Forest Ecology and Management 480 (2021) 118689

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

The snag's the limit: Habitat selection modeling for the western purple martin in a managed forest landscape

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ARTICLE INFO

Keywords:
Songbird
Swallow
Cavity-nesters
Early seral forest
Aerial insectivore
Habitat selection

ABSTRACT

The western purple martin (*Progne subis arboricola*), an avian insectivore, is a species of conservation concern throughout the Pacific Northwest. Compared to the well-studied eastern subspecies (*Progne subis subis*), little is known of the life history and biology of the western subspecies. Availability of breeding habitat is believed to be a major limiting factor for western purple martins in forested habitat, but fundamental information on their current distribution and selection of nesting habitat is deficient. To fill this gap, we compared habitat characteristics at three spatial scales (snag-level, stand-level [48.6 ha], landscape-level [314 ha]) surrounding nest snags occupied by purple martins in western Oregon to unoccupied sites. We found habitat for nesting purple martins was defined by the presence of moderately decayed snags with nest cavities, located well away from closed-canopy forest in sufficiently large (>15 ha) open areas. Our modeling efforts suggested suitable habitat was rare within the study region because: 1) snags were scarce on private industrial forest lands and 2) large disturbed patches were uncommon on federal lands. We conclude that a disturbance regime characterized by infrequent but major stand-replacing events, such as fire or timber harvest, is likely the key to maintaining breeding habitat for purple martins in upland forests in western Oregon.

1. Introduction

Long-term population declines of the purple martin (*Progne subis*), an avian insectivore and the largest swallow in North America, has raised concerns for the conservation of this charismatic species in many parts of its range (Sauer et al., 2013; Tautin et al., 2008). As a long-distance migrant species, purple martins are subject to many potential threats, ranging from habitat loss on the wintering grounds (Fraser et al., 2012), to negative effects of insecticides (Hallmann et al., 2014; Airola, 2020). For conservation purposes, it is critically important to recognize the distinction between the relatively abundant eastern purple martin subspecies (*Progne subis subis*), with >10 million birds in eastern North America (Rich, 2004), and the western purple martin subspecies (*P.s. arboricola)*, with an estimated <5000 pairs distributed between southwestern BC and southern CA (Western Purple Martin Working Group, 2018). All individuals of the eastern subspecies nest in human-provided artificial housing (Tarof and Brown, 2013). In contrast, the western subspecies is a species of conservation and management concern throughout its breeding range (Wildlife Act R.S.BCE, 1996; Shuford and Gardali, 2008; ODFW, 2017; WDFW, 2017), where a large portion of the population can still be found nesting in natural cavities in the forests of Oregon and California (Bettinger, 2003; Horvath, 1999). Availability of breeding habitat is suspected to be a major limiting factor for the western subspecies within forested habitat (Rockwell, 2019), because compared to the well-studied eastern subspecies, little information exists pertaining to nest site location and selection (Tarof and Brown, 2013).

Declines in western purple martin (hereafter referred to as purple martin) populations in the Pacific Northwest have been attributed to competition with non-native cavity nesting birds and the reduction of natural nesting habitat as a result of forest management activities (Rockwell, 2019). As cavity-nesters and aerial insectivores, purple martins require nesting structures in open habitat (Horvath, 1999; Hagar and Sherman, 2018) where legacy trees and snags provide nesting substrate in productive early-seral forest following disturbances such as fire or clear-cut timber harvest (Tarof and Brown, 2013). However, availability of nesting habitat in post-disturbance forest has been reduced over many decades of snag removal during timber harvest and timber salvage following wildfire (Rose et al., 2001). Furthermore, although the regeneration harvest regime typically used on private lands

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https://doi.org/10.1016/j.foreco.2020.118689
Received 2 July 2020; Received in revised form 2 October 2020; Accepted 8 October 2020
Available online 23 October 2020
0378-1127/© 2020 Published by Elsevier B.V.

in this region may provide early seral conditions, availability of nest snags is likely to decrease as any remaining legacy snags decay and are not replaced under short-rotation harvest schedules (≤40 years). The opposite set of conditions currently occurs on federal forests, where snags and large trees are more abundant, but historic policies of fire suppression and curtailment of timber harvesting under the Northwest Forest Plan (USFS and BLM, 1994) in the early 1990′s has reduced the availability of early seral habitat (Kennedy and Spies, 2004; Swanson et al., 2011; Phalan et al., 2019). Although the combination of two critical elements of purple martin nesting habitat — open-canopy and residual snags — has not been promoted by forest management practices on either private or public forest lands for several decades, anecdotal reports of single pairs or small colonies nesting in snags on forest land are not uncommon. Information on current distribution and quantification of habitat associations of snag-nesting purple martins is needed for conservation planning especially in managed forests in the Pacific Northwest (Rockwell, 2019).

