

**SELECTION OF DAY-ROOST HABITAT BY FLAMMULATED OWLS (*Psiloscops*  
*flammeolus*) IN COLORADO**

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By

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## **Abstract**

Flammulated Owls (*Psiloscops flammeolus*) are small insectivorous raptors that breed in ponderosa pine ecosystems in Western North America. These owls depend on old-growth ponderosa pine forests for nesting, foraging, and day-roosting habitat. Old-growth pine forests are at risk due to shifting fire regimes and increased anthropogenic disturbance. Understanding how Flammulated Owls use old-growth forests can help us predict how changes in forest composition may impact Flammulated Owl communities. Flammulated Owl habitat selection has been well documented regarding their nocturnal foraging and nesting behaviors, but less is known about how they select day-roosting habitat. I sought to address this gap in knowledge by compiling data on the traits of day-roost sites selected by radio-tagged male Flammulated Owls in the 1980s and 2020s. I examined patterns in roost habitat use across three spatial scales: (1) the stand of trees in which roosts were located, (2) the roost tree proper, and (3) the perch the owl selected. I then assessed habitat selections by comparing roost sites to available but unused sites. Understanding characteristics of day-roosting habitat can help us predict how the loss of old-growth forests in the American West may impact Flammulated Owl habitat selection, influencing conservation and management strategies for the species. My results suggest that at each spatial scale, Flammulated Owls primarily selected traits that maximized the amount of foliage cover surrounding the roost. Additionally, results suggest that while Flammulated Owls rely on ponderosa pines and Douglas-firs for day-roosting, they may rely more heavily on mature rather than old-growth trees.

## Introduction

Migratory birds are confronted with many choices throughout their annual cycle, including where to settle in their summer destinations and which habitats to select for breeding. Available resources vary across space, with some locations being more suitable to a particular species' life history (Fretwell & Lucas, 1969). Birds that choose lower-quality habitats are less likely to survive and reproduce and are therefore selected against, making habitat selection an important aspect of behavior, particularly for migratory birds (Fretwell & Lucas, 1969). Understanding habitat selection can provide scientists insight into what qualifies as high-quality habitat and what resources are important to different species of birds (Finne et al., 2000; Pearse et al., 2017). Patterns in habitat selection can be used to influence management decisions, allowing for more informed conservation plans, protecting habitat that birds have demonstrated to be important to them (Pearse et al., 2017).

Among migratory birds, habitat selection occurs across multiple spatial scales (Wiens, 1987). These scales are defined as: first-order: geographic range, second-order: home range, third-order: microhabitats for specific activities such as feeding or sleeping, and fourth-order: the specific item chosen, such as food item, or the branch on which to nest (Johnson, 1980). The patterns of habitat selection may change depending on the scale observed, making it important to investigate habitat selection across multiple scales (Chalfoun & Martin, 2007; Wiens, 1987). For example, at the home range scale of habitat selection, Flammulated Owls (*Psiloscops flammeolous*) avoid locations with high-severity burns (Yanco & Linkhart, 2018). However, at the third-order scale, these owls do not display a strong avoidance of burned habitat (Yanco & Linkhart, 2018). Studying only third-order habitat selection wouldn't provide a complete understanding of how burn-severity impacts Flammulated Owl habitat selection. Examining

habitat selection across multiple spatial scales provides insight into how animals use and select resources across space, giving us a more complete understanding of their ecology (Chalfoun & Martin, 2007).

At the third-order, selection of roost habitat may greatly impact an individual's ability to survive and successfully reproduce. Roosts have been demonstrated to benefit birds in two primary ways: by providing protection from predators, and by reducing metabolic costs (Körtner & Geiser, 1998). Suitable roosts may reduce predation by either concealing or camouflaging the bird (Körtner & Geiser, 1998). Additionally, roosts may reduce exposure to precipitation, wind, and cold and heat stress, reducing the costs of thermoregulation (Körtner & Geiser, 1998). By selecting a suitable roost, a bird can increase its chances of survival by reducing the risk of depredation and conserving energy.

Flammulated Owls are Neotropical migrants that winter in southern Mexico and Central America and breed in Western North America (Linkhart et al., 2016; Linkhart & McCallum, 2020; Nelson et al., 2009). These insectivorous raptors primarily occupy pine forests, specifically ponderosa pine (*Pinus ponderosa*) ecosystems (Linkhart & McCallum, 2020). Previous studies conducted on the habitat selection of Flammulated Owls demonstrated that they preferentially selected home ranges containing old-growth ponderosa pine habitat (Linkhart et al., 1998). Old-growth forests are known for their high temporal stability and structural heterogeneity, both of which have the potential to promote biodiversity (Spies, 2004). Due to anthropogenic disturbances, such as commercial logging, fire suppression, and the elimination of Indigenous forest management practices, many old-growth forests are being replaced by dense stands of young trees (Covington & Moore, 1994; Kaufmann et al., 2007).

The structure of old-growth ponderosa pine forests in the American West was historically maintained by frequent, low-intensity fires (Covington & Moore, 1994; Graham & Jain, 2005; Reynolds et al., 2013). However, fire suppression, higher temperatures, and drier conditions have shifted fire regimes, increasing the frequency of high-severity, stand-replacing fires (Covington & Moore, 1994; Reynolds et al., 2013). As a fire-adapted species, old-growth ponderosa pines are often able to survive low and mixed-intensity fires (Graham & Jain, 2005; Huckaby et al., 2003; Reynolds et al., 2013). These fire regimes promote stands with a variety of tree age classes present, creating high structural heterogeneity (Kaufmann et al., 2007; Reynolds et al., 2013). High-intensity fires, however, frequently kill all trees in a stand, reducing the prevalence of old-growth trees, and promoting stands of even-aged trees with low structural diversity (Covington & Moore, 1994; Reynolds et al., 2013). As the climate shifts and high-intensity fires become more frequent, old-growth stands are at high risk (Steel et al., 2022). These intense, stand-replacing fires have the potential to severely reduce the amount of high-quality old-growth habitat that Flammulated Owls and many other species rely on.

Though analyses on third-order habitat selection by Flammulated Owls have been conducted for multiple owl behaviors, previous studies focused primarily on nesting and foraging habitats, with less emphasis on day-roost selection. While Yanco and Linkhart (2018) and Linkhart et al. (1998) studied Flammulated Owl day-roost selection, the former examined it in the context of habitat impacted by the high-severity Hayman Fire, and the latter only addressed general patterns of roost selection. Additionally, little is known about fourth-order selection for the day-roosting behavior of this owl. This study seeks to fill this gap in knowledge by collecting data on Flammulated Owl day-roost sites across multiple spatial scales. I examined day-roost selection at three spatial scales (1) the stand of trees used for roosting, (2) the roost tree

proper, and (3) the perch the owl selected. I compared used roost sites to available but unused sites within the owls' home range. To examine fourth-order selection, I collected data on the characteristics of the branch used as a perch by the owl. This study aims to gain a better understanding of what habitat characteristics Flammulated Owls select for in their day-roosts, and if patterns in selection of this owl change across spatial scales. More specifically, this study aims to determine if characteristics of old-growth forests are as important for day-roost habitat as they are for nesting and hunting habitat.

Understanding what characteristics Flammulated Owls look for in day-roost sites has important implications for conservation of the species. Due to commercial logging, the amount of old-growth ponderosa pine habitat within the Flammulated Owl's range has greatly decreased (Linkhart et al., 1998; Linkhart & McCallum, 2020). Additionally, due to a combination of climate change, fire suppression, and the exclusion of Indigenous forest management, changing fire regimes in western North America from the historic frequent low-intensity fires of ponderosa pine ecosystems to high-intensity stand-replacing fires pose threats to these habitats (Covington & Moore, 1994; Linkhart et al., 1998; Linkhart & McCallum, 2020). Current management strategies to reduce the frequency of stand-replacing fires include mechanical stand thinning, prescribed burns, and reducing understory surface fuels (Graham et al., 1999; Graham & Jain, 2005; Pollet & Omi, 2002). It is important to understand the life history requirements of Flammulated Owls in order to manage forests in a way that returns the system to a natural fire regime while promoting habitat features that Flammulated Owls require to survive.

Understanding Flammulated Owl habitat use will contribute to our understanding of this species' response to climate and landcover change, which is increasingly important as temperatures warm and anthropogenic activity continues.

My research aims to determine which habitat characteristics Flammulated Owls select for in their day-roosts. I predicted that at the tree stand scale, Flammulated Owls would select forest overstory similar to what they use for foraging; namely old-growth stands of ponderosa pine and Douglas-fir (*Pseudotsuga Menziesii*) (Linkhart et al., 1998). Additionally, I expected that owls would select stands of trees in proximity to their nest sites, as was observed by Yanco & Linkhart (2018). At the tree scale, I expected owls to select old-growth ponderosa pines and Douglas-firs, which contain many trees with large diameters and crown volumes that provide critical vegetative cover for protection from predators and weather (Linkhart et al., 1998). At the perch scale, I predicted owls would select branches surrounded by dense foliage, as observed by Linkhart et al. (1998). I also predicted they would select north-facing perches to reduce direct sun exposure and heat stress, as found in other studies of owl day-roost habitat selection (Barrows, 1981). I predicted that Flammulated Owls would primarily rely on old-growth ponderosa pine/Douglas-fir habitat for day-roosting, as they do for nesting and hunting habitat (Linkhart et al., 1998).

## **Study Area and Methods**

### *Study Area*

I conducted this study in the Manitou Experimental Forest in Teller County, central Colorado, in July and October of 2023. I collected data in the 511 ha Hotel Gulch Study Area (HGSA), which has been part of a long-term demographic study on Flammulated Owls since 1981 (Linkhart & Reynolds, 2006; Linkhart et al., 2007). Forests in the study area are primarily composed of (1) ponderosa pine mixed with Douglas-fir on ridgetops and southwest-facing slopes, (2) quaking aspen (*Populus tremuloides*) on lower slopes and drainage bottoms, (3) quaking aspen mixed

with blue spruce (*Picea pungens*) in moist drainage bottoms and lower slopes, and (4) Douglas-fir mixed with blue spruce on higher elevation north-facing slopes (Linkhart et al., 1998).

Elevations in the study area ranged between 2550-2855 m.

