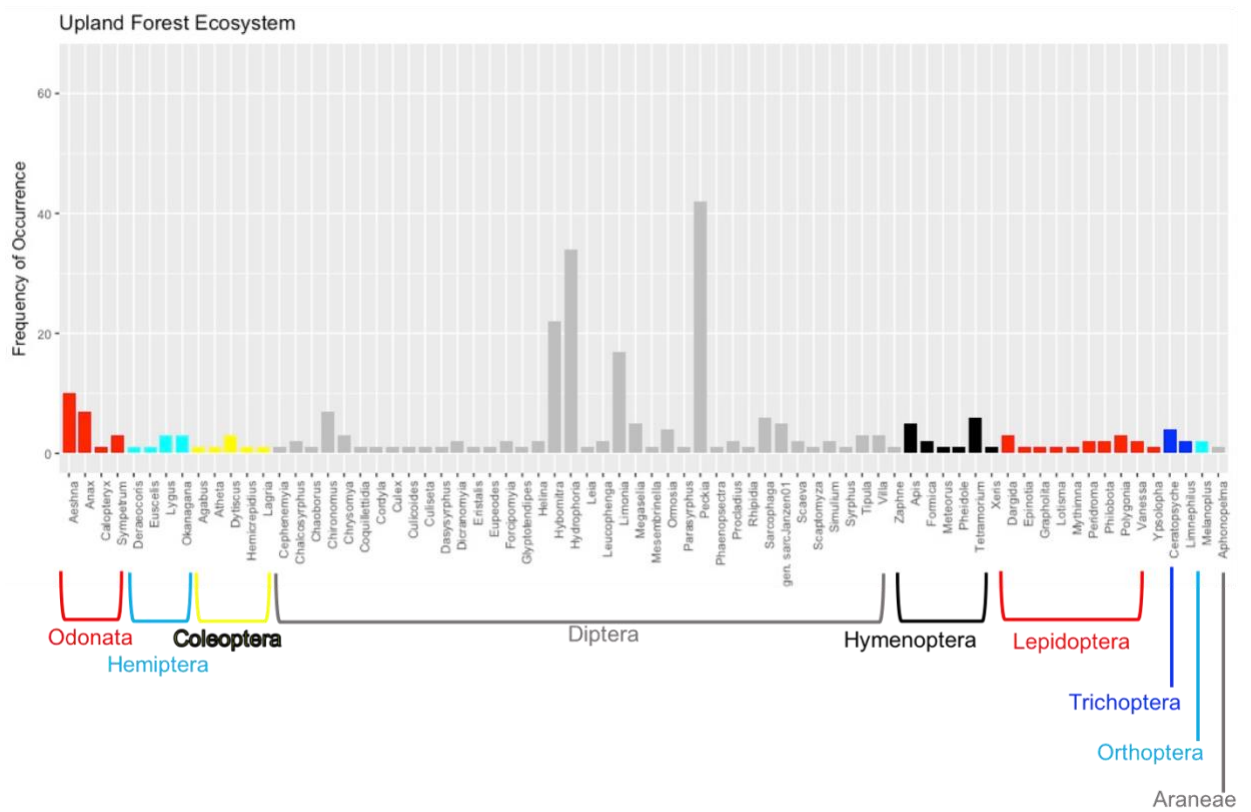


Figure 3.9. A bar graph showing the frequency of occurrence of prey taxa by arthropod genus in nestling fecal samples with a y-axis break at 65 FOO for the upland forest ecosystem. Prey genera are grouped and color coded by taxonomic order.