Recent revisions to the Bureau of Land Management (BLM) forested

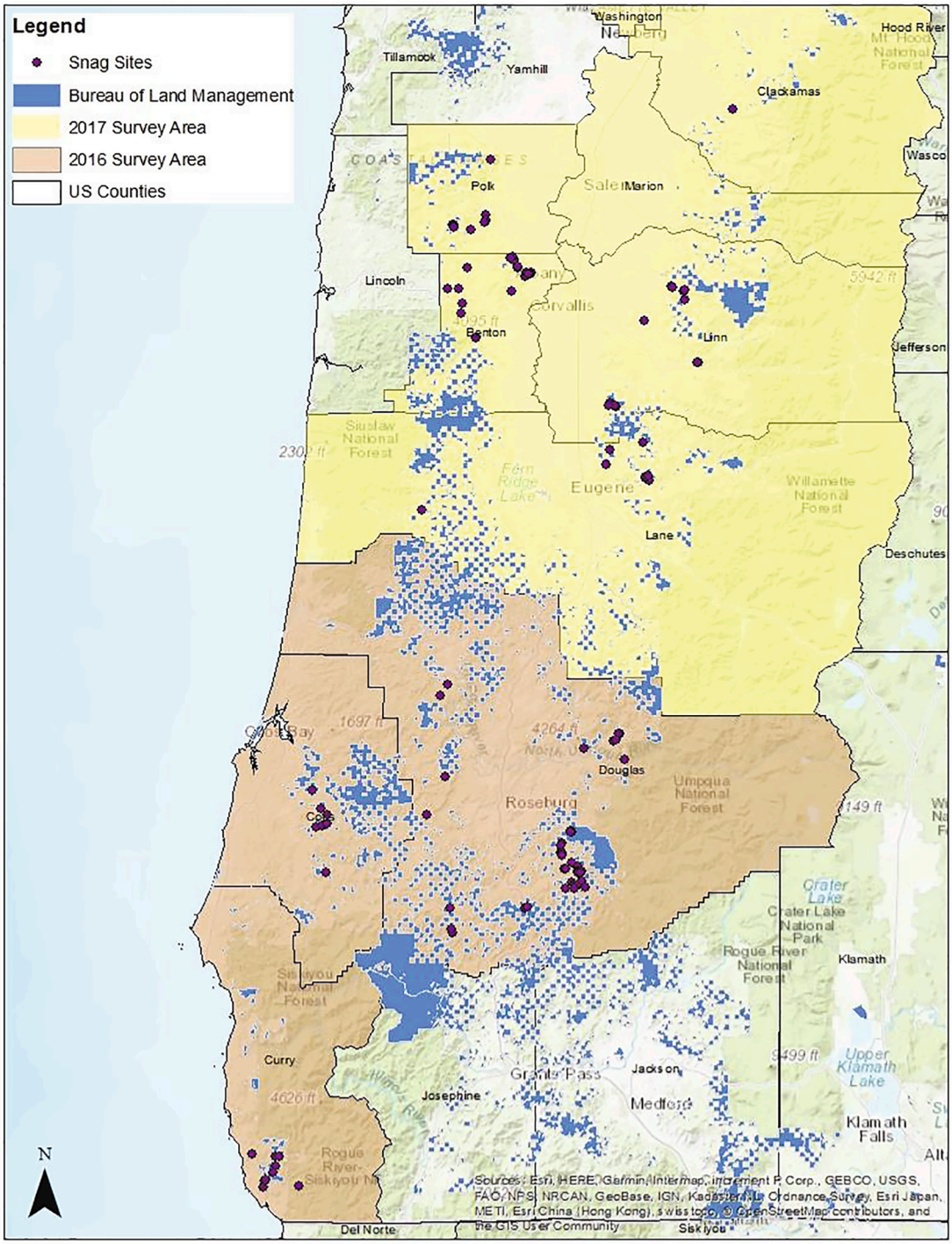

Fig. 1. The study area and locations of surveys of snag-nesting purple martin habitat at snag sites in western Oregon, USA. The orange areas represents the counties included in the 2016 survey, and the yellow areas counties surveyed in 2017. Sites with measured snag and habitat characteristics that were included in the habitat selection model are shown as red dots. Land under the jurisdiction of the USDI Bureau of Land Management is shown as blue polygons. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

lands management plan in western Oregon (USDI BLM, 2016) have reintroduced regeneration harvesting as a management tool. The revisions offer a unique opportunity to restore potential nesting habitat for the purple martin while maintaining the agency's timber harvest goals. However, fundamental information on the characteristics of snags, surrounding patches, and landscape used by breeding purple martins is necessary to guide design of harvest units intended to provide nesting habitat. Although both Horvath (1999) and Bettinger (2003) described individual- and site-level characteristics of snags occupied by nesting purple martins on forest lands in western Oregon, neither survey quantified characteristics of unoccupied sites, so inferences about habitat selection cannot be made from these data. The goal of our study was to facilitate conservation and management of the western purple martin by filling information gaps on distribution in western Oregon and habitat associations at the snag, patch, and landscape scale. We conducted surveys on public and private forest lands in western Oregon to address three specific objectives: 1) assess occurrence rates of purple martins in potentially nesting habitat throughout western Oregon; 2) identify and quantify key characteristics of upland forest sites used for nesting; and 3) develop a predictive model from data collected in-field to identify current and future nesting habitat in western Oregon. We intended the results of this work to be useful for identifying locations for future surveys and for guiding management, particularly the design of harvest units, on forest land where conservation of purple martins and other early seral species is a goal.