### *Radio Telemetry*

The Colorado College Flammulated Owl research crew and I captured three male Flammulated Owls during the nestling period in early July 2023. We targeted only breeding males because they are more likely to be recaptured than non-breeding males (Linkhart et al., 2007), and because females roost in nest cavities during the incubation and most of the nestling stages (Linkhart et al., 1998). Owls were captured at their nests, following prey delivery to their mates and young (Linkhart et al., 1998). After capture, owls were outfitted with radio transmitter backpack units (Advanced Telemetry Systems<sup>TM</sup>, model A1030), which have an estimated battery life of 40 days. We attached the transmitters to owls as per the methods outlined in McGinn (2018), with a backpack harness made from nylon fishing line. Transmitters weighed 2 grams each (3.9% of a male's average body mass). To track owls, we used a hand-held R-1000 telemetry receiver and a 3-element RA-165 yagi antenna (Communication Specialists Inc.<sup>TM</sup>). Owls were tracked between 1000 hr and 1700 hr MDT. We followed the strongest transmitter signal in concentric circles until we located the roost tree. We then searched for the owl in the tree using binoculars and confirmed a tree as a roost if we found the owl. Once a roost was confirmed, we recorded the GPS coordinates and flagged the tree, then vacated the area to avoid disturbing the bird with our presence. If the exact tree was not found, we simply recorded site characteristics, however, these data were not included in my analyses. We determined locations of roost trees between July 6-24.



### *Habitat quantification*

During October of 2023, I collected data on habitat characteristics of roost sites. I quantified day-roost habitat at three distinct spatial scales: (1) the stand of trees the roost was located in, (2) the roost tree itself, and (3) the branch the owl was perched on. At the tree stand scale, I recorded the dominant species and size of trees making up the overstory, the position of the stand on the slope, the slope aspect, the grade of the slope, and the distance of the stand to the nest tree. I used the point-centered quarter method (Cottam & Curtis, 1956) to calculate tree density immediately surrounding roost trees, and in order to determine if tree density differed across size classes, I assessed tree density in two arbitrary size classes, trees  $< 20$  cm DBH (diameter at breast height) and trees  $\geq 20$  cm DBH (hereafter small tree density and large tree density, respectively).

Additionally, I counted the number of trees in a clump, which I defined as a group of trees with interlocking crowns, including the roost tree (Dickinson et al., 2014). I examined these clumps to explore how the foliage of nearby trees and the structure of the forest impacted roost selection, as this type of tree group is characteristic of ponderosa pine forests maintained by frequent low-intensity fires (Reynolds et al., 2013). At the tree scale, I recorded tree species, height (assessed with a range finder), DBH, canopy closure (assessed with a densiometer), and crown volume (See Yanco & Linkhart (2018) for the literature source for this calculation, and for other tips for describing habitat quantification). At the perch scale, I recorded the approximate diameter of the perch, the direction the perch was facing, the direction the owl was facing, how far up the tree the perch was, and the distance of the owl from the trunk of the tree.

To determine habitat selection by owls at the tree stand and tree scales, I compared habitat characteristics of roost sites to available but unused sites. I did not assess habitat selection of perches, as I did not compare used branches to available branches; instead, I simply looked at

trends in perch characteristics. To determine which available trees to sample for the tree stand and individual tree scales, I used ArcGIS Pro (ArcGIS Pro for Desktop v3.1; ESRI 2024) to generate one random point for each confirmed roost location. To ensure that these trees were available to owls, I generated points only within a 213m radius of the owl's nest, which is the average radius of a Flammulated Owl territory (Linkhart et al., 1998). Due to the small sample size of roost trees in 2023, I combined these data with data collected in the HGSA in 1982-1983 (Linkhart et al., 1998). These latter data added 45 unique roost locations for seven male owls.

### *Data Analysis*

I analyzed roosts used before fledging occurred to avoid introducing error that may result from changes in adult owl behavior as they take care of their newly fledged young. To determine which characteristics best predicted the use of a tree as a day-roost, I first tested each variable for normality using Shapiro-Wilk tests. I then compared characteristics of roost sites and available sites using Mann-Whitney U tests for non-normal data, and unpaired two-tailed t-tests assuming unequal variance for normal data. I used IBM SPSS statistics (V29; IBM Corp 2023) for the Shapiro-Wilk and Mann-Whitney U tests and Microsoft Excel (V16.84; Microsoft Corporation 2024) for t-tests. Variables that did not significantly differ between roost sites and available sites were left out of subsequent analyses. Additionally, I used the same tests to compare data between 2023 and 1982-1983. I performed these tests on each individual variable to determine if they differed between time periods. If there was no significant difference between my data and the 1982-1983 data, I combined the data sets for further analysis. Because of my small sample size, I considered anything with a p-value  $\leq 0.1$  to be significant (Goguen, 2012).

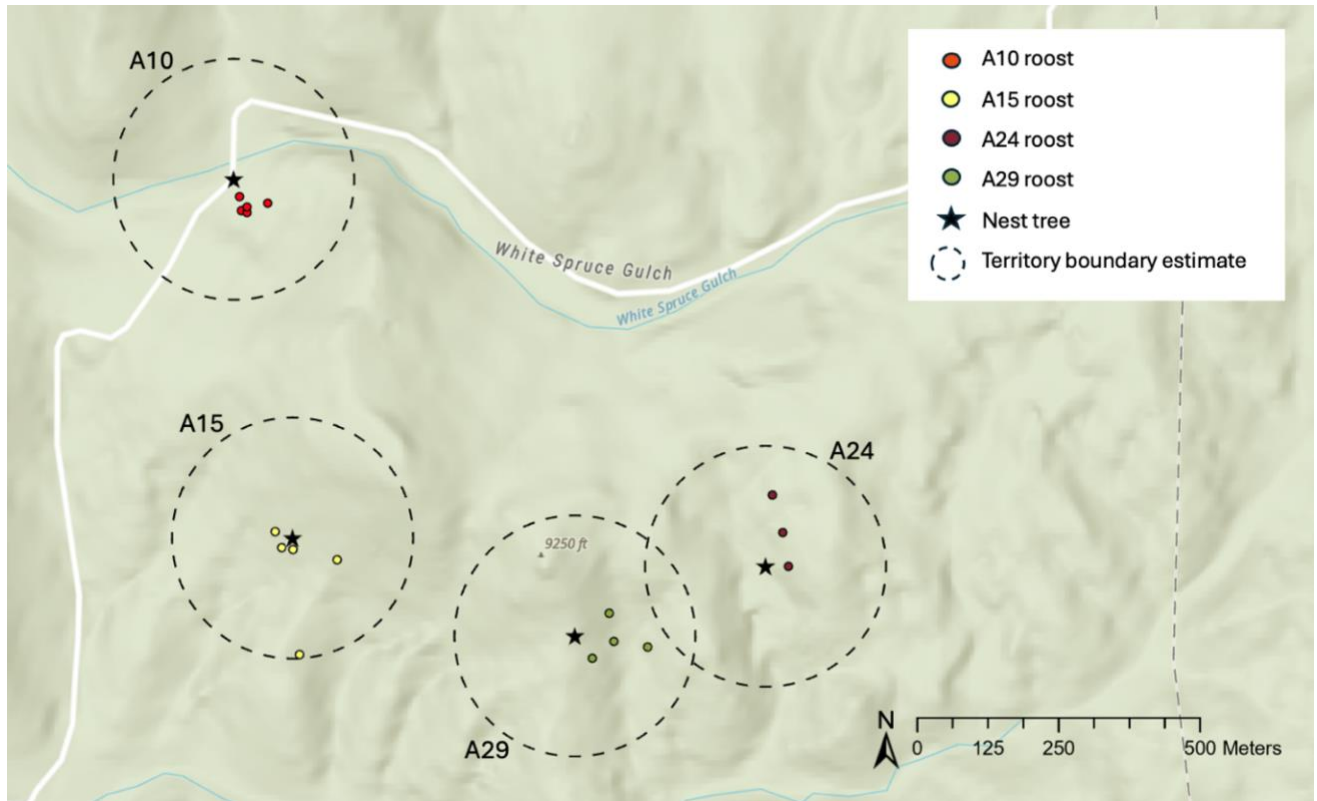
To examine roost selection across all years at the tree stand scale and the individual tree scale, I fit global binary logistic regressions using the programming language R (V4.3.1; R Core Team 2023). Use across time periods was the response and roost characteristics at respective scales that varied significantly between selected roosts and available locations were the predictors. No data were collected at the tree stand scale for available sites in 1982-1983, so combined 2023 and 1982-1983 roost site data were compared only to 2023 available site data. Data on the number of trees per clump were not recorded in 1982-1983, so this characteristic was excluded from the joint analysis. Data on canopy closure taken from the ground were not recorded in 1982-1983, and I was unable to calculate crown volume for 2023 trees, so these characteristics were absent from their respective analyses.

To examine which combination of roost characteristics best predicted use at the tree stand scale and the individual tree scale for individual time periods, I fit univariate binary logistic regressions in which use was the binary response and vegetation characteristics were predictors. Independent analyses were conducted separately for each time period, but an analysis was not conducted at the tree stand scale for 1982-1983 because available tree stand data were not reported for that time period. I estimated Akaike's Information Criterion corrected for small sample sizes ( $AIC_c$ ) using the "AICcmodavg" package (V2.3.3; Mazerolle 2023). Models within 2  $AIC_c$  values of the top model were considered competitive, and models with the lowest  $AIC_c$  were considered best (Ausprey & Rodewald, 2011). Variables that informed competitive models were subsequently added to additional models until they were no longer competitive. Variables were not included in the same model if they were highly correlated with one another  $|r| \geq 0.6$  (Lambertucci & Ruggiero, 2013). I used McFadden's pseudo  $R^2$  to measure the variance explained by top models (Lambertucci & Ruggiero, 2013). McFadden's pseudo  $R^2$  values

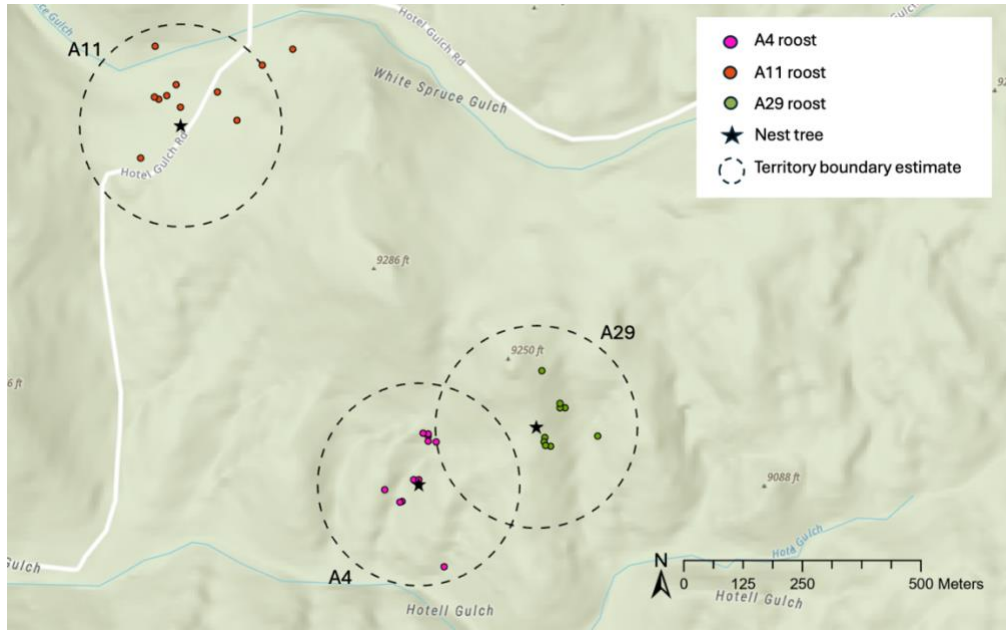
between 0.2 and 0.4 indicate good model fit (Lambertucci & Ruggiero, 2013). I conducted AIC<sub>c</sub> model selection for the 2023 data and the 1982-1983 data separately and did not combine data sets. At the perch scale, I used chi-square tests to determine if perches with specific traits were used more frequently than would be expected by chance using a p-value of  $\leq 0.1$  to determine the critical value.