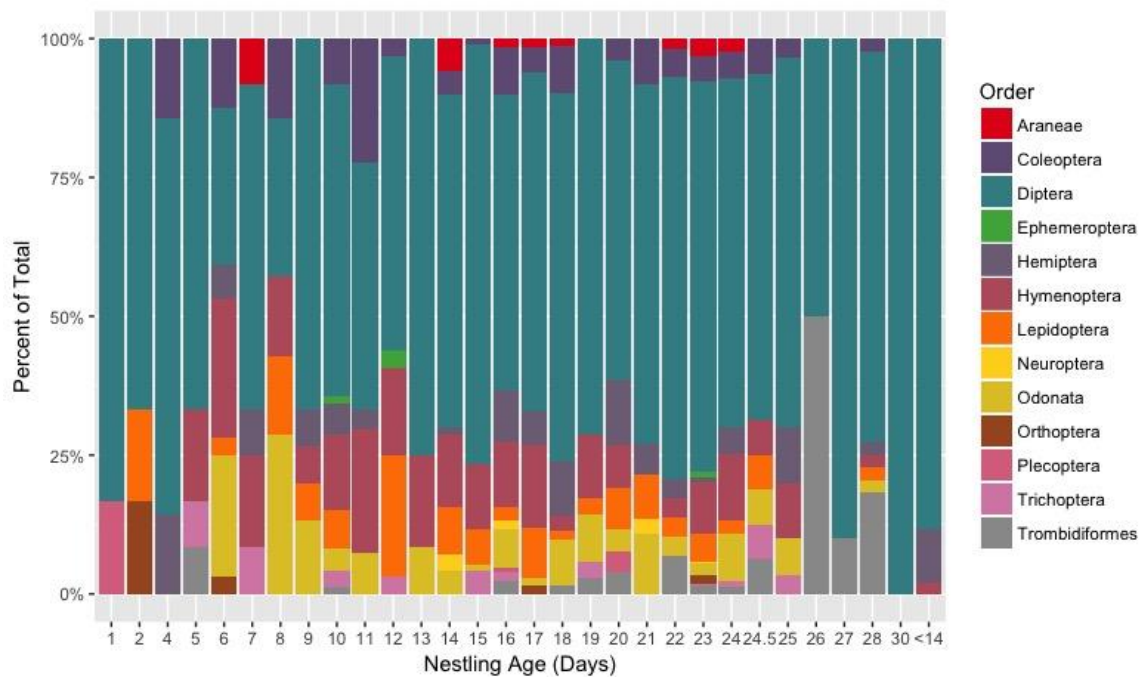


Figure 3.10. A stacked bargraph displaying the percent composition of prey items found in all fecal nest samples by nestling age across all ecosystems. Ecosystems were standardized by the number of samples in each. The <14 age category represents all nestling fecal samples that were under 14 days of age but were not aged to a specific age by the technician.

