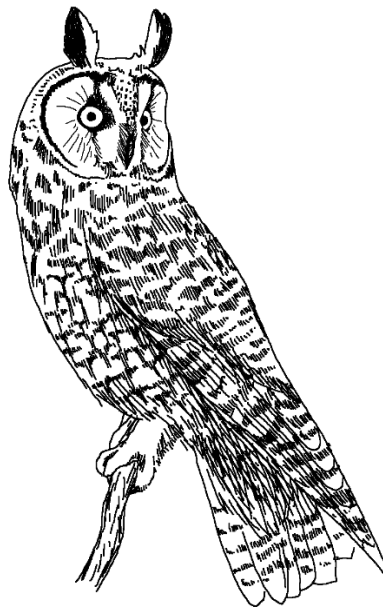DIURNAL ROOST SITE SELECTION

IN LONG-EARED OWLS (*ASIO OTUS*)

Tyler Christensen

Advanced Ecological Data Analysis

Final Project Report

Introduction

Long-eared Owls (Asio otus) are a medium-sized owl with a holarctic distribution. Due to their strict nocturnality, cryptic appearance, and furtive habits, the Long-eared Owl is among the least-studied owls in North America (Gross 2010). In New Jersey Long-eared Owls are a threatened species whose state population is thought to be declining (Beans and Niles 2003), Bosakowski et al. 1989). Long-eared Owls form gregarious roosts during the winter, with up to a dozen or more owls roosting together in a single tree or shrub or on adjacent stems.

Winter is associated with the highest mortality rates for most birds of prey (Newton et al. 2016). Predation and starvation are the primary causes of mortality in Long-eared owls (Tome 2011). Benefits of selecting suitable roost sites likely include protection from wind, precipitation, predation, and mobbing behaviors of other birds (Bosakowski 1984). Perhaps for these reasons, owls roost in areas with greater vegetation density and overhead cover (Churchill 2000).

The contrast between published accounts of roost site characteristics and my own observations at roost sites located via radiotelemetry in 2018 motivated this study. Although many published studies have involved locating and visiting Long-eared Owl roosts (e.g., the hundreds of studies on Long-eared Owl diets; see Birrer 2009), these studies pose one or more of the following problems for interpreting roost habitat preferences: (1) Roost site selection was not the primary focus of the studies, and consequently roost descriptions were only cursory; (2) Roost descriptions mostly focused on compositional, rather than structural, attributes of the vegetation (e.g., "[the roost] was located … among a stand of 15 pine trees (*Pinus pinea*), two field elms (*Ulmus minor*), and one pecan (*Carya illionensis*);" Charter et al. 2012) , which are likely not the ultimate basis for their selection by owls (Churchill 2000); (3) there have been few if any attempts to describe the process of roost site selection quantitatively (Holt 1997), e.g., by comparing the structural environment at selected habitats with that of non-selected habitats; and (4) no study of which I am aware used unbiased survey methods to detect roosts, e.g., radiotelemetry – other methods of locating owls and owl roosts, such as visual detection, have resulted in biased and incorrect conclusions about roost habitat preferences in other, more abundant, owls (Churchill 2000).

The present study attempts to address some of these shortcomings of the current literature when it comes to elucidating Long-eared Owl roost site selection processes. Knowledge of roost site characteristics may lead to a better understanding of their habitat requirements, possibly contributing to the ability to evaluate and manage habitats for their ability to support winter roosts of Long-eared Owls.

I radio-tracked 19 Long-eared owls to their roosts during the winters of 2019-2020 and 2020-2021 to characterize their structural attributes. I compared these with paired sites situated in the forest surrounding each roost. This comparison provided insights about the process of selection of roost sites in Long-eared Owls during winter.

Methods

Data Collection – During the winters of 2019-2020 and 2020-2021, 16 Long-eared Owls were captured and fitted with either VHF or VHF-GPS transmitters. Owls were captured using a combination of mist nets with audio lures playing calls of conspecifics, or bal-chatri traps baited with live mice and augmented with audio lures playing recordings of meadow vole (*Microtus pennsylvanicus*) vocalizations. VHF radio transmitters (Advanced Telemetry Systems model) weighed 3.6g and were mounted to a central rectrix following the methods of Kenward (1985). GPS transmitters with VHF beacons weighing an average of

9.5g were attached to owls using a custom backpack made of tubular Teflon® webbing following the methods of Steenhof (2006). Owls were released at or near the point of capture and tracked the following day using a handheld receiver (Icom R10) and 3-element Yagi antenna (Wildlife Materials, Inc.). Roost trees were identified by the presence of owls and/or the presence of pellets and whitewash (excrement) directly underneath the roosts, were marked with forestry tape, and were then revisited in February and March 2021 for data collection, once owls had left.