## **Results**

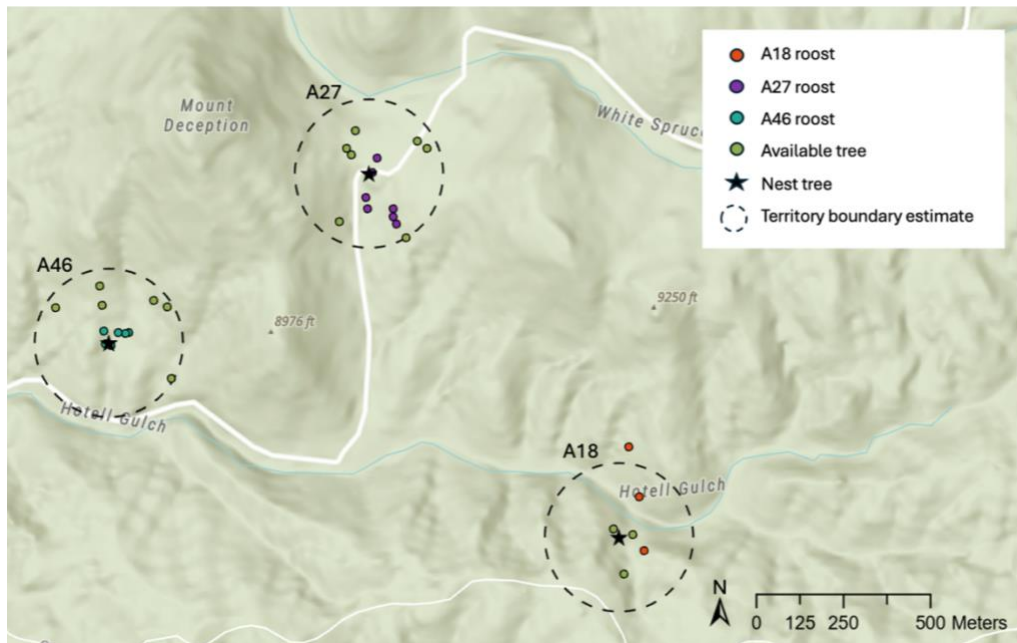
In total I analyzed 61 distinct roost trees, 45 from 1982-1983 and 16 from 2023, with data from four owls in 1982 (Figure 1), three owls in 1983 (Figure 2), and three owls in 2023 (Figure 3). Each roost site I analyzed was a confirmed roost location, as I excluded sites without visual confirmation of the owl from my analysis. 60 roost trees were alive, and one was a snag. In 1982, all focal owl territories were within two territories of each other, and two were adjacent territories (Figure 1). In 1983, two focal owl territories were adjacent to one another, with the third approximately two territories away (Figure 2). In 2023, all focal owl territories were separated by between one and three other territories (Figure 3).



**Figure 1.** Estimated territory boundaries, nests, and day-roost trees of Flammulated Owls in central Colorado in 1982.



**Figure 2.** Estimated territory boundaries, nests, and day-roost trees of Flammulated Owls in central Colorado in 1983.



**Figure 3.** Estimated territory boundaries, nests, day-roost trees, and available but unused trees of Flammulated Owls in central Colorado in 2023.

### *Habitat Selection at Tree Stand Scale*

Tree stands at roost sites contained a greater number of trees per clump than at available sites, as well as a higher density of large trees (Figure 4; Figure 5). The average number of trees per clump for stands at roost sites was  $14.3 \pm 1.7$  (SE) and  $8.9 \pm 2.1$  for available sites (Mann-Whitney  $U = 77.5$ ,  $n_1 = n_2 = 16$ ,  $p < 0.1$  two-tailed). The average density of large trees for roost stands was  $275 \text{ tree/ha} \pm 20$  and  $189.1 \text{ trees/ha} \pm 37.8$  for available stands (Mann-Whitney  $U = 314.5$ ,  $n_1 = 61$   $n_2 = 16$ ,  $p = 0.03$  two-tailed). Tree stands at roost sites occurred more frequently on south-facing slopes than on north-facing slopes (70.5% vs 18%; Figure 6). In contrast, 50% of available stands were on south-facing slopes, and 31.3% on north-facing slopes (Figure 6). Stands on east and west-facing slopes were used at approximately the same rate as they were available in the environment. However, southwestern-facing slopes were used most frequently for roosting, hosting 54% of used stands and 37.5% of available stands (Figure 6). Roost site stands were significantly closer to the nest tree than available stands were, with the average roost tree being  $86.4\text{m} \pm 7.2$  away from the nest, compared to  $140\text{m} \pm 14.6$  for random trees (Mann-Whitney  $U = 241$ ,  $n_1 = 61$   $n_2 = 16$ ,  $p = 0.001$  two-tailed) (Figure 7). Notably, in 2023, roost sites were significantly closer to the nest in the 5 days preceding fledging (Figure 8). In 2023, Roosts used within 5 days of fledging were on average  $33.9\text{m} \pm 10$  away from the nest, while all other roosts were an average of  $123.1\text{m} \pm 21.3$  away from the nest (Mann-Whitney  $U = 3$ ,  $n_1 = 9$   $n_2 = 7$   $p = 0.003$  two-tailed).

For my combined analysis at the tree stand scale, the only characteristics shared between time periods that differed significantly between roost sites and available sites were the following: distance of the tree stand from the nest tree, large tree density, and slope aspect. According to the combined global model, which explained a modest amount of variation in data across all years

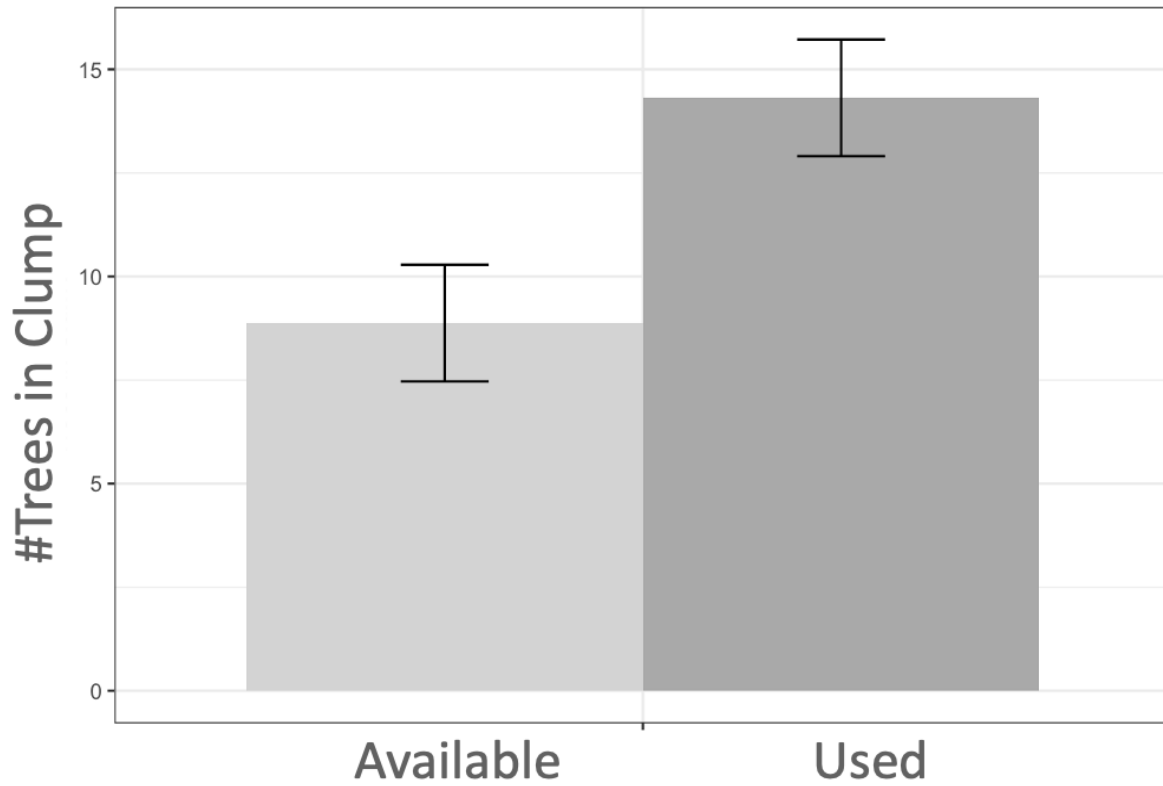
( $R^2 = 0.30$ ), individuals were more likely to use tree stands on south-facing slopes ( $\beta_{SA} = 0.87$ ;  $SE = 0.83$ ), closer to nest sites ( $\beta_{DN} = -0.021$ ;  $SE = 0.007$ ), and with higher large tree density ( $\beta_{TD} = 0.007$ ;  $SE = 0.003$ ).

For my individual time period analysis, which I conducted only for 2023 data, the model that best predicted use at the tree stand scale carried 74% of the  $AIC_c$  model weight and was informed by large tree density, distance from the nest, and slope aspect (Table 1). This model explained a modest amount of variation in the 2023 data ( $R^2 = 0.53$ ). Roosting tended to be more likely in stands on south-facing slopes ( $\beta_{SA} = 2.53$ ;  $SE = 1.59$ ) and was significantly more likely in stands where distance to nests was smaller ( $\beta_{DN} = -0.043$ ;  $SE = 0.019$ ) and where large tree density was higher ( $\beta_{TD} = 0.013$ ;  $SE = 0.006$ ).