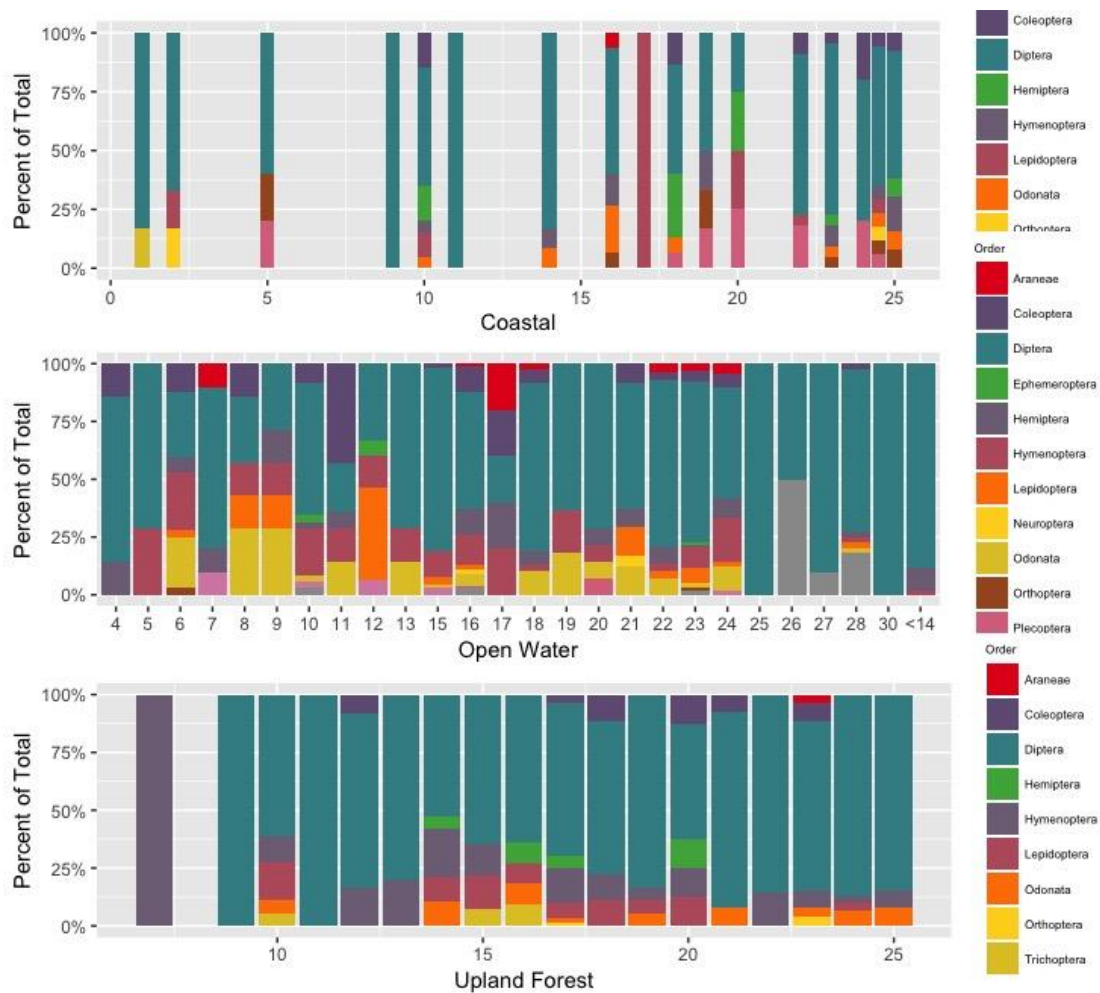


Figure 3.11. A stacked bargraph displaying the percent composition of prey orders found in all fecal nest samples by nestling age for the coastal, open water, and upland forest ecosystems. Ecosystems were standardized by the number of samples in each.