Vegetation and roost site characteristics were measured within a 5m-radius circular plot centered on the roost tree. This space was thought to represent the approximate area within which vegetation characteristics would have direct effects on the conditions experienced by roosting owls, even though the surrounding habitat almost certainly influences the thermal environment, risk of predation, probability of disturbance, maneuverability to and from the roost, etc., thereby impacting overall roost habitat suitability. In some cases, owls were distributed among several trees proximate one another in a "roost complex", in which cases the plot was centered on the centroid among roost trees.

Thirteen variables were measured within each plot (Table 1). Variables were chosen based on published information on habitat use by Long-eared Owls and other owl species (e.g., Bosakowski 1984, Churchill 2000, Blakey et al. 2019) or my own knowledge of Long-eared Owl biology and observations of past roost site characteristics. To derive estimates of overhead cover, canopy photographs were taken at the plot center and at five meters in each cardinal direction using smartphones mounted on tripods facing upwards from a height of 1m above the ground (see Data Analysis). Canopy height and roost tree height were measured using a clinometer app for smartphones (Tree Height Estimator).

To compare plots utilized as roost habitats to "available" habitat in the area surrounding the roost, the same thirteen variables were measured at a "control plot" chosen by traveling in a random direction (0 – 359°) and at a random distance (10 – 50m) from the roost plot and centering the plot on the nearest tree (Churchill 2000, Sutton et al. 2010).

Data Analysis – Canopy closure photographs were analyzed using ImageJ and values were averaged for each plot. Invasive and evergreen closure were derived by multiplying estimated proportions for each class by the canopy closure estimates taken at respective measurement location(s) within the plot.

The remaining analyses were performed in R version 3.6.2. I used a binomial logistic regression approach to determine the relationships between plot residency status and habitat covariates. To conform to assumptions of binomial regression, each observation's status (control versus roost) received the designation of 0 or 1, respectively.

One missing CanopyHeight value was imputed using the factor mean. Distributions for each of the 13 factors were visualized using Cleveland dot plots (Fig. 1). Distributions among the two plot status levels (roost vs. non-roost) were visualized using boxplots (Fig. 2). In order to compare the effect sizes of factors in the models, all 13 variables were scaled and centered.

Since factor independence is an assumption of linear models, only predictor variables whose effects on the response are independent of one another were desired for candidate models. Collinearity among the 13 predictors, the presence of which is a violation of the assumption of factor independence, was assessed in two ways: first visually, by plotting all combinations of predictors against one another (Fig. 3), and then quantitatively, by calculating pairwise Pearson's correlation coefficients. Variables with correlation coefficients greater than 0.7 were considered collinear (Dormann et al. 2013).

Table 1. List and descriptions of variables measured at Long-eared Owl roosts and their respective controls.

Variable	Description
CanopyHeight	Average height of canopy at four cardinal points and plot center
CanopyClosure	Average canopy closure at cardinal points and plot center
StemsUnder2.5	Number of stems under 2. 5cm
StemsOver2.5	Number of stems above 2. 5cm
Stems	Total number of stems (sum of above)
EvergreenClosure	Percent evergreen closure
RoostCanopyClosure	Canopy closure directly above roost(s)
InvasiveClosure	Percent invasive closure
RoostVineClosure	Percent vine closure at roost(s)
CanopyHeightRoostAve	Height of canopy above roost(s)
RoostTreeDBHAve	Average DBH at roost tree(s)
RoostTreeHeightAve	Roost tree height(s)
DistanceToTreeAve	Distance to nearest tree(s)

Among pairs of collinear variables, each individual variable was used to fit a bivariate (i.e., the effect of the single predictor on the response) generalized linear model (glm) using the `stats::glm()` function. Because the response was binary, I used a binomial error structure and a logit link function. Model fit was assessed using Akaike's Information Criterion (AIC), and the variable with the bivariate glm that produced the lower AIC was retained for inclusion in the global model. The variable with the higher AIC score of each pair was eliminated.