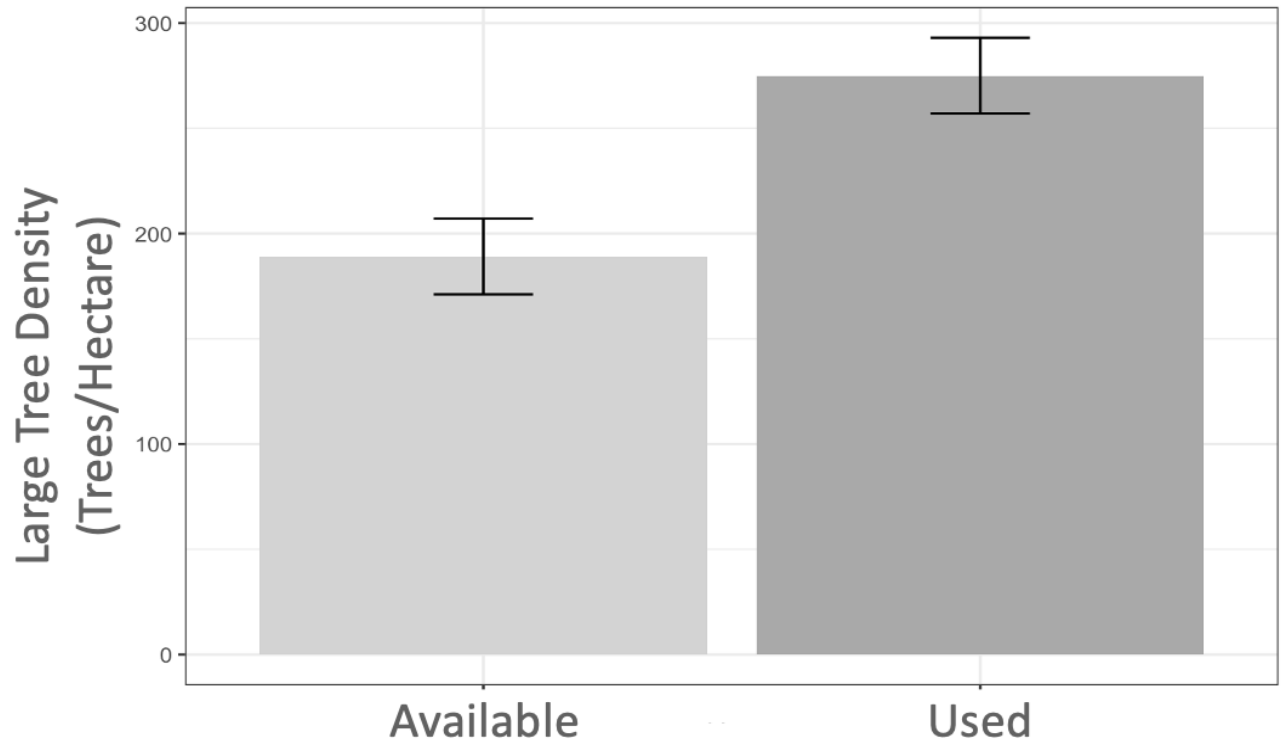
**Table 1.** Models for Flammulated Owl day-roost use in 2023 at the tree stand scale. K is the number of parameters in a model,  $AIC_c$  is Akaike's Information Criterion corrected for small sample sizes,  $\Delta AIC_c$  is the difference between  $AIC_c$  values of each model and the top model,  $AIC_{cwt}$  is the  $AIC_c$  weight of the model,  $Cum_{wt}$  is the cumulative weight of each model, and LL is the Log likelihood of each model. DN is the distance of the focal site from the nest tree. TD is the density of trees  $\geq 20$ cm in DBH. SA is the aspect of the slope the stand is on. CN is the number of trees in a clump with the focal tree. Null is the null model.

Model	K	$AIC_c$	$\Delta AIC_c$	$AIC_{cwt}$	$Cum_{wt}$	LL
SA + DN + TD	4	26.29	0.00	0.74	0.74	-8.15
SA + DN + TD + CN	5	28.83	2.54	0.21	0.95	-7.84
SA + DN	3	31.80	5.51	0.05	1.00	-12.33
SA	2	38.64	12.34	0.00	1.00	-17.05
DN	2	42.84	16.55	0.00	1.00	-19.21
TD	2	43.93	17.64	0.00	1.00	-19.76
CN	2	44.78	18.49	0.00	1.00	-20.18
Null	1	46.49	20.20	0.00	1.00	-22.18

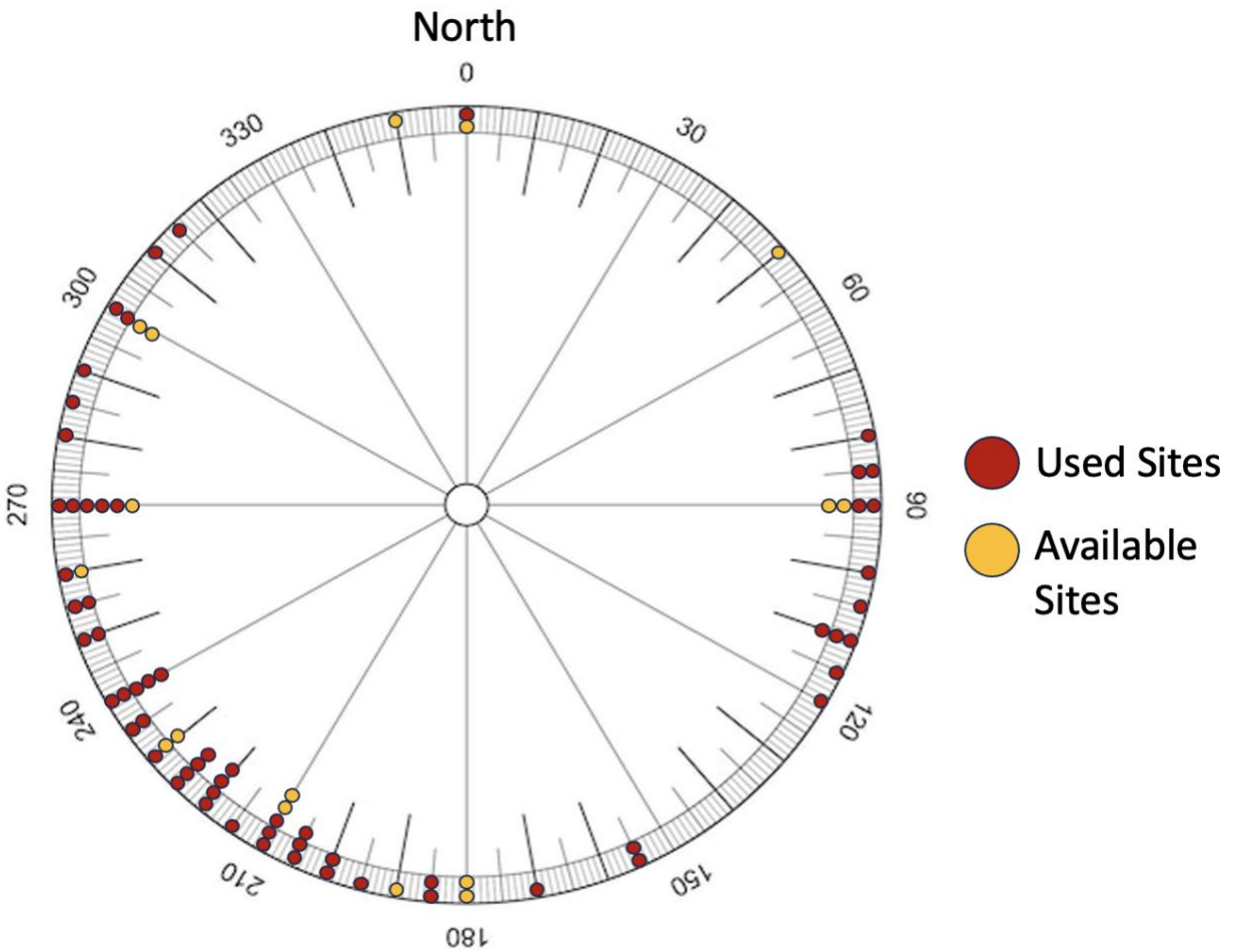




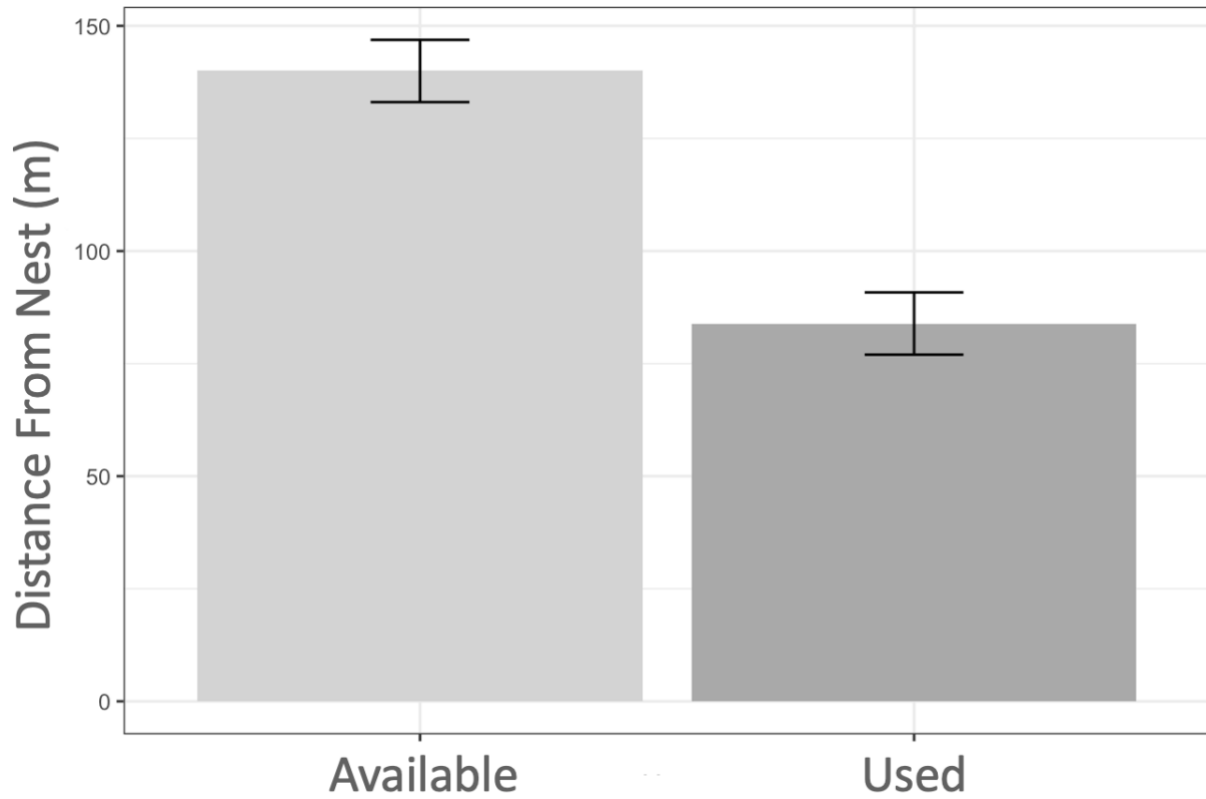
**Figure 4.** Average number of trees in a focal tree's clump for Flammulated Owl roost habitat (N=16) and available habitat (N=16) in central Colorado. The number of trees in a clump differed significantly between roost sites and available sites, as I considered anything with a p-value  $\leq 0.1$  to be significant ( $p=0.1$ ).