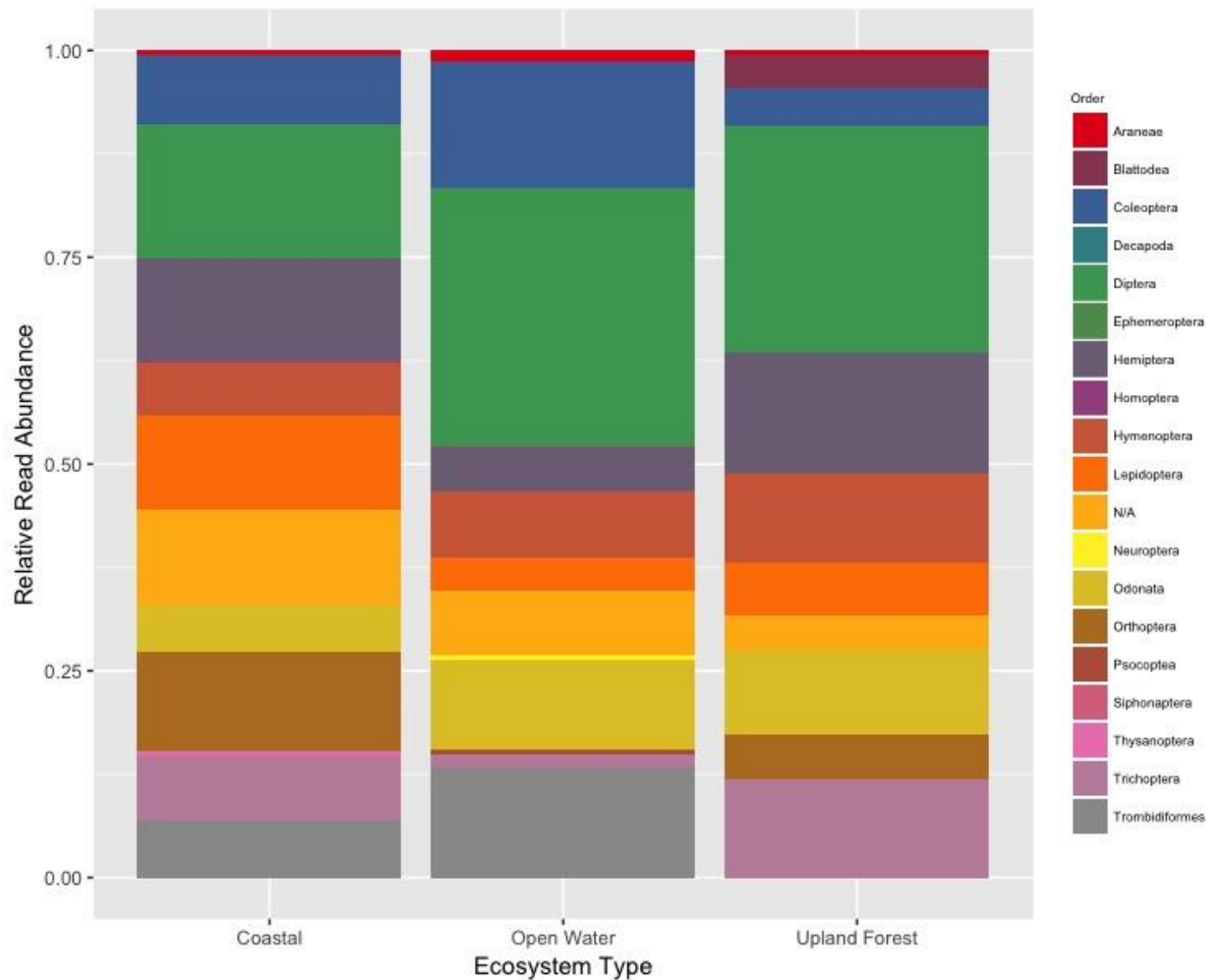


Figure 3.12. A stacked bargraph displaying the mean relative read abundance of purple martin nestling prey orders averaged across nest level fecal samples for each ecosystem type (coastal, open water, and upland forest). Ecosystems were standardized by the number of samples in each.

Table 3.1. The number of successful and unsuccessful extraction amplifications using different Qiagen extraction kits by ecosystem type, where 0 = failed amplification and 1 = successful amplification.

ECOSYSTEM AND KIT TYPE	0	1	TOTAL
COASTAL	8	33	41
POWERFECAL DNA	8	33	41
OPEN WATER	52	75	127
DNEASY BLOOD & TISSUE	30	10	40
QIAAMP FAST DNA STOOL	2	2	4
POWERFECAL DNA	20	63	83
UPLAND FOREST	9	31	40
POWERFECAL DNA	9	31	40
WPMWG	13	27	40
DNEASY BLOOD & TISSUE	13	5	18
POWERFECAL DNA	0	22	22
TOTAL	82	166	248

Table 3.2. The most frequently detected arthropod prey order, family, genus, and species for coastal, open water, and upland forest ecosystems.

Ecosystem	Most Frequent - Order	Most Frequent - Family	Most Frequent - Genus	Most Frequent - Species
Coastal	Diptera (FOO: 0.58)	Chironomidae (FOO: 0.16)	Chironomus (FOO: 0.07)	<i>Chironominae</i> <i>sp.</i> (FOO: 0.05)
Open Water	Diptera (FOO: 0.66)	Chironomidae (FOO: 0.29)	Chironomus (FOO: 0.15)	<i>Chironomus sp.</i> (FOO: 0.12)
Upland Forest	Diptera (FOO: 0.69)	Sarcophagidae (FOO: 0.19)	Peckia (FOO: 0.15)	<i>Peckia intermutans</i> (FOO: 0.13)

Table 3.3. Summary table of the mean Relative Read Abundance (RRA) of prey orders in nestling diet for each ecosystem type (coastal, open water, and upland forest). RRA was averaged by ecosystem type and then standardized to be out of 100%.

Order	Coastal	Open Water	Upland Forest
Araneae	0.6%	1.5%	0.6%
Blattodea	0	0	4.2%
Coleoptera	9.6%	16.4%	4.8%
Decapoda	0	0.2%	0
Diptera	18.3%	33.1%	28.5%
Ephemeroptera	0	0.6%	0
Hemiptera	14.0%	5.9%	15.3%
Homoptera	0.2%	0.1%	0
Hymenoptera	7.2%	8.7%	11.3%
Lepidoptera	12.9%	4.4%	6.6%
Neuroptera	0	0.6%	0
Odonata	6.3%	11.8%	10.6%
Orthoptera	13.5%	0.1%	5.6%
Psocoptea	0	0.4%	0
Siphonaptera	0.2%	0	0
Thysanoptera	0.6%	0	0
Trichoptera	8.8%	1.7%	12.4%
Trombidiformes	7.8%	14.4%	0
Total	1	1	1

Table 3.4. Summary table of the mean Relative Read Abundance (RRA) of prey genera by order in nestling diet for each ecosystem type (coastal, open water, and upland forest). RRA was averaged by ecosystem type and then standardized to be out of 100%.