2. Materials and methods

2.1. Study area

The study area included portions of the Cascade Mountain Range, Coast Range, and the Willamette Valley in western Oregon (Fig. 1), and ranged in elevation from 70 to 1219 m. Highly productive forestland makes up about 80% of western Oregon. The land ownership of these forests is broken down as follows: about 52% owned by federal public agencies, 41% private entities, and 7% nonfederal public agencies (Campbell, 2003). The study area had a checkerboard pattern of land ownership alternating between private timberlands and lands administered by the BLM, with each 259 ha parcel designated by ownership. The major stand-replacing disturbance events in the study area were timber management and wildfire. The maritime climate of this region is characterized by mild temperatures year-round (mean high temperatures of low 80°F's in the summer and low 50°F's in the winter) with dry summers and seasonally heavy precipitation in the winter (annual precipitation of 40–80 in. with about 50% of the annual occurring December-February; Taylor and Bartlett, 1993).

Vegetation cover of the study area 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*). In addition to Ecological Systems Landcover Classes (ESLF)(Grossmann et al., 2008) including early seral forest as defined later, our habitat selection model included the ESLF land classes we deemed as potential foraging and nesting habitat due to their openness and based on known habitat associations (Tarof and Brown, 2013): 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.

2.2. Survey site selection

The study was designed to quantify habitat characteristics for purple martins by only surveying sites that met the following criteria for potential nesting habitat: 1) early post-disturbance (15 years or less) or low tree density (<8/ha); 2) elevation <1220 m (Bettinger, 2003); and 3) presence of at least one snag. The BLM produced a list of forest stands on public lands in Oregon west of the Cascade Mountains that met the first two of these criteria, but information on snag presence was not available during this phase of site selection. We surveyed 74 stands on BLM land randomly selected from this list in 2016. Stands with no potential nest snags were dropped after the first survey as not meeting criteria for potentially suitable sites and replaced by stands randomly selected from the list of potential stands. We encountered numerous sites that met the criteria for stand age and had potential nest snags while crossing private timberlands to access BLM sites. We obtained permission to survey private land where these conditions were opportunistically encountered. For this reason, a large portion of our survey sites in 2017 were not randomly selected, but we are confident these sites were representative of purple martin nesting habitat in western Oregon because they met the three criteria for nesting habitat listed above.

2.3. Breeding status surveys

We surveyed each site from one to five times between 15 May and 15 August to incorporate the entire breeding season (nest establishment through fledging). We visited sites with no purple martin detections at least three times. Whereas, sites with purple martins detections were visited until we could confirm the breeding status, which happened on the first visit in some cases. The first survey was conducted between 1 h before and two hours after sunrise at all sites with at least one snag present, for a duration of at least 20 min. Purple martins are territorial and respond vocally to other individuals entering their territory, so at sites where no purple martins were detected on the first visit, we 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 >80%, as calculated by dividing the number of surveys with purple martin detections by the total number of surveys at those sites. In addition to their vocalizations, purple martins are approximately 3× the mass and 1.3× the wingspan of other native swallow species (Winkler, 2011; Tarof and Brown, 2013), making them easily identifiable based on size alone. We followed a standardized protocol to determine breeding status with four site status categories (Cousens and Airola, 2006): "Unoccupied" sites had no purple martin observations; "Present" sites had observations of purple martins, but not using potential nest snags; "Occupied" sites had observations of purple martins perching on or using potential nest snags; and "Active Cavity" sites had evidence of nesting such as incubation behavior or feeding nestlings.

2.4. Habitat data collection

Habitat data collection was in accordance with the Manly et al., (2007) Design 1 assessment by sampling used and unused sites without identifying individual purple martins. As such, inferences are at the population level, not the individual colony level. At each survey site, snags with cavities approximately 2″ in diameter and larger were identified as being large enough for use by purple martins. For each potential nest snag, regardless of use by purple martins, we recorded snag height (m), diameter-at-breast-height (DBH; cm), cavity height (m), decay class, tree species, cavity origin, and number of cavities. Decay class was a categorical variable where 0 = live tree; 1 = recently killed, hard snag, fine branches still intact; 2 = dead several years, fine branches missing; 3 = soft, only stubs of large branches remain, bark sloughing; 4 = very soft, no bark, missing top (Cline et al., 1980) Cavity origin was determined by examining the size and shape of the cavity entrance.