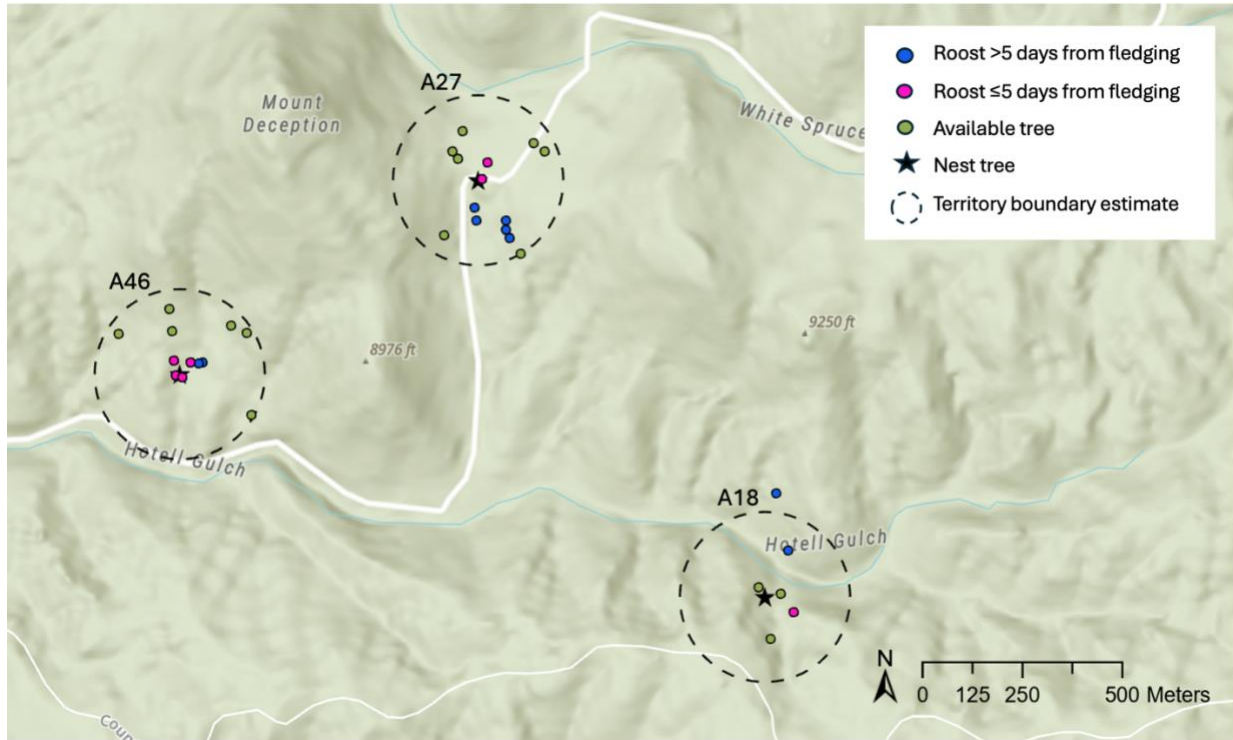
**Figure 5.** Density of large trees ( $20\text{cm} \leq \text{DBH}$ ) per hectare in Flammulated Owl roost stands ( $N= 61$ ) and available stands ( $N=16$ ) in central Colorado. Roost stands had a significantly higher density of large trees than available stands ( $p=0.03$ )



**Figure 6.** Slope aspect (shown in degrees) of Flammulated Owl roost sites (N=61) and available sites (N=16) in central Colorado. Roost sites are shown in red and available sites are shown in yellow. Roost sites were located on south-facing slopes more often than available sites. Roost sites were most frequently on southwestern-facing slopes. South-facing slopes were used as roost sites at a significantly higher rate than they were available in their environment [ $\chi^2(1, N = 70) = 13.7, p < 0.001$ ].



**Figure 7.** Average distance (in meters) of Flammulated Owl roost stands (N=61) and available stands (N=16) from an owl's nest tree in central Colorado. Roost stands were significantly closer to nests than available stands ( $p=0.001$ ).



**Figure 8.** Territory boundary estimates, nests, day-roost trees used >5 days from fledging, day-roost trees used  $\leq 5$  days from fledging, and available but unused trees of Flammulated Owls in central Colorado in 2023.

#### *Habitat Selection at Individual Tree Scale*

Roost trees in 1982-1983 had significantly larger DBHs than available trees did, however, there was no significant difference between the DBH of roost trees and available trees in 2023 (Figure 9). In 1982-1983, roost trees had an average DBH of 31.8cm  $\pm$  1.5 and available trees had an average DBH of 25.5  $\pm$  1.4 (Mann-Whitney U = 814.5,  $n_1 = 45$   $n_2 = 59$ ,  $p \leq 0.001$  two-tailed). In 2023, the average DBH was 36.2cm  $\pm$  2.3 for roost trees and 35.8cm  $\pm$  2.6 for available trees (Mann-Whitney U = 116,  $n_1 = n_2 = 16$   $p = 0.67$  two-tailed). Available trees were significantly larger in 2023 than they were in 1982-1983, but there was no significant difference between the size of 2023 and 1982-1983 roost trees [DBH: (Roost: Mann-Whitney U = 260,  $n_1 = 16$   $n_2 = 45$ ,  $p$

= 0.103 two-tailed) (Available: Mann-Whitney  $U = 195$ ,  $n_1 = 16$   $n_2 = 59$ ,  $p < 0.001$  two-tailed)] [Height: (Roost:  $t = -1.6$ ,  $df = 39$ ,  $p = 0.13$  two-tailed) (Available:  $t = -2.2$ ,  $df = 22$ ,  $p = 0.04$  two-tailed)] (Figure 9; Figure 10). In 1982-1983, roost trees were significantly taller than available ones, but there was no significant difference between the height of roost trees and available trees in 2023 (Figure 10). In 1982-1983 the average height was 13.9m +/- 0.62 for roost trees and 11.1m +/- 0.47 for available trees ( $t = 3.5$ ,  $df = 84$ ,  $p < 0.001$  two-tailed). In 2023 the average height was 15.4m +/- 0.71 for roost trees and 13.6m +/- 1 for available trees ( $t = 1.4$ ,  $df = 27$ ,  $p = 0.16$  two-tailed). 58% of roost trees were Douglas-firs, and 31% were ponderosa pines, with 31% of available trees being ponderosa pines, but only 50% of available trees being Douglas-firs (Figure 11). 14% of available trees were quaking aspens, but no quaking aspens, or any other deciduous trees, were used as roosts, with the owls roosting only in conifer species (Figure 11). Roost trees had significantly larger crown volumes than available trees (Figure 12). The average crown volume was 166.3m<sup>3</sup> +/- 25.2 for roost trees and 57.3m<sup>3</sup> +/- 9.1 for available trees (Mann-Whitney  $U = 521$ ,  $n_1 = 44$   $n_2 = 55$ ,  $p < 0.001$  two-tailed).

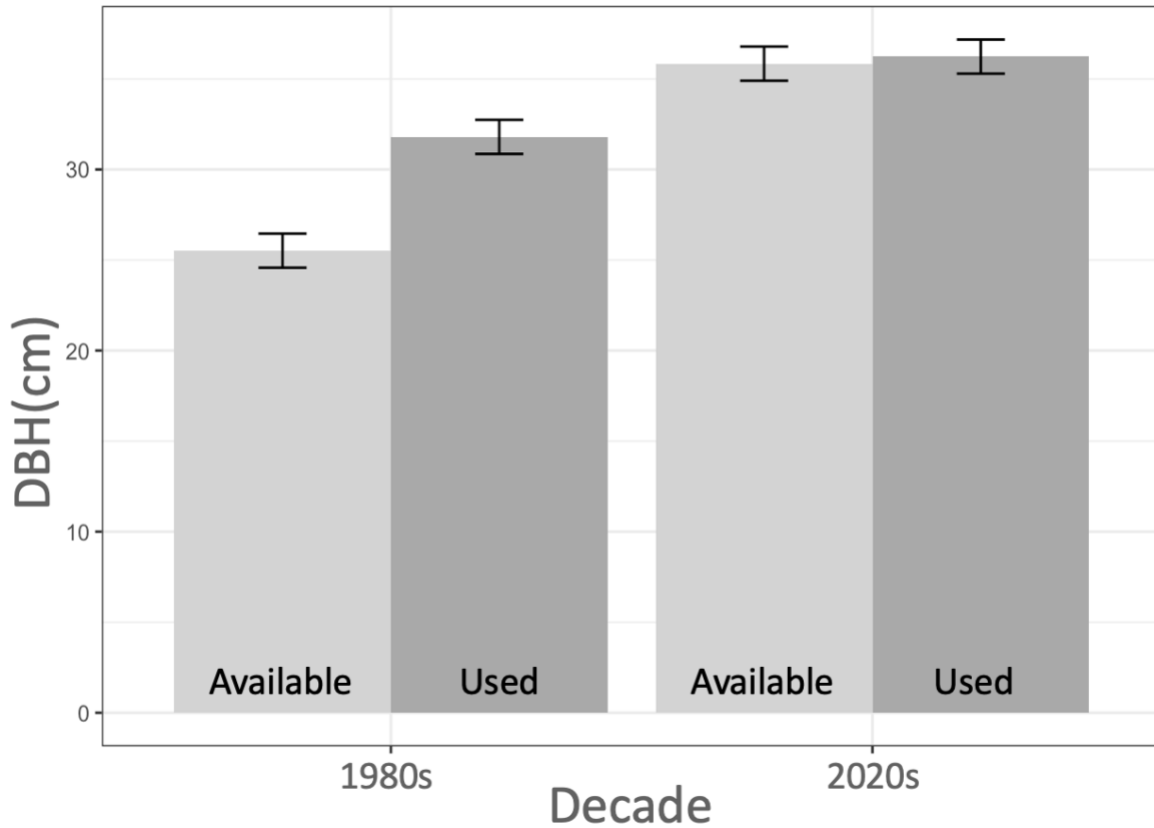
There were no shared characteristics between time periods at the individual tree scale that differed significantly between roost trees and available trees, so a combined analysis was not done at this scale. It should be noted that I was unable to calculate crown volume for the 2023 trees, so the only characteristic analyzed for 2023 was tree species.