Prey Genera	Coastal	Open Water	Upland Forest
Araneae	0.2%	1.2%	0.1%
Anyphaena	0.2%	0.1%	0.0%
Aphonopelma	0.0%	0.0%	0.1%
Argiope	0.0%	0.0%	0.0%
Bathypantes	0.0%	0.6%	0.0%
Brachypelma	0.0%	0.1%	0.0%
Clubiona	0.0%	0.1%	0.0%
Nesticella	0.0%	0.0%	0.0%
Pholcus	0.0%	0.0%	0.0%
Steatoda	0.0%	0.1%	0.0%
Tetragnatha	0.0%	0.3%	0.0%
Coleoptera	7.4%	19.4%	4.8%
Acilius	0.0%	2.4%	0.0%
Agabus	0.0%	0.1%	0.1%
Aphthona	0.0%	0.1%	0.0%
Atheta	0.0%	0.0%	1.6%
Bembidion	0.0%	0.0%	0.0%
Buprestis	0.0%	5.3%	0.0%
Ceruchus	0.1%	0.0%	0.0%
Coccinella	0.0%	0.1%	0.0%
Colymbetes	0.4%	2.0%	0.0%
Coquillettida	0.6%	0.5%	1.0%
Dytiscus	0.9%	3.2%	1.3%
Harmonia	0.0%	0.1%	0.0%
Hemicrepidius	5.5%	2.6%	0.7%
Hippodamia	0.0%	0.8%	0.0%
Hydaticus	0.0%	0.0%	0.0%
Lagria	0.0%	0.0%	0.0%
Niphona	0.0%	0.1%	0.0%
Pterostichus	0.0%	0.0%	0.0%
Rhantus	0.0%	0.0%	0.0%
Xestoleptura	0.0%	1.8%	0.0%
Decapoda	0.0%	0.0%	0.0%
Caridina	0.0%	0.0%	0.0%

Diptera	31.2%	46.4%	46.2%
Ablabesmyia	0.2%	0.1%	0.0%
Aedes	0.0%	0.2%	0.0%
Anopheles	0.0%	0.0%	0.0%
Archytas	0.0%	0.3%	0.0%
Asteromyia	0.0%	0.0%	0.0%
Atrichomelina	1.4%	0.0%	0.0%
Chalcosyrphus	0.4%	1.0%	0.0%
Chaoborus	0.0%	0.7%	0.3%
Chironomus	3.1%	1.9%	1.7%
Chrysomya	0.3%	0.0%	1.0%
Coenosia	0.0%	0.1%	0.0%
Cordyla	0.0%	0.0%	0.1%
Cryptochironomus	0.0%	0.0%	0.0%
Cryptomeigenia	0.0%	0.1%	0.0%
Culex	0.0%	0.4%	4.8%
Culicoides	0.6%	0.0%	0.0%
Culiseta	0.1%	0.8%	0.1%
Cuterebra	0.0%	0.0%	0.0%
Daphnia	0.0%	0.0%	0.0%
Dasysyrphus	0.0%	0.0%	0.7%
Dicranomyia	1.0%	4.4%	3.9%
Dicrotendipes	0.2%	0.1%	0.0%
Drosophila	0.0%	4.5%	0.0%
Erioptera	0.0%	0.0%	0.0%
Eristalis	0.0%	0.1%	1.4%
Eupeodes	0.2%	0.0%	3.7%
Forcipomyia	0.0%	0.2%	0.3%
Glyptotendipes	0.6%	0.7%	1.0%
Gymnophora	0.0%	7.0%	0.0%
Helina	0.0%	0.0%	1.1%
Hybomitra	3.2%	2.4%	2.7%
Hydrellia	0.3%	0.0%	0.0%
Hydrophoria	1.1%	2.0%	1.9%
Katatopygia	0.5%	0.0%	0.0%
Leia	5.4%	0.3%	0.1%
Leptocera	0.0%	0.1%	0.0%
Leucophenga	0.0%	0.0%	0.8%
Limnophora	0.0%	0.0%	0.0%