For the habitat selection model, we estimated the distance from each snag to the nearest edge of closed canopy forest (>75% canopy cover) 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 having an average quadratic mean diameter (QMD) of <10 cm (Betts et al., 2010) and with either a conifer- or broadleaf- dominant tree species composition. We classified pasture and other non-forest vegetation types separately from early seral forest. We used a 48.6 ha (120 acre) circular plot around each snag to represent stand-level characteristics, based on the maximum allowable clearcut size under the Oregon Forest Practices Act. We 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. We 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). We averaged the early seral area for all overlapping landscape level plots centered on snags within the site. The GNN model predicts forest structural characteristics at a 30-m pixel resolution by utilizing Forest Inventory Analysis (FIA) plots, mapped environmental data, and Landsat Thematic Mapper Imagery (Ohmann and Gregory, 2002). At larger spatial scales, GNN predictions more closely match observed values for vegetation characteristics, including QMD (Ohmann and Gregory, 2002).

2.5. Statistical analysis

Our approach was to compare candidate models developed from measured habitat characteristics using Akaike information criterion (AIC; Burnham and Anderson, 2011) and select a final model that could be used to map potential nesting habitat for purple martins in western Oregon. To identify and quantify key habitat characteristics, we conducted univariate tests to compare the medians of habitat variables between used and unused snag groups. We used a two-sided Mann-Whitney test for these comparisons because variables did not meet assumptions of normal distribution.

To quantify the relationship between breeding status and habitat characteristics at multiple spatial scales (snag-, stand-, and landscape-level), we created a set of candidate generalized, linear, mixed-effects models (GLMM) using a binomial distribution and a logit link fit to the data. The response variable was the binary breeding status (snag-status), where 0 represented lack of evidence of nesting, or the "Unoccupied" and "Present" categories combined, and 1 represented evidence of nesting by at least one pair of purple martins, or the "Occupied" and "Active Cavity" categories combined. We were unable to include all explanatory variables in the model due to a small sample size. We chose variables based on our observations and knowledge of purple martins, choosing those we believed to be most useful for land managers in creating and retaining snag habitat. The snag-level explanatory variables we chose for model selection were: snag cavity height (cavhgt), DBH (dbh), and decay class (dec); stand-level variables were distance from the snag to closed canopy forest (dist), area of early seral forest within the 48.6 ha plot (es120), and elevation (elev); the single landscape-level explanatory variable was area of early seral forest within the 314 ha plot (es1km). All response variables except for decay class were continuous variables. The explanatory variable dbh was not included in candidate model sets because there was no evidence for a statistical difference in dbh between snags used and not used by purple martins in univariate tests ($U = 3128.5$, $p = 0.2951$). We performed correlation analyses to prevent highly correlated variables from occurring together in a model. The Pearson's Correlation Coefficient (PCC) for es1km and es120 was 0.74, so no model included both terms. However, all other pairwise PCC values between explanatory variables were <0.46. Due to the nested nature of the study design, every candidate model contained a random effect representing variation among stands and a random effect representing variation among landscape level plots. We standardized all explanatory variables to account for their different scales of measurement using the training data mean and standard deviation. All statistical analyses were done in R version 3.4.4 (2018-03-15).

The sample size at the landscape level was insufficient ($N = 59$) to allow inclusion of all explanatory variables in the full model, so we started by fitting sets of three explanatory variables at a time, followed by sets of two-variable models, then single-variable and a null model. We calculated AICc with the AICc() function and an K, ΔAICc, and AICc weights using the AICtab() function in the AICcmodavg package (Mazerolle, 2020). The model with the smallest AICc value was considered the best, and models within 4 AIC_c of the best were considered equally plausible (Burnham and Anderson, 2011).

We verified that assumptions of uniformity and linearity of residuals from the best model were met by graphically checking residuals using the DHARMa package (Hartig, 2018).

3. Results

3.1. Breeding status surveys

We surveyed a total of 96 unique sites on public land over both years of the study (including 7 BLM sites surveyed in both years, for a total of 103 surveys on public land sites) to assess colony persistence at upland forest sites. We surveyed a total of 77 upland forest sites under private ownership over both years of the project, 6 of which were surveyed in both years (for a total of 83 surveys on private land sites). Of the 77 total upland forest sites, 3 sites with gourd racks and 1 with nest boxes were surveyed but excluded from analysis.

Snag-nesting purple martins were uncommon but widely distributed throughout the study area in western Oregon. We found 17 nests at 16 occupied sites (occurrence rate = 15%) out of a total of 96 sites surveyed on public lands in both years (96 unique sites with 7 of the same sites surveyed in both years). The occurrence rate on BLM land alone was 14% (11 sites used for nesting out of 78 sites surveyed). We found 58% of the sites we surveyed on private lands to have at least one pair of nesting purple martins (45 sites used for nesting out of 77 site surveys). A post-hoc analysis showed that privately owned sites averaged 15 ha more of early seral within the stand-level 48.6 ha plot than publicly owned sites ($P < 0.0001$, Mann-Whitney test). Of the 7 sites surveyed in both years, 6 were occupied in both years; one BLM site that was occupied and produced fledglings in 2016, was unoccupied in 2017.