In my individual time period analysis conducted for the 2023 data, no models outcompeted the null model (Table 2). Tree species informed the second ranked model, which was not competitive with the null model and carried 10% of the AIC<sub>c</sub> model weight. This model explained very little variation in the 2023 data ( $R^2 = 0.07$ ). According to this second-ranked model, roosting tended to be more likely in Douglas-firs ( $\beta_{SP} = 0.13$ ,  $SE = 0.52$ ), but the

relationship was not significant. For 1982-1932 data, the top model was informed by crown volume and carried 44% of the  $AIC_c$  model weight (Table 2) and explained a modest amount of variation in the 1982-1983 data ( $R^2 = 0.24$ ). Roosting was more likely in trees with larger crown volumes ( $\beta_{CV} = 0.012$ ,  $SE = 0.003$ ). The second ranked model was informed by crown volume and tree species. This model was competitive with the top model and carried 41% of the  $AIC_c$  model weight (Table 2) and explained a modest amount of variation ( $R^2 = 0.30$ ). Roosting was more likely in trees with larger crown volumes ( $\beta_{CV} = 0.011$ ,  $SE = 0.003$ ) and in Douglas-firs ( $\beta_{SP} = 0.42$ ,  $SE = 0.54$ ).

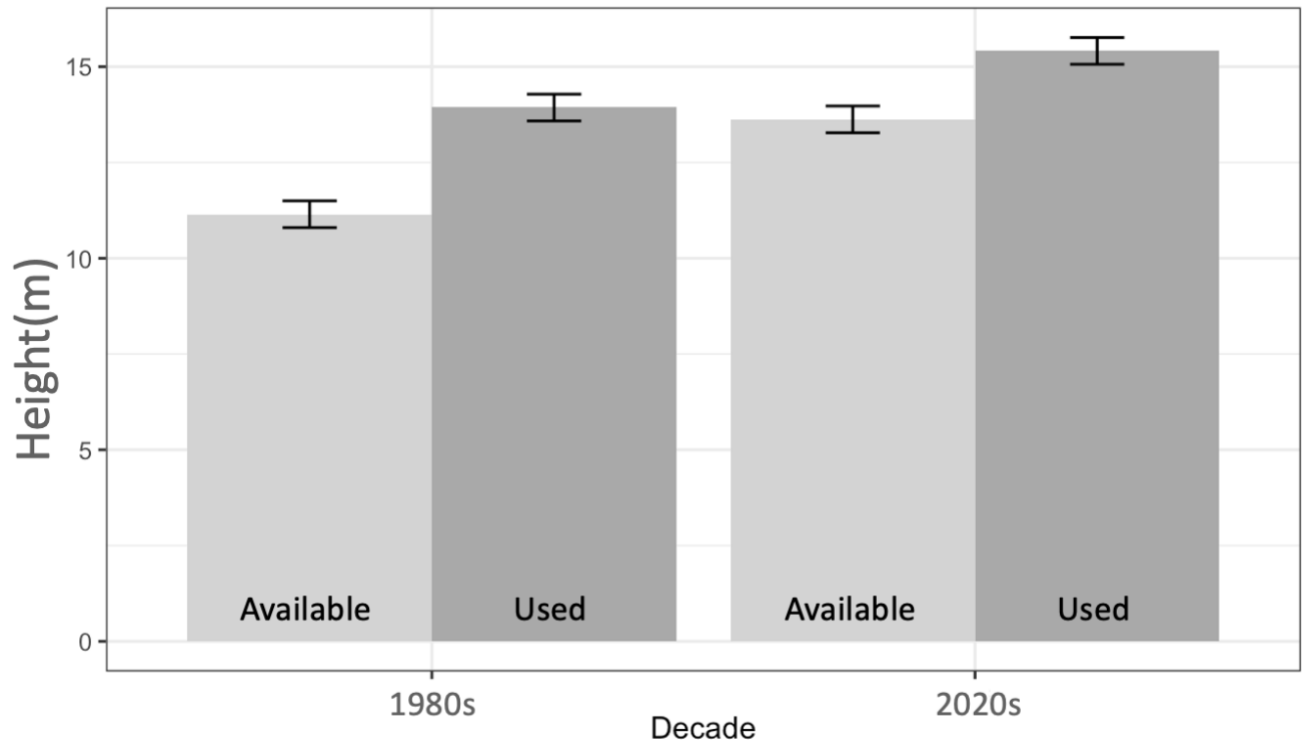
**Table 2.** Models for Flammulated Owl day-roost use at the tree scale. K is the number of parameters in a model,  $AIC_c$  is Akaike's Information Criterion corrected for small sample sizes,  $\Delta AIC_c$  is the difference between  $AIC_c$  values of each model and the top model,  $AIC_{cwt}$  is the  $AIC_c$  weight of the model,  $Cum_{wt}$  is the cumulative weight of each model, and LL is the Log likelihood of each model. CV is crown volume, SP is tree species, TH is tree height, DB is DBH, and Null is the null model.

Year	Model	K	$AIC_c$	$\Delta AIC_c$	$AIC_{cwt}$	$Cum_{wt}$	LL
2023	Null	1	46.49	0.00	0.9	0.9	-22.18
	SP	4	50.94	4.44	0.1	1.00	-20.73
1982-1983	CV	2	117.08	0.00	0.44	0.44	-56.48
	CV+SP	6	117.22	0.14	0.41	0.85	-52.15
	CV+TH	3	119.20	2.13	0.15	1.00	-56.47
	TH	2	133.88	16.81	0.00	1.00	-64.88
	SP	2	136.93	19.85	0.00	1.00	-63.16
	DB	2	137.20	20.12	0.00	1.00	-66.54
	Null	1	144.32	27.25	0.00	1.00	-74.14

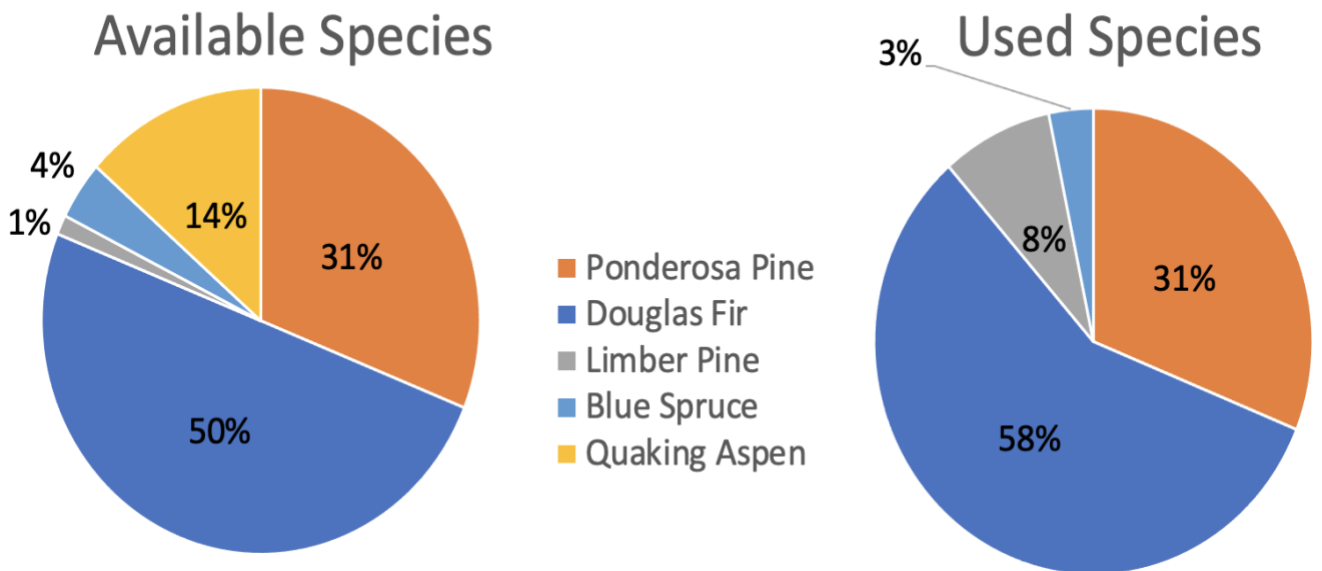


**Figure 9.** Average DBH (in centimeters) of Flammulated Owl roost trees and available trees in 1982-1983 and 2023 in central Colorado. In 1982-1983 Roost trees (N=45) had significantly higher DBHs than available trees (N=59) ( $p < 0.001$ ). There was no significant difference between the DBHs of roost trees (N=16) and available trees (N=16) in 2023 ( $p = 0.67$ ). 2023 available trees were significantly larger than 1982-1983 available trees ( $p < 0.001$ ). There was no significant difference between the DBH of 2023 and 1982-1983 roost trees ( $p = 0.103$ ).