In the case of the three variables related to stem density within plots (*StemsUnder2.5*, *StemsOver2.5*, and *Stems*), a slightly different approach was taken: Two of the three variables were collinear (*StemsUnder2.5* and *Stems*). Of the collinear pair, the bivariate glms for *StemsUnder2.5* and *Stems* had similar AIC scores (AIC = 56.68 and 56.67, respectively). Even though *Stems* had a slightly lower AIC, since it represented the sum of *StemsUnder2.5* and *StemsOver2.5*, I decided to eliminate *Stems* in favor of retaining the mutually exclusive *StemsUnder2.5* and *StemsOver2.5* variables.

With the remaining set of non-collinear variables, `glm()` encountered issues with overfitting. This can occur when there is a perfect separation of response levels, i.e., the model was able to perfectly predict every case, resulting in undefined likelihoods. Practically this may occur when there are too many predictor variables for the given sample size, which would be unsurprising in this case given the relatively small number of roosts and controls (n = 38). My solution was to reduce the number of variables further, though other solutions to overfitting do exist, including some Bayesian methods or penalized likelihoods (Scheipl et al. 2013), or variable reduction techniques such as regression using principal components.

I eliminated *InvasiveClosure* since owls were unlikely to be selecting roosts according directly to plant nativity status. If owl selection was related to plant nativity in some way, the reasons would likely be indirect, and may have more to do with structural differences than compositional differences. These structural differences would hopefully be captured by the other variables in the set that related to vegetation structure directly. I eliminated *DistanceToTreeAve* and *RoostTreeHeightAve* next because they both had low performance according to bivariate glms: each had high AIC scores for their bivariate glms compared to other variables in the model set; their slope coefficients were small and statistically insignificant, with standard errors that included zero; and results of Welch's t-tests indicated that differences in the predictor means between the two response levels had high probabilities ($p > 0.4$) of occurring at the observed magnitude or larger under null scenarios.

After the elimination of each variable, I attempted to fit a new glm to see whether the overfitting issues had been resolved. Once the variables above had been eliminated the model converged. Retained predictor variables were *CanopyHeight*, *StemsUnder2.5*, *StemsOver2.5*, *EvergreenClosure*, *RoostCanopyClosure*, *RoostVineClosure*, and *RoostTreeDBHAve*. A global model was fit to the data using the factors retained during variable selection. A backward stepwise selection procedure was used to test nested models derived from the global model using `stats::step()`, which used AIC to select the most parsimonious model at each step (Zuur et al. 2009). All models were assessed for goodness of fit using AIC scores. Models that were within 2 ΔAIC of the top-ranked model were considered to have relatively high support, and results from those models were reported.

The linear model assumptions of normally- and homoskedastically-distributed residuals were assessed using the package `DHARMa`. To investigate the source of the deviations from normality and homoskedasticity, I plotted standardized residuals against each predictor variable retained in the final model. This procedure also indicates patterns of factor dependence/independence, which has implications for overall model fit (Zuur et al. 2009). Remaining multicollinearity within the top-ranked model was assessed by calculating variance inflation factors for each variable using the function `stats::vif()`. The `summary()` function was used to generate p-values and other summary statistics for the set of top-ranked models that were within 2 ΔAIC. To test the performance of the top-ranked models, they were compared to the global model and to a null model using AIC.

To test a hypothesized inverse relationship between the amount of coniferous evergreen vegetation and vine closure in the canopy at roost sites, I calculated a Pearson's correlation coefficient for these two variables among the subset of data containing only Long-eared Owl roost plots, and plotted the two predictors against one another.

Results

Six models were produced by backward stepwise model selection that were ranked within 2 ΔAIC of the top-performing model, indicating a high level of support (Table 2). All six of the top models contained the variables *RoostCanopyClosure* and *RoostVineClosure*. In the top-ranked model none of the coefficients had statistically significant *p*-values, though the effects of *RoostCanopyClosure* and *RoostVineClosure* approached significance (Table 3).