3.2. Comparison of habitat characteristics

Snag-level characteristics - In total, we measured habitat characteristics at 155 snags (60 used and 95 not used) to develop the habitat model. Of the five snag-level variables we tested, three were significantly different between occupied and unoccupied sites (Table 1). The heights of snags and cavities were both lower for nest snags than for unused snags, while snags used for nesting were characterized by greater decay (Table 2). In addition, the most commonly used snag species was Douglas-fir ($n = 101$ total cavities; 61% of all occupied cavities). Other snag species with nest cavities were: 6 in big-leaf maple, and 1 each in red alder (*Alnus rubra*), Pacific madrone, quaking aspen (*Populus tremuloides*), and western red-cedar (*Thuja plicata*). Nest cavities in snags originated from excavation by northern flicker (*Colaptes auratus*), hairy woodpecker (*Leuconotopicus villosus*), and pileated woodpecker (*Dryocopus pileatus*), as well as branch breakage, and other types of tree decay.

Stand- and landscape level characteristics - All four of the stand- and landscape-scale variables differed significantly between used and unused sites (Table 1), but stand-level area of early seral habitat was one of the most important predictors of snag use for purple martins (es120 estimate = 1.18; CI = 1.10–1.29; Fig. 2). The amount of early seral at the stand scale surrounding used snags was more than three times as great (3.46 times) as at unoccupied sites and was more than twice as great (2.38 times) for occupied sites at the landscape scale (Table 1). Median

Table 1
Comparison of habitat characteristics centered on snags used for nesting by western purple martins (*Progne subis arboricola*) and unoccupied snags in upland forest of western Oregon from in-field data collected in 2016 and 2017. Decay class was a categorical variable ranging from 0 for live trees to 4 for very well-decayed snags (Cline et al., 1980).

	Nest Snags (N = 60)	Unoccupied Snags (N = 95)	Mann-Whitney Test
Snag-level	Median (SE)	Median (SE)	P-value
Snag height (m)	15.2 (1.64)	22.0 (1.47)	< 0.0001
Cavity height (m)	10.0 (1.76)	19.0 (1.27)	< 0.0001
Snag DBH (cm)	66.5 (6.97)	76.2 (4.84)	0.29
Decay class	3 (0.15)	2 (0.16)	0.01
Number of cavities	2.0 (0.39)	2.0 (0.50)	0.17
Stand-level			
Early seral in 0.48-km radius plot (ha)	51.6 (4.21)	14.9 (2.60)	< 0.0001
Distance to closed canopy forest (m)	150.0 (16.95)	90.0 (12.19)	< 0.0001
Elevation (m)	1138.7 (112.94)	1828.8 (84.18)	< 0.001
Landscape-level			
Early seral in 1-km radius plot (ha)	148.1 (11.31)	62.1 (8.68)	< 0.0001

Table 2
Comparison of average snag and cavity height (m) and average decay class () for potential nest snags that were used as nest sites and potential nest snags that were not used as nest sites by western purple martins (*Progne subis arboricola*) in western Oregon from in-field data collected in 2016 and 2017. Decay class was a categorical variable ranging from 0 for live trees to 4 for very well-decayed snags (Cline et al., 1980).

Snag Status	Snag Height Average (m)	Cavity Height Average (m)	Decay Class Average
Unused Snags	23.1	18.8	2.5
Nest Snags	16.1	13.6	2.8

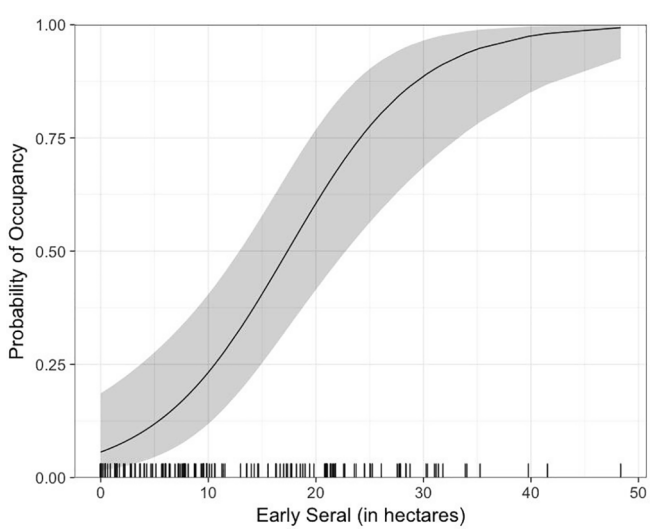

Fig. 2. Probability of snag use by breeding purple martins (*Progne subis arboricola*) in western Oregon as a function of area of early seral habitat within a 90-ha plot centered on the snag (Model "ac" in Table 1) based on in-field data collected in 2016 and 2017. The gray ribbon is the 95% confidence interval and the solid line indicates the estimated values. Black tick marks represent observed values.

distance to forest edge was also greater at occupied sites by 60 m.