Limonia	1.6%	1.1%	2.5%
Lispe	0.0%	0.1%	0.0%
Megaselia	1.4%	0.0%	1.1%
Megasyrphus	0.0%	0.2%	0.0%
Mesembrinella	0.0%	0.0%	1.2%
Molophilus	0.1%	0.5%	0.0%
Nilodorum	0.0%	0.2%	0.0%
Ochlerotatus	0.0%	1.3%	0.0%
Ormosia	1.2%	1.0%	0.4%
Orthocladus	0.0%	0.0%	0.0%
Parasyrphus	0.0%	0.0%	0.9%
Peckia	1.5%	0.0%	3.1%
Pentacricia	0.0%	0.0%	0.0%
Phaenopsectra	0.0%	0.0%	0.4%
Phylidorea	0.0%	0.0%	0.0%
Phytobia	0.1%	0.0%	0.0%
Procladius	0.0%	0.4%	0.5%
Psectrotanypus	0.0%	0.3%	0.0%
Psychoda	0.0%	0.5%	0.0%
Rachispoda	1.9%	0.1%	0.0%
Ravinia	0.1%	0.0%	0.0%
Rheocricotopus	0.0%	0.0%	0.0%
Rhipidia	2.0%	1.2%	0.6%
Sarcophaga	0.5%	0.0%	1.0%
Sarcophagidae gen. sarcJanzen01	0.3%	3.5%	0.2%
Scaeva	0.0%	0.0%	0.1%
Scaptomyza	0.0%	0.2%	0.6%
Simulium	0.0%	0.2%	0.8%
Spilogona	0.0%	2.4%	0.0%
Sylvicola	0.0%	0.0%	0.0%
Symplecta	0.9%	2.0%	0.0%
Syrphus	0.1%	0.0%	2.5%
Tipula	0.0%	3.4%	0.4%
Toxomerus	0.6%	0.0%	0.0%
Urophora	0.0%	0.2%	0.0%
Villa	0.2%	0.0%	4.2%
Zaphne	0.0%	0.0%	0.1%
Ephemeroptera	0.0%	0.2%	0.0%

Hexagenia	0.0%	0.0%	0.0%
Maccaffertium	0.0%	0.2%	0.0%
Hemiptera	24.2%	11.1%	8.6%
Banasa	0.0%	3.1%	0.0%
Belostoma	0.0%	0.0%	0.0%
Callicorixa	0.0%	0.2%	0.0%
Cenocorixa	0.2%	1.5%	0.0%
Chlorochroa	0.0%	0.2%	0.0%
Corisella	0.0%	0.1%	0.0%
Deraeocoris	0.0%	0.1%	0.9%
Dikrella	0.0%	0.7%	0.0%
Essigella	0.0%	0.1%	0.0%
Euscelis	0.0%	0.0%	0.6%
Hesperocorixa	0.3%	0.6%	0.0%
Lygocoris	7.9%	0.0%	0.0%
Lygus	7.5%	0.3%	1.2%
Mollitrichosiphum	0.0%	0.2%	0.0%
Myzus	0.0%	0.2%	0.0%
Notonecta	1.4%	1.7%	0.0%
Okanagana	7.0%	1.3%	5.9%
Ophiothrix	0.1%	0.0%	0.0%
Paracolopha	0.0%	0.0%	0.0%
Phytocoris	0.0%	0.8%	0.0%
Homoptera	0.1%	0.0%	0.0%
Acyrtosiphon	0.1%	0.0%	0.0%
Idiocerus	0.0%	0.0%	0.0%
Hymenoptera	9.6%	7.4%	19.9%
Aeshna	0.3%	1.0%	1.0%
Apis	1.5%	2.5%	2.1%
Callibaetis	0.0%	1.0%	0.0%
Cephenemyia	0.0%	0.0%	0.3%
Dolichovespula	0.0%	0.8%	0.0%
Formica	6.7%	0.3%	0.1%
Meteorus	0.0%	0.0%	5.7%
Pheidole	0.0%	0.1%	0.4%
Tetramorium	0.0%	1.7%	2.8%
Urocerus	0.0%	0.0%	0.0%
Vespula	1.0%	0.0%	0.0%
Xeris	0.0%	0.0%	7.4%