The `DHARMa` residual diagnostics indicated heteroskedasticity among the standardized residuals in the top-ranked model, particularly within the upper 0.75 quantile and among middle values of the predictors (Fig. 4). A QQ plot indicated deviations from normality. Plotting the residuals against each of the

Table 2. Top-ranked models (those within 2 ΔAIC) generated by backward stepwise model selection. AIC and ΔAIC of the global and null models are also shown. EV = *EvergreenClosure*, CAN = *RoostCanopyClosure*, VIN = *RoostVineClosure*, DBH = *RoostTreeDBHAve*, SU = *StemsUnder*2.5, SO = *StemsOver*2.5,

Model	AIC	ΔAIC
EV + CAN + VIN + DBH	30.57	0.00
SO + EV + CAN + VIN	31.11	0.54
SO + EV + CAN + VIN + DBH	31.51	0.95
CAN + VIN + DBH	31.65	1.08
EV + CAN + VIN	32.12	1.55
SU + EV + CAN + VIN + DBH	32.25	1.68
Global model	35.24	4.68
Null model	54.68	24.11

predictor variables suggested that *RoostCanopyClosure* and *RoostTreeDBHAve* had heteroskedastic residual distributions, which may have contributed to the deviations some of the top models (Fig. 5).. The second model in the top-ranked set (*RoostStatus* ~ SO + EV + CAN + VIN) did not violate assumptions of residual normality and homogeneity according to DHARMa residual diagnostics. The variance inflation factor (VIF) scores for the variables in the top-ranked model were all < 2.0, indicating low multicollinearity among the factors in the final model.

The estimated β coefficients indicate that canopy closure had the greatest effect on the probability that a plot was one that contained a Long-eared Owl roost. Roost plots had greater mean canopy cover (79.7% ± 2.5% SE) than non-roost plots (53.8% ± 4.7% SE). Canopy closure was followed in importance by vine closure at the roost tree, roost tree diameter, and amount of evergreen vegetation in the canopy. Evergreen vegetation at roosts was 34.7% ± 5.6% versus 19.3% ± 5.2% at non-roosts. Bivariate probability plots showed how the estimated probability of a plot containing a Long-eared Owl roost relates to each of the four predictor variables appearing in the top-ranked model (Fig. 6). An increase in the amount of any of the four variables resulted in an increased probability that a plot was occupied. At roost plots, vine cover and evergreen cover were strongly negatively correlated (-0.71, p < 0.001; Fig. 7)

Discussion

These findings represent perhaps the first attempts to (1) describe Long-eared Owl roost site selection quantitatively, and (2) use a survey methodology by which to locate roosts that avoids introducing potential observer biases. The increased probability of plot residency by a roost of long-eared owls when canopy closure, evergreen closure, and vine closure were greater indicate that vegetation density is indeed an important part of the process of roost site selection in Long-eared Owls. This is consistent with other owl species that utilize dense cover to protect against winter weather, predation, and disturbance (Curchill 2000, Blakey et al. 2019). That owl roosts were associated with greater levels of vine cover, particularly

Table 3. β coefficients, standard errors, and p-values for factors retained in the top AIC-ranked model.

Factor	β	SE	p
EvergreenClosure	1.14	0.75	0.13
RoostCanopyClosure	2.01	1.19	0.09
RoostVineClosure	1.91	1.04	0.07
RoostTreeDBHAve	1.26	0.80	0.11

when evergreen closure was low, was an unanticipated but perhaps explicable finding: Since vegetation density is important in selecting roost sites, it stands to reason that when roosts lacked evergreen cover, they tended to be beneath dense vine cover instead.

Because patterns of resource selection can proceed across multiple spatial scales, defining "availability" in use-availability analyses has important implications for their interpretation (Mayor et al. 2007, McGarigal 2016). While there is no consensus definition for availability, particularly across multiple spatial scales and for organisms displaying a dramatically broad array of spatial behaviors, there is general agreement that it should be defined in such a way that is biologically meaningful and interpretable. In this case, a radius of 50m surrounding the roost was intended to represent habitat that was (1) accessible to a mobile animal like a Long-eared Owl, such that control roosts were situated in habitat that was easily available and exploitable; and (2) within forest of similar age and stand composition, so that any differences among paired plots were due to heterogeneity at the microhabitat or mesohabitat scale.