3.3. Habitat model

Models that contained the stand-level variable area of early seral forest within the 48.6 ha plot (es120) consistently out-performed all other models (Table 3). Three top-performing models were equally plausible according to the criterion of $\Delta AIC_c < 4$ (Burnham and Anderson, 2011): a single variable model (es120), a two-variable model (es120 and snag decay class), and a three-variable model (es120, cavity height, and snag decay class; Table 3). We selected the simplest model containing only es120 (ac), with a ΔAIC_c of 4.5, for the applied habitat model for the primary reason that the current lack of contiguous snag data in Oregon would make application of a model with snag variables impractical. Land managers would be unable to utilize a model requiring snag decay data. According to our final model, the probability of use of snags in recently disturbed areas encompassing less than 10 ha was <25%, but increased steeply to near 90% at 30 ha (Fig. 2).

4. Discussion

Our results confirmed and quantified the importance of early seral conditions as nesting habitat for purple martins. Our major finding was snag-nesting purple martins were widely distributed throughout western Oregon, but that the probability of nest site use was strongly and positively related to stand-level area of early seral habitat. The strong positive association with recently disturbed forests likely explains why purple martins were relatively rare on public forest lands, where past policies of fire suppression and reductions in timber harvest over the last two decades in support of the Northwest Forest Plan's primary goal of restoring mature forest have decreased the availability of post-disturbance forest (Kennedy and Spies, 2004; Swanson et al., 2011; Phalan, 2019). Forest regrowth at many sites on BLM land that had been previously clearcut apparently rendered the sites no longer suitable for nesting, despite the presence of large snags. In contrast, continuous

Table 3
Comparison of candidate model characterizing purple martin (*Progne subis arboricola*) nesting habitat in upland forest sites in western Oregon using Akaike's information criterion with a correction for small sample size (AICc), delta AICc (ΔAICc), and Akaike weights (AICcWt) based on in-field data collected in 2016 and 2017. Due to a small sample size (N = 59 landscapes), the full model would not converge. Sets of 3 explanatory variables in the model were fit first, followed by sets of 2 explanatory variables, then individual explanatory variables. The bolded models were contenders for the best fitting model.

Model ID	Model Description[1]	K	AICc	ΔAICc	AICcWt
acdec	**snagstatus ~ es120 + dec**	**8**	**152.70**	**0.00**	**0.62**
acsnag	**snagstatus ~ es120 + cav + dec**	**9**	**154.61**	**1.91**	**0.24**
ac	**snagstatus ~ es120**	**4**	**157.20**	**4.50**	**0.07**
accav	snagstatus ~ es120 + cav	5	158.20	5.49	0.04
acdist	snagstatus ~ es120 + dist	5	159.26	6.56	0.02
acstand	snagstatus ~ es120 + dist + elev	6	160.28	7.58	0.01
kmsnag	snagstatus ~ es1km + cav + dec	9	167.72	15.02	0.00
kmdec	snagstatus ~ es1km + dec	8	167.83	15.13	0.00
kmstand	snagstatus ~ es1km + dist + elev	6	169.48	16.78	0.00
km	snagstatus ~ es1km	4	170.00	16.99	0.00
kmdist	snagstatus ~ es1km + dist	5	171.03	18.33	0.00
el	snagstatus ~ elev	4	180.23	27.53	0.00
cav	snagstatus ~ cav	4	181.44	28.74	0.00
dist	snagstatus ~ dist	4	183.31	30.61	0.00
dec	snagstatus ~ dec	7	184.72	31.76	0.00
null	snagstatus ~ [1]	3	184.72	32.02	0.00

[1] Variable definitions: snagstatus = binary status of snag (used or not used for nesting); es120 = area of early seral forest within a 48.6 ha plot centered on a snag; dec = decay class of the snag; cav = snag cavity height; dist = distance from the snag to closed canopy forest; elev = elevation; es1km = area of early seral forest within a 314 ha plot centered on a snag.

cycles of regeneration harvesting on private lands maintained sufficiently large areas of early seral habitat for purple martins. Our estimates of purple martin occurrence rates on private lands across western Oregon should be interpreted with caution because survey sites were non-randomly selected based on having a component of early seral forest and where we could obtain access permits. Nonetheless, we believe the evidence of a large difference in occurrence rates between public and private forest lands is real. Despite the non-random survey design, we selected sites to survey based on disturbance history and presence of snags, regardless of the presence of purple martins.

Although our model predicts that the probability of use by purple martins increases with area of early seral habitat, the presence of snags is imperative to support nesting purple martins. Therefore, the low availability of snags was likely a primary factor limiting use of early seral forest for breeding (Lund, 1978; Horvath, 1999). Evidence of a scarcity of natural nest sites included observations of rapid occupation by purple martins of artificial housing immediately after installation in clear-cut harvest units (Hagar and Sherman, 2018; Vesely, 2014), and competitive interactions with other cavity-nesting species. Although we observed purple martins co-occurring in the same snag with other cavity-nesting species (e.g. western bluebird [*Sialia mexicana*]) when multiple cavities were available, competitive interactions at sites where cavities were scarce suggested the number of cavities were a limiting factor for purple martins and other cavity nesting birds (Newton, 1994).