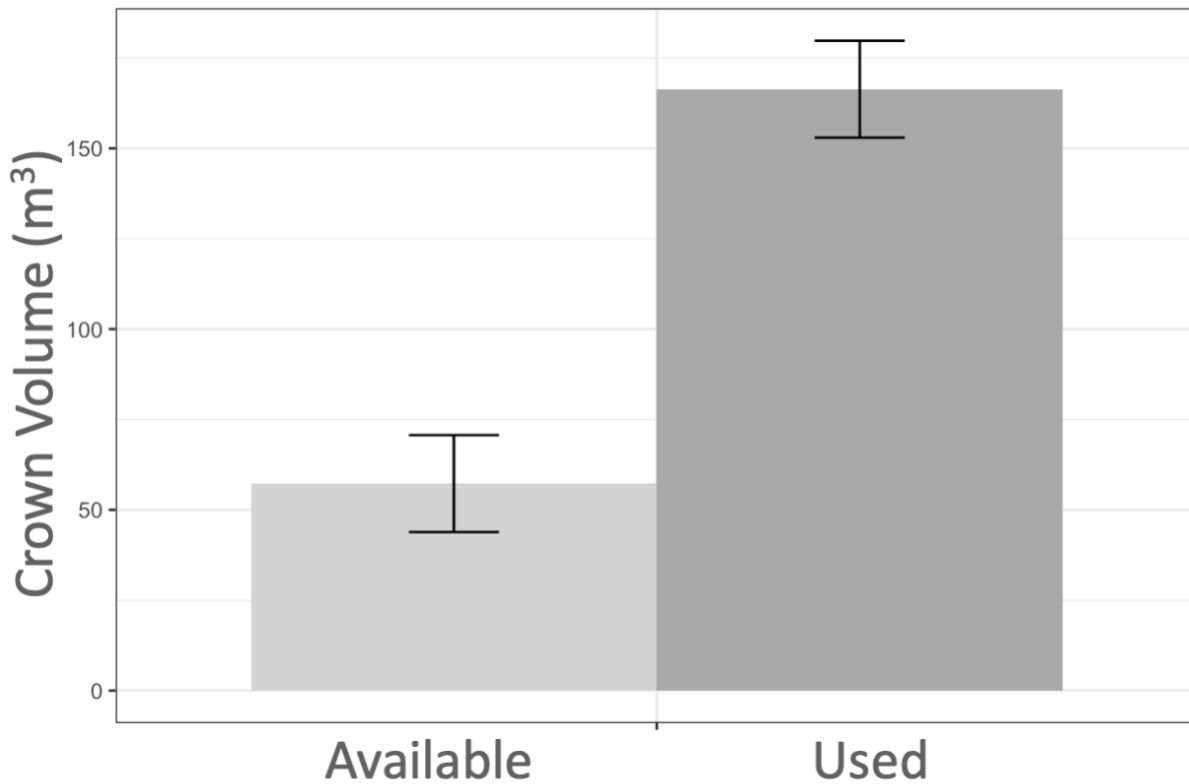




**Figure 10.** Average height, in meters, of Flammulated Owl roost trees and available trees in 1982-1983 and 2023 in central Colorado. Roost trees were significantly taller than available ones in 1982-1982 ( $p < 0.001$ ), but not in 2023 ( $p = 0.16$ ). 2023 available trees ( $N = 16$ ) were significantly taller than 1982-1983 available trees ( $N = 59$ ) ( $p = 0.04$ ). There was no significant difference between the height of 2023 ( $N = 16$ ) and 1982-1983 ( $N = 45$ ) roost trees ( $p = 0.13$ ).



**Figure 11.** Species makeup of Flammulated Owl roost trees and available trees in central Colorado. Douglas-firs were used at a higher rate than they were available in the environment. Quaking aspen trees were never used as roosts but made up 14% of available trees.

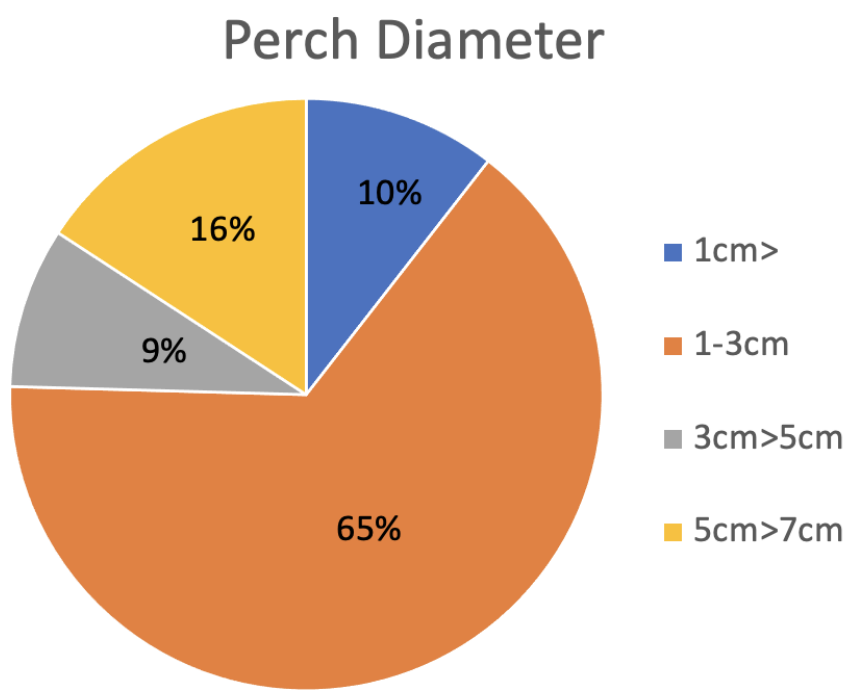


**Figure 12.** The average crown volume, in meters<sup>3</sup>, of Flammulated Owl roost trees and available trees in central Colorado. Roost trees (N=45) had significantly higher crown volumes than available trees (N=59) ( $p < 0.001$ ).

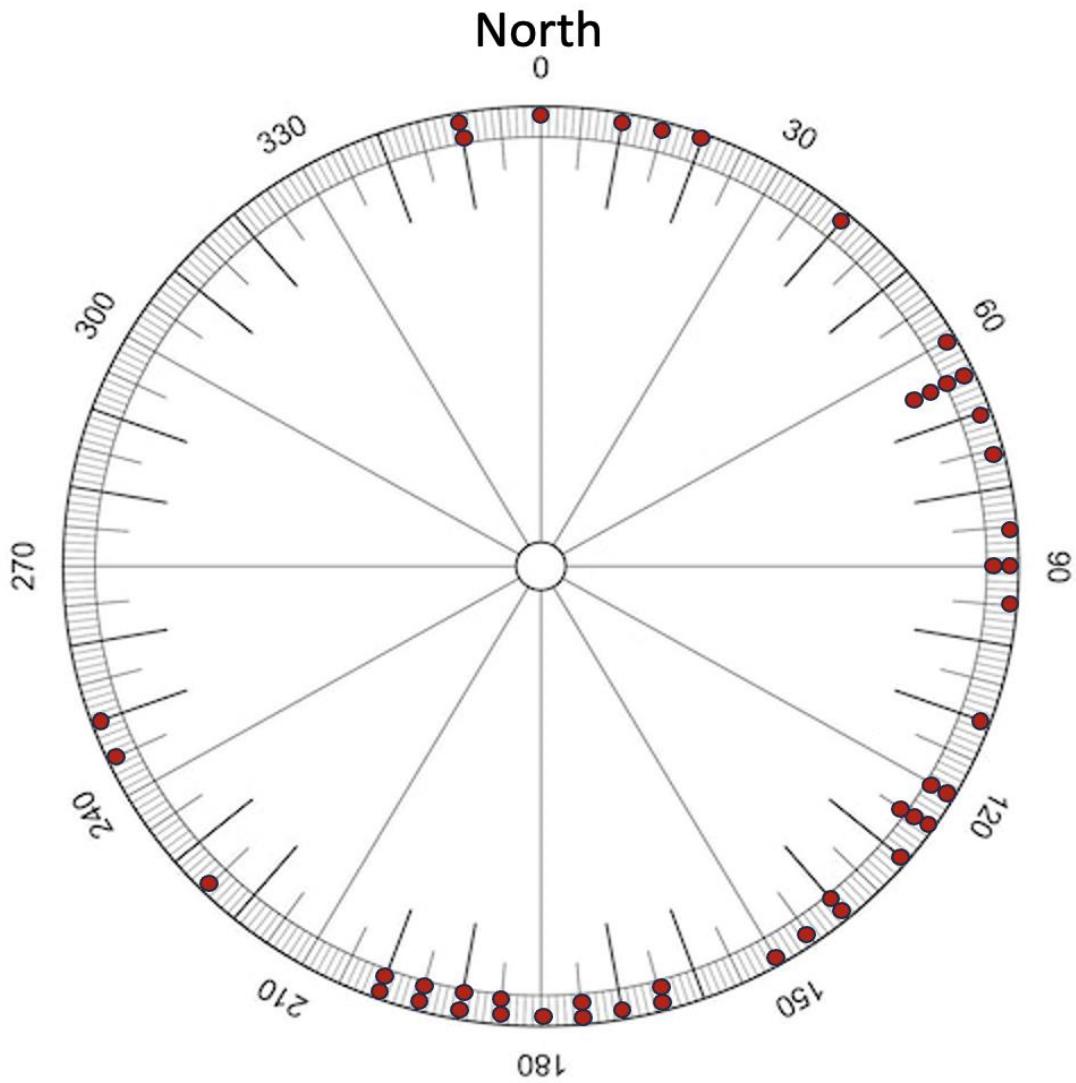
### *Perch Scale*

At the perch scale, owls typically chose perches with small diameters. 65% of perches were between 1 and 3 cm in diameter, and no perches exceeded 7cm in diameter (Figure 13). They frequently roosted close to the trunk of the tree, with owls touching the trunk on 69.4% of perches. Owls were never observed to roost more than 4m away from the trunk of the tree. There was no significant difference between the canopy cover in the direction the perch was facing compared to the other three cardinal directions. Owls did not face any singular direction more than would be expected by chance. North and south-facing perches were not used at a

significantly different rate; however, east-facing perches were used significantly more frequently than west-facing perches [ $X^2(1, N = 44) = 3.7, p = 0.05$ ] (Figure 14). 93.8% of perches were in the upper 50% of a tree, with 68.8% of perches in the upper 75%.



**Figure 13.** Diameters (in cm) of perches used by Flammulated Owls in central Colorado. The majority of perches were between 1 and 3 centimeters in diameter. No perches were larger than 7cm in diameter.



**Figure 14.** Compass orientation of perches used by Flammulated Owls in central Colorado. Each dot represents one perch. Use did not differ between north and south-facing perches. East-facing perches were used more frequently than would be expected by chance [ $X^2(1, N = 44) = 3.7, p = 0.05$ ].

## Discussion

### *Tree Stand Scale*

My results suggest that at the tree stand scale, male Flammulated Owls maximized the amount of cover provided by surrounding trees. Stands of trees at roost sites had significantly higher densities of large trees than available stands. However, there was no significant difference between the total density of trees or the density of small trees in roost stands and available stands. Trees with DBHs above 20cm are typically taller than trees with DBHs below 20cm, and, in the case of both ponderosa pines and Douglas-firs, younger trees have denser crowns toward their bases than their tops (Huckaby et al., 2003; Ishii et al., 2016). While the crowns of younger trees may reach the heights at which owls typically roost, their sparse upper crowns would likely provide little cover. Older trees, however, are more likely to have dense crowns at the height of owl roosts, providing high canopy cover to roost sites. Roost stands also had a greater number of trees in a clump with the roost tree. This higher number of interlocking crowns is also likely to provide a large amount of foliage cover to roosting owls.