Because study plots were concerned with variables within 5m of each roost, and because "available" control plots were restricted to within a 50m radius of roost plots, the findings of this study extend only to fine-scale habitat selection processes. This leaves much unanswered about how Long-eared Owls are choosing habitats across larger spatial scales. For example, decisions about where to situate winter activity ranges may include factors related to prey abundance, proximity to habitat with structural attributes optimal for foraging, levels of predators or noise pollution, or other factors less pertinent at the micro- or mesohabitat scales. Because of the paucity of literature on their roost habitat preferences across all levels of organization, the impacts of forest management practices on the availability and quality of forested habitats for Long-eared Owls are unknown (Holt 1997). Adequate understanding of Long-eared Owl habitat requirements will have to integrate information about habitat selection across multiple spatial scales, ranging from fine-scale vegetation structural preferences at the roost to optimal configurations of macrohabitats within the landscape.

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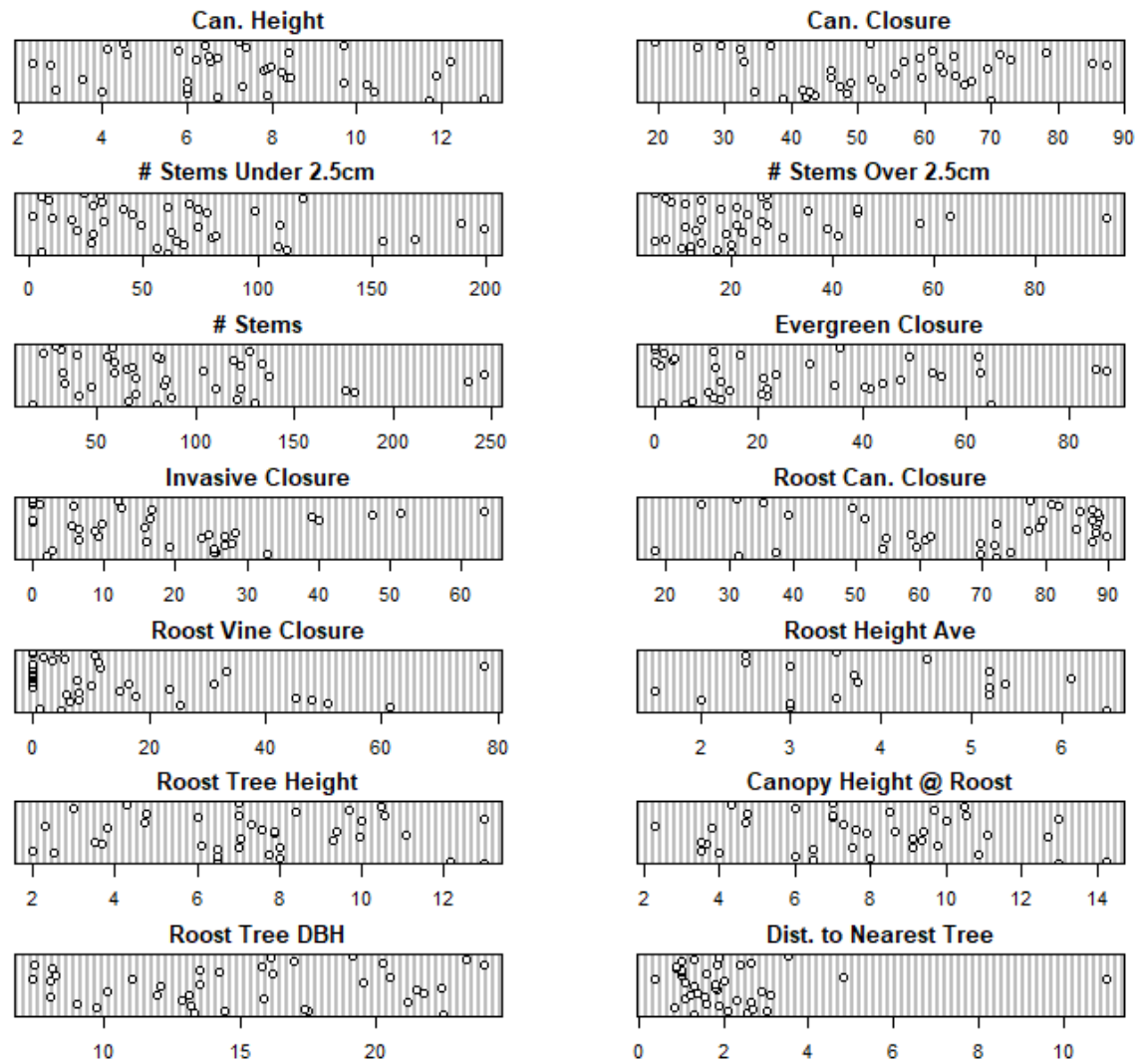   models and extensions in ecology with R. Springer, New York.