Several characteristics that differed between used and unused snags, including decay stage, snag and cavity height, and distance of snag to closed canopy forest, offer some insight into possible drivers of nest site selection. Decay stage of snags influences availability of cavities created by primary excavators (i.e., woodpeckers; Mannan et al., 1980; Chambers et al., 1997), which are a critical resource for purple martins and many other species of secondary cavity-nesters (Martin and Eadie, 1999). Use of snags by primary excavators generally increases with snag age up to at least a decade (Arnett et al., 2010; Barry et al., 2018), so snags in the early stages of decay (Decay class 1) likely have not had sufficient time for formation of cavities from excavators (Mannan et al., 1980; Chambers et al., 1997). On the other hand, cavities in snags in advanced stages of decay (i.e., decay class 4) may lack sufficient structural integrity to support a purple martin nest and are rarely used by most cavity-nesting species (Bevis and Martin, 2002). Therefore, the usefulness of snags as nesting substrates for purple martins and other secondary cavity-nesting species may be limited to middle stages of decay (Barry et al., 2018). This potential limitation is supported by our finding that the average decay class of used snags was 2.8 on a scale of 0–4 (Table 2).

The lower heights of snags and cavities in used compared to unused snags may seem counterintuitive, but was likely related to the limited availability of large snags. As previously mentioned, we found purple martins nesting in small snags when such snags were the only substrate available. Nest cavities in snags with small diameters (e.g., 30–60 cm dbh) were likely limited to heights at which internal volume or structure was able to accommodate a clutch of purple martins, typically 4–6 nestlings (Bunnell, 2013; Tarof and Brown, 2013). In addition, we found a positive correlation of snag diameter and cavity height ($r = 0.37$), providing further evidence that cavity height was likely limited by snag diameter.

Given the limited availability of snags in an early seral setting from which purple martins could select, many snags that were used by purple martins on our sites may not well represent the best nest sites. For example, the lack of difference in diameter between used and unused snags might be a consequence of the limited availability of snags from which to select. Additionally, early migrants may select the largest diameter nest snags, leaving smaller diameter snags for later returning purple martins. Historical reports indicate that purple martins select nest snags that can support multiple-pair colonies over isolated single-cavity sites (Morton et al., 1990), but we found purple martins attempting to nest in snags with DBH as small as 20 cm DBH and as short as 3.0 m when such snags were the only substrate available in clearcut harvest units (Fig. 3a). In contrast, Horvath (1999) found the mean DBH

Fig. 3. a. (left) A 22.9-cm DBH, 2.5-m high red alder snag with 2 cavities in which a pair of purple martins attempted to nest; b. (right) A 175 cm DBH and 28-m high Douglas-fir snag that supported 5 nesting pairs of purple martins. Both snags were on private timberlands in southwestern Oregon. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

of snags used by purple martins in western Oregon was 120 cm. Snags of that size were uncommon on early seral sites in our study area, but where large legacy snags had been retained in harvest units from previous old stands, they provided nesting opportunities for multiple pairs of purple martins and other cavity-nesting species simultaneously (Fig. 3b). Limits on colony size resulting from a lack of concentrated nesting opportunities, whether in one large "apartment" snag or multiple single-cavity snags, can result in lower fecundity for purple martins (Morton et al., 1990; Stutchbury, 1991). In addition, the risk of predation may be greater for small colonies because the effectiveness of mobbing to deter predators likely increases with colony size (Arroyo et al., 2001).

As the largest swallow in North America, purple martins are morphologically and behaviorally suited to flight in open spaces (Tarof and Brown, 2013), so it is not surprising that nest snags tended to be further from closed canopy forest than unused snags. Quantifying used snags only, Horvath (1999) found a mean distance of 195 m between nest sites and closed canopy forest, which is consistent with our data indicating that snags <100 m from a forest edge were infrequently used for nesting. We did not incorporate nesting success into this finding, so we recommend future studies attempt to quantify the optimum range of distance to closed canopy forest edge for nest snag retention and creation. Selecting nest sites away from forest edges may lower risk of predation by forest-dwelling predators (Tautin, 2005; Tarof and Brown, 2013; Ray, 2014). Combined with the positive relationship between probability of nesting and area of early seral condition, the significantly larger distance to closed canopy forest for nest snags compared to unused snags highlights the importance of snags in the open as nesting substrates for purple martins.