The dominant DBH size class of tree stands did not significantly differ between roost sites and available sites. However, the significance of a high density of large trees suggests that the presence of mature and old-growth trees is an important factor at this scale. All but one of the 2023 roost trees occurred in clumps. These clumping dynamics are characteristic of the historic structure of ponderosa pine forests in the American Southwest, the structure of which was maintained by frequent low-intensity fires (Graham & Jain, 2005; Reynolds et al., 2013). This suggests that historic fire regimes continue to affect selection of day-roost habitat even after more than a century of fire suppression.

The distance of a stand from the nest tree was an important characteristic in determining use at the tree stand scale. Roost sites were significantly closer to the nest than available sites; this is consistent with previous studies in which the majority of roost trees were within 100m of nests (Yanco & Linkhart, 2018). Roosting closer to nest sites could reduce the amount of energy owls spend traveling between roost and nest sites and allow the male to monitor the nest site during the day. Linkhart et al. (1998) found that all male owls roosted within 20m of their nest sites in the four days preceding fledging. I also observed males roosting significantly closer to their nests in the 5 days before fledging. However, due to the small size of my data set, I did not separately analyze roost sites close to fledging. When comparing 2023 roosts >5 days from fledging and available trees, there was no significant difference between the distances. However, I believe this is due to the small data set, which had one notable outlier that greatly increased the average distance of roost trees from the nest. Given this, I believe further studies separately analyzing roosts used within 5 days of fledging would be required to fully understand the significance of this trait.

I had originally anticipated that Flammulated Owls would select roost locations that helped them reduce heat stress. Barrows (1981) observed that Spotted Owls (*Strix occidentalis*), which have a low tolerance for hot temperatures, roost in cooler closed-canopy forest often on north-facing slopes. However, Flammulated Owls used stands of trees on south-facing slopes at a higher rate than they were available in the environment. South-facing slopes are significantly warmer and drier than north-facing slopes. While roosting on warmer slopes may enable Flammulated Owls to remain warm when conditions are cool, daily temperatures during this study were frequently above 25°C; so, it seems unlikely that owls were trying to warm themselves.

Most roost sites were on slopes positioned in the southwest quadrant of the compass. Ponderosa pine stands are most frequently found on southwest-facing slopes, as are older trees (Graham & Jain, 2005; Linkhart et al., 1998; Reynolds et al., 2013). Although stand DBH size class and species makeup were not significant predictors of use in my analyses, this could suggest that owls are selecting for slopes that contain these stand types. Historic fire regimes in ponderosa pine ecosystems facilitated the formation of open park-like stands dominated by clumps of older trees (Dickinson et al., 2014; Graham & Jain, 2005; Reynolds et al., 2013). However, fire suppression has resulted in increased tree densities in these ecosystems (Covington & Moore, 1994; Reynolds et al., 2013). Notably, south-facing slopes in the Colorado Front Range generally support lower densities of trees, resulting in more open stands (Dickinson et al., 2014; Finney et al., 2003). Given this, the selection of south-facing slopes could suggest that owls are selecting day-roost habitat that is similar in structure to historic ponderosa pine forests before fire suppression.

### *Tree Scale*

Flammulated Owls appeared to select roosts that maximized foliage cover at the tree scale. Use was significantly more likely in trees with larger crown volumes. Though not always true, larger trees (in terms of both DBH and height) often have greater crown volumes (Graham & Jain, 2005). In 1982-1983 specifically, the DBH of roost trees was significantly larger than available trees. Conversely, in 2023 there was no significant difference between the DBH of used roost trees and available trees, which may be a result of a low sample size. The average available tree in 2023 was larger than in 1982-1983, as they have had 40 years to grow, but roost trees did not significantly differ in size between decades. Even though there was no apparent difference



between the DBH of roost trees and available trees in 2023, the average DBH of roost trees in 2023 was greater than in 1982-1983 (though not significantly), suggesting that larger trees may be valuable for Flammulated Owl roosting.

The two species of tree that were most frequently used as day-roosts were Douglas-fir and ponderosa pine. Douglas-firs were used more frequently than every other species combined, likely because they tend to have the largest crowns (Linkhart et al., 1998; Yanco & Linkhart, 2018). These results are consistent with previous studies that found Flammulated Owls roost most frequently in Douglas-firs and in trees with large heights and DBHs (Linkhart et al., 1998; Yanco & Linkhart, 2018). Old-growth ponderosa pines and Douglas-firs generally have sparser crowns than mature trees (Franklin et al., 1981; Graham & Jain, 2005; Huckaby et al., 2003; Reynolds et al., 2013; Washington State Department of Natural Resources). Given this, it seems that mature trees may be most important to Flammulated Owls at this scale, as their crowns are likely to provide the birds with the most cover. Previous studies found that the best predictor of use at the tree scale was whether a tree was alive or a snag (Linkhart et al., 1998; Yanco & Linkart, 2013). This trait was not included in my analyses, however, only one roost tree in this study was a snag, which corroborates prior research and indicates that live foliage is important for roosting.

High foliage cover can provide many benefits to roosting birds (Finne et al., 2000; Walsberg, 1983). Basal and thermostatic metabolism account for approximately 40-60% of the energy expenditure of wild birds (Walsberg, 1983). Roosts that shield birds from wind and precipitation are known to greatly decrease metabolic costs by reducing the amount of energy lost due to radiative and convective heat loss (McCafferty et al., 2001; Shaw, 1979; Walsberg, 1983). Additionally, roosts with dense foliage cover are hypothesized to decrease predation risk

(Finne et al., 2000). Trees with larger crowns typically have more foliage, providing more cover from predators and adverse weather. Therefore, roost trees with large crown volumes are likely to provide Flammulated Owls with thermoregulatory benefits and reduce their risk of predation.

### *Perch Scale*

At the perch scale, Flammulated Owls overwhelmingly chose perches with small diameters. These smaller branches are likely easier for the small owls to hold on to for extended periods of time. Individuals roosted most frequently in the upper portions of a tree's crown. Mature ponderosa pines and Douglas-firs typically have denser crowns higher in the tree, and Flammulated Owls appeared to roost most frequently in the upper third of trees and in areas with denser foliage cover (Huckaby et al., 2003; Ishii et al., 2016, *pers observation*). However, more research is required to fully understand how owls may select perches regarding foliage cover. Individuals also perched with their bodies touching the trunk of the tree, which likely serves to reduce the visibility of their bodies. Owls often perched facing east more than any other direction, which potentially reduced the amount of direct sun exposure individuals experienced during the day.

### *Conclusion*

My results suggest that Flammulated Owls selected day-roost locations that maximized the amount of foliage cover they receive at each spatial scale I examined. Roosts with high vegetative cover have been documented to reduce both radiative heat loss and convective heat loss to wind (McCafferty et al., 2001). In Barn Owls (*Tyto alba*), metabolic heat production was observed to decrease when the birds roosted in locations with high cover, such as in trees with

dense foliage, or in human buildings (McCafferty et al., 2001). Roosting in trees with high foliage cover can therefore greatly reduce the energy Flammulated Owls spend thermoregulating, allowing them to allocate energy to other activities. This is especially important during the breeding season, as feeding nestlings requires extensive effort and energy.

Multiple avian species are suspected to roost in locations that reduce their risk of predation, and in the case of raptors, locations that reduce the risk of mobbing by smaller birds (Pavey, 1998; Townsend, 2009). While predation of adult Flammulated Owls is poorly documented, mortality due to diurnal accipiter hawks has been recorded (McCallum, 1994). Little is known about the mobbing of Flammulated Owls; however, I observed roosting Flammulated Owls adopting a concealing posture in response to American Crow (*Corvus brachyrhynchos*) vocalizations. This suggests that they view Crows, which are known to engage in mobbing behavior (Barash, 1976), as a threat. Thus, roosting in areas with dense foliage could decrease the likelihood that potential predators or mobbing birds will spot the owls during the day, increasing their chances of survival.

Old-growth trees are important for many other aspects of Flammulated Owl habitat selection, such as hunting and nesting habitat (Linkhart et al., 1998). However, mature ponderosa pines and Douglas-firs typically have denser crowns with greater volumes than old-growth trees of the same species (Franklin et al., 1981; Graham & Jain, 2005; Huckaby et al., 2003; Reynolds et al., 2013; Washington State Department of Natural Resources). This suggests that mature trees rather than old-growth ones may be most important for Flammulated Owl day-roosting habitat. The significance of a high density of large trees indicates the importance of both mature and old-growth trees at the tree stand scale, though exclusively old-growth habitat does not seem to be necessary.

Historic structures of ponderosa pine forests, such as typical clumping dynamics, also appear important for day-roost habitat. These forest structures are maintained by frequent low-intensity fires; however, stand-replacing crown fires are becoming more frequent in the American Southwest (Covington & Moore, 1994; Reynolds et al., 2013). Fire suppression resulting in increased fuel loads, combined with elevated global temperatures, greatly increases the risk of high-severity fires in these ecosystems (Covington & Moore, 1994; Reynolds et al., 2013). These high-severity fires have the potential to decimate old-growth and mature forests, resulting in forests of small, young trees with homogeneous horizontal structures (Reynolds et al., 2013). The loss of high-quality day-roost habitat could have adverse implications for the species by greatly increasing their risk of predation and elevating energy expenditure. Therefore, reducing the frequency of high-severity crown fires and promoting low-intensity ground fires will be vital in maintaining the availability of high-quality day-roosting habitat for this species.

This study reveals important trends in Flammulated Owl day-roost selection behavior. However, even with the addition of the 1982-1983 data, my data set was quite small. Additionally, I had no crown volume data for 2023, which was the most important characteristic at the tree scale, so more recent crown volume data is required. Due to the difficulty of accessing owl perches, data at the perch scale would benefit from more accurate procedures, specifically foliage cover. Thermoregulatory benefits are some of the most important aspects of avian roost selection (Körtner & Geiser, 1998; McCafferty et al., 2001; Walsberg, 1986). Future studies comparing the temperatures inside roosts to ambient temperatures could provide us with important insights into how these owls use day-roosts to thermoregulate. This information could be especially important to the species' conservation as the global climate continues to shift.

This study revealed the importance of mature, mixed ponderosa pine and Douglas-fir forests for Flammulated Owl day-roost habitat. Maintaining a high availability of this habitat throughout the Flammulated Owl's range will therefore be vital to the conservation of the species. Reducing the logging of mature and old-growth forests and promoting frequent low-intensity fires can help conserve these important habitats. Thinning younger trees and reducing understory fuel loads are strategies that could help reduce catastrophic high-intensity fires that threaten these forests (Graham & Jain, 2005; Pollet & Omi, 2002). While these results provide information that can help influence management strategies, the scope of this study was limited. Further research into Flammulated Owl day-roost selection is required to fully understand what resources they rely on for this aspect of their behavior.

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