Lepidoptera	15.9%	4.9%	6.5%
Batia	0.0%	0.0%	0.0%
Caloptilia	0.0%	0.0%	0.0%
Ceroctena	0.3%	0.0%	0.0%
Dargida	0.0%	1.3%	2.1%
Dismorphia	0.0%	0.0%	0.0%
Epinotia	0.0%	0.9%	0.3%
Eupithecia	0.5%	0.6%	0.0%
Glyphipterix	8.3%	0.0%	0.0%
Grapholita	0.0%	0.0%	0.0%
Hyles	0.0%	0.6%	0.0%
Lotisma	0.0%	0.0%	0.5%
Mythimna	1.5%	0.0%	0.0%
Noctua	0.0%	0.4%	0.0%
Parornix	0.0%	1.0%	0.0%
Peridroma	3.5%	0.0%	1.2%
Philobota	1.0%	0.0%	0.8%
Polygonia	0.0%	0.0%	1.4%
Prionoxystus	0.0%	0.1%	0.0%
Synanthedon	0.9%	0.0%	0.0%
Vanessa	0.0%	0.0%	0.1%
Ypsolopha	0.0%	0.0%	0.0%
Neuroptera	0.0%	0.3%	0.0%
Chrysoperla	0.0%	0.1%	0.0%
Hemerobius	0.0%	0.2%	0.0%
Sisyra	0.0%	0.0%	0.0%
Odonata	2.9%	3.5%	8.1%
Aeshna	0.0%	0.0%	4.9%
Anax	0.8%	0.5%	2.5%
Calopteryx	0.0%	0.0%	0.0%
Enallagma	0.0%	0.1%	0.0%
Neodythemis	0.0%	0.0%	0.0%
Sympetrum	2.1%	2.8%	0.7%
Orthoptera	3.8%	0.0%	1.1%
Kosciuscola	0.0%	0.0%	0.0%
Melanoplus	0.0%	0.0%	1.1%
Prumna	3.8%	0.0%	0.0%
Thysanoptera	0.2%	0.0%	0.0%
Haplothrips	0.2%	0.0%	0.0%

Trichoptera	2.5%	1.5%	4.9%
Ceratopsyche	0.0%	0.0%	2.4%
Limnephilus	2.5%	0.0%	2.5%
Philorheithrus	0.0%	1.2%	0.0%
Wormaldia	0.0%	0.2%	0.0%
Trombidiformes	2.2%	4.1%	0.0%
Limnesia	0.0%	1.7%	0.0%
Piona	2.2%	2.4%	0.0%
Total	100.0%	100.0%	100.0%

Table 3.5. Summary data of nestling provisioning collected visually surveying photos of purple martin nest sites in upland forest, inland open-water, and coastal ecosystems. All photos were collected by motion sensor game cameras.

Ecosystem	Upland Forest	Open water	Coastal
Average Provisioning Rate	37.44	50.4	51.5
Minimum Visits On a Single Day	12	23	11
Maximum Visits On a Single Day	82	94	68
Total Recorded Visits	1011	1109	515

CHAPTER 4. SYNOPSIS AND CONCLUSIONS

Lorelle Sherman

As a species of conservation concern in the Pacific Northwest, it is crucial to utilize conservation resources on populations of purple martins that can sustain themselves. To sustain snag-nesting populations, an understanding of the processes driving the population dynamics of purple martin colonies is necessary to guide management decisions. Based on the little information we have of western purple martin life history and biology, I assume that prey availability and nest site availability are the two key components of habitat quality. Martins may be subject to both nest site and prey availability limitations in western Oregon. The combined results of my second and third chapter begin to describe the potential limitations martins are subject to in each of the three ecosystem types they nest in. Understanding what colonies in different ecosystem types are limited by will help guide management decisions about where to focus efforts in efficiently bolstering populations.

The snag-nesting population of purple martins in western Oregon may represent an opportunity to maintain self-sustaining populations in the Pacific Northwest. Snag-nesting purple martins are widely distributed in small numbers throughout western Oregon. Martins are primarily (45 out of 174 sites) occupying private timberlands as opposed to public lands (16 out of 174 sites). The area of early seral habitat within a stand affects the probability of occupancy by a breeding pair of purple martins. Interestingly, purple martins rarely occupied snags less <100m from mature forest edge. They are used cavities in a wide range of DBH classes. According to my data, there is a 0.5 probability of occupancy when there is approximately 46 acres of early seral within a 314 ha stand. This implies that as long as snags are left at least 100m from mature forest edge in stands with a component of early seral forest, the probability of occupancy is moderately high.

I created a predictive habitat suitability model that identifies purple martin habitat throughout western Oregon. This is a valuable tool for identifying sites for future occupancy surveys. Users can decide on a suitable threshold of probability of

occupancy and extract all locations above this threshold for on the ground occupancy and reproduction surveys. A major limitation of the model is the lack of landscape-level data on snag distribution. With no contiguous snag data available for western Oregon, sites identified as having high probability of occupancy values based on area of early seral must be visited to check for the presence of cavities in leave trees or snags. The AUC fit index of 0.8134 infers that there will be some false positives in the model output. In this situation, the model would identify a site lacking available nest snags as having a high probability of occupancy by nesting martins due to favorable measures of other habitat variables.