Figure 1. Cleveland dot charts to visualize distributions of each factor measured at Long-eared Owl roost sites and paired controls.
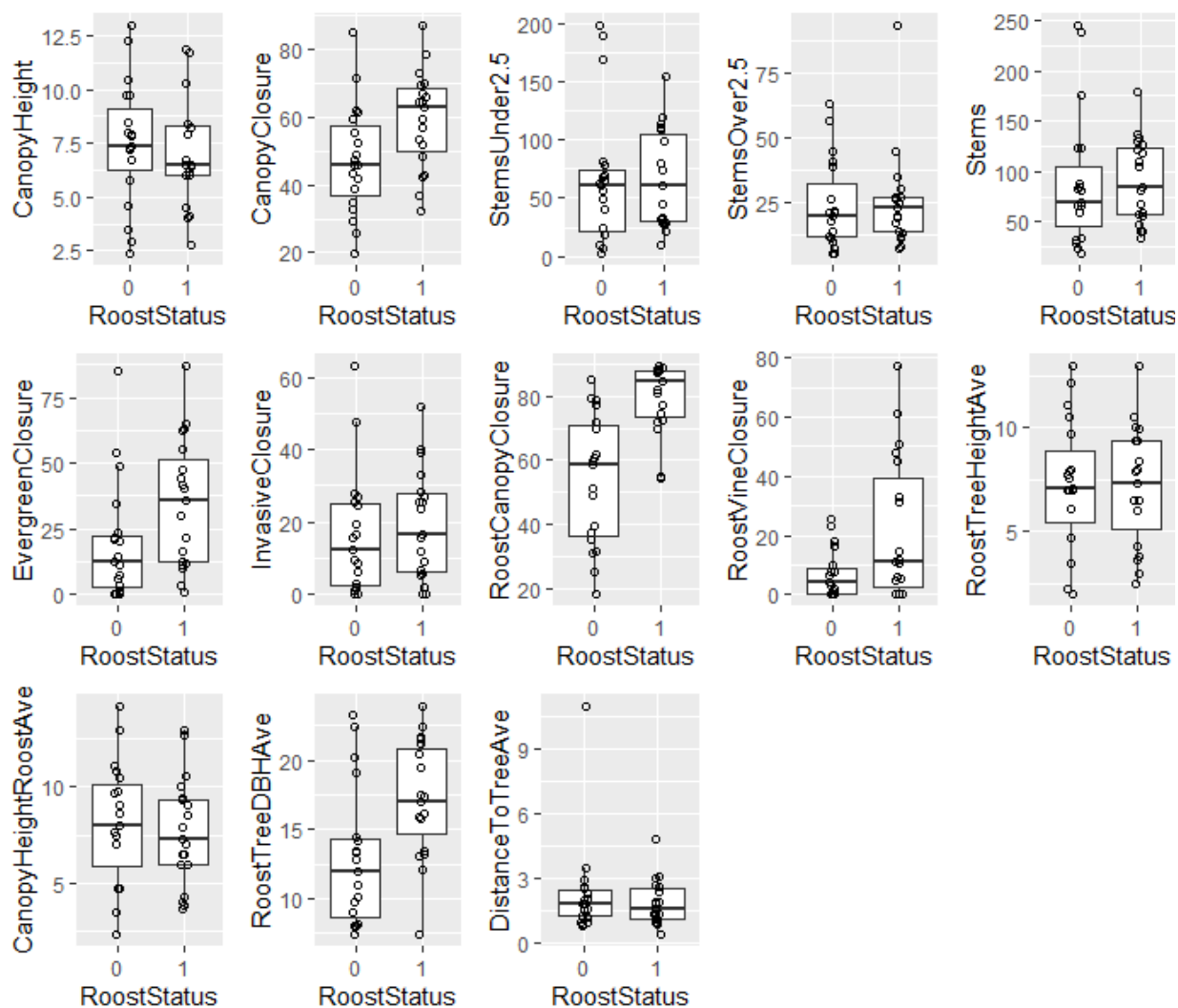
Figure 2. Boxplots displaying differences in the distributions of predictor covariates stratified by response factor level (0 = control, 1 = roost)

Figure 3. Correlograms produced by the `pairs()` function in r. Evident patterns indicate collinearity among predictors.