In summary, breeding habitat for purple martins on forest lands in our study region was defined by the presence of moderately decayed snags with nest cavities, located well away from closed-canopy forest in sufficiently large open areas. We found these conditions to be currently rare on public lands following decades of management focused on restoration of mature forest under the Northwest Forest Plan. Although purple martins were found more frequently in recent clearcuts on private industrial forest land (Bettinger, 2003; this study), the large snags that are currently an important source of nesting habitat are primarily remnants from original old-growth forest, and are unlikely to be replaced in the future (Mike Rochelle, Weyerhaeuser Co., personal communication). Recruitment of replacement snags is precluded by short rotation cycles (<50 years) typically practiced on private industrial timberlands, which limit the maximum diameter trees can attain (Adams et al., 2002), in turn limiting the size of future snags.

A disturbance regime that is characterized by infrequent but major stand-replacing events is likely the key to maintaining breeding habitat for purple martins on forest lands. Long intervals between major disturbances that create large early seral patches, such as intensive forest management or fire, allow time for the development of large trees that can become large snags. Relative to other ownerships that practice short harvest rotation schedules, federal forest lands harbor more large live trees and snags (Davis et al., 2015), so the recent reintroduction of regeneration harvesting under revised management plans on BLM lands offers the opportunity to emulate this disturbance pattern. Continuation of forest succession and tree growth on federal forest lands under the Northwest Forest Plan may provide a critical source of future large snags that could be available as purple martin nesting habitat following natural or anthropogenic disturbances.

4.1. Management implications/recommendations

Intentional creation of snags from live trees retained at harvest is one way to provide the essential combination of nesting substrate in early seral habitat for purple martins. However, at least two modifications of existing practices for snag creation may be necessary to provide nest sites. First, the current practice of retaining intentionally created snags at the edges of clear-cut harvest, which minimizes safety hazards and is more convenient for harvesters, may not be an effective means of providing nest sites. Instead, our results suggest that snags intended for use by purple martins should be >100 m from the edge of closed-canopy forest. Secondly, in current practice, snags are created at the time of timber harvest, and are not usable by purple martins for several years because of the time necessary for cavity formation through processes of decay and woodpecker activity (Chambers et al., 1997). Temporal limitations on the usefulness of created snags as a nesting substrate are exacerbated under management for rapid reestablishment of conifers. By the time snags have decayed enough to provide nest cavities, development of the next stand has narrowed the window of open-canopy conditions for purple martins. Therefore, where management goals include provision of nesting habitat for purple martins and other cavity-nesters that use snags in open environments, we suggest retention of existing snags during harvest operations whenever possible. Another possible approach to increasing the length of functional early seral nesting habitat may be to create snags 3–5 years before regeneration harvest, resulting in snags that are decayed and ready for use by purple martins at the time of harvest. To our knowledge, this strategy has not yet been tried, but is worthy of experimentation.

Finally, the use of artificial housing is a potential strategy for mitigating snag scarcity and for bridging gaps in nest site availability between creation of new snags and the formation of cavities. The establishment of artificial housing has been successfully undertaken in the Pacific Northwest (Cousens and Lee, 2012), but it requires long-term commitments and a reliable and consistent network of volunteers. Additionally, artificial housing must only be utilized as a short term conservation measure while focusing efforts on habitat creation and improvement. Although purple martins readily inhabit artificial housing (Tarof and Brown, 2013), snags offer the significant advantage of providing nesting, roosting, and foraging habitat for other native cavity-users in addition to purple martins (Mannan et al., 1980; Rose et al., 2001; Hayes, 2003). The loss of large multi-cavity snags is a conservation concern threatening cavity-nesting species locally and globally (Lindenmayer et al., 2012), and the key elements of nesting habitat for western purple martin — the presence of snags in productive early seral conditions — are the same as those required by many other species that use early post-disturbance environments as their primary habitat (Swanson et al., 2011; Hagar, 2007). Ensuring the presence of snags in early seral forest may be the best strategy for both maintaining self-sustaining populations of wild purple martins and contributing to the maintenance of biodiversity by supporting a host of other cavity-nesting species that are unable to persist in closed canopy forests.

CRediT authorship contribution statement

Lorelle Sherman: Data curation, Writing - original draft, Investigation, Visualization, Formal analysis. **Joan Hagar:** Conceptualization, Methodology, Writing - review & editing, Funding acquisition, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

For the habitat modeling and statistical analysis, we thank Ariel Muldoon with Oregon State University and Patti Haggerty with USGS. For the occupancy surveys, we thank Roli Espinosa, Josh Johnson, Matt Hane, and Doug Meekins for the resources and support they provided. Thanks to Miranda Martin and Carolyn Coyle for their help in the field. This research would not have been possible without funding from the

Interagency Special Status/Sensitive Species Program, United States, (L16PG00043) and the Purple Martin Conservation Association, United States, (2019-640). A special thanks to Bruce Cousens for his continued willingness to share his extensive knowledge of purple martins. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Funding

This work was supported by the Interagency Special Status/Sensitive Species Program [grant number L16PG00043, 2017] and the Purple Martin Conservation Association [grant number 2019-640, 2018]. The funding sources had no involvement in the conduct of research or article preparation.

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