I successfully utilized metabarcoding techniques to non-invasively study the diet of a sensitive status species. The results of this study revealed a potential preferential use of Dipteran prey for nestling diet. Dipteran prey were found to be a frequent part of nestling diet across all nestling ages and all ecosystem types. Trevelline et al. 2018 suggests that Dipterans may be preferentially chosen as nestling prey items due to a combination of increased digestibility and increased foraging efficiency. Purple martins in open water ecosystems are utilizing a more taxonomically diverse array of arthropod prey items than coastal and upland forest ecosystems. This suggests the potential for nestlings in open water ecosystems to be more resistant to changes in composition and abundance of prey compared with nestlings in upland forest and coastal ecosystems.

The observational data collected on the impacts of extreme heat events on nestling health was a serendipitous result of game camera use and nestling color banding. Nestling provisioning rates were severely reduced during the hottest part of the day during the four-day extreme heat event. Many nestlings prematurely fledged the nest, sought refuge on the artificial nest platform, or were emaciated at the time of banding. Purple martins remain relatively inactive in shaded cavities for the entirety of their nestling phase. Artificial housing units may not buffer internal cavity temperatures as efficiently as snag cavities do. I recommended that future studies examine the relationship between internal cavity temperature and cavity wall material

and thickness. In the context of climate change, certain styles of artificial housing units may become lethal during extreme heat events.

The scope of this study is limited to western purple martin populations in western Oregon. However, similar ecosystem types exist throughout the Pacific Northwest where nesting structure and prey taxa are likely comparable to that of my study. Wildlife and forest managers in Oregon should be cautioned in using these results outside of the region encompassed by the study area, because forest management practices vary widely regionally and with different land owners. This study revealed several habitat characteristics associated with purple martin occupancy that are relevant to land managers. The optimal distance from mature forest and amount of early seral within a stand and landscape are attainable through common forest management practices. Using the prediction model, wildlife and land managers can identify locations with moderate to high probability of occupancy values for habitat enhancement opportunities, such as the creation of snags or additional early seral forest acreage. Once candidate sites for habitat enhancement have been identified, sampling for prey availability can provide additional support for management decisions before extensive resources are expended. My results on diet composition are exploratory, but they can be used to refine future studies of prey availability by utilizing sampling techniques shown to effectively catch known prey types. Now that we know what purple martins in western Oregon are consuming, prey taxa populations can be monitored long-term.

I recommend the development of a snag data component for inclusion in future model versions. Reliable and geographically continuous snag data is challenging to collect due to their highly variable spatial distribution, which requires complex and intensive sampling methods (Wing et al. 2015). There have been attempts to create an algorithm to extract snag presence from LiDAR (Wing et al. 2015) and Landsat (Frescino et al. 2001) data. However, these studies are plagued by variable detection rates and several methodological limitations. For example, Bater et al. (2009) successfully retrieved live and dead tree data from the use of LiDAR based

on the assumption that the presence of standing dead trees and vertical stand structure are strongly related. This may be true for naturally regenerating forest and may not be true for snags retained during clearcut harvesting. Martinuzzi et al. (2009) found higher accuracy of snag detection in mature multistory and old growth forest than in young multistory and understory reinitiation forests. I suggest that improvements in snag-detection algorithms for early seral forest are needed for use in purple martin habitat models. The estimates of snag densities and heights in harvest units and recent burns would substantially improve the model. Snag density data may allow for estimates of current population size and of the current total amount of suitable purple martin habitat in western Oregon.

The use of metabarcoding for diet analysis in its current state yields qualitative results. The primers I used in this study show some taxonomic bias during PCR amplification. Thus, I am unable to infer the exact proportions or biomass of prey taxa in the diet. However, some innovative ideas and techniques for attaining quantitative results could be explored for avian diet analysis. For example, the application of stochastic labelling is a recently suggested technique for use with PCR that has been used in microbial ecology to identify actual community proportions instead of relative proportions (Hoshino and Inagaki 2017). A random barcode or infinite sequence combinations is inserted between the genomic DNA and the adapter sequence. All random barcode combinations are equally efficiently amplified during PCR, allowing for a quantitative read abundance calculation during the bioinformatics stage. Another potentially quantitative method is the analysis of species haplotypes in the sequence data output, though this would only work for species with intraspecific genetic variation within a certain range (Rytönen et al. 2019). I recommend testing this method by extracting DNA from a known number of arthropod species haplotypes, amplifying and sequencing the DNA, then comparing the number of haplotypes in the sequence output with the initial sample.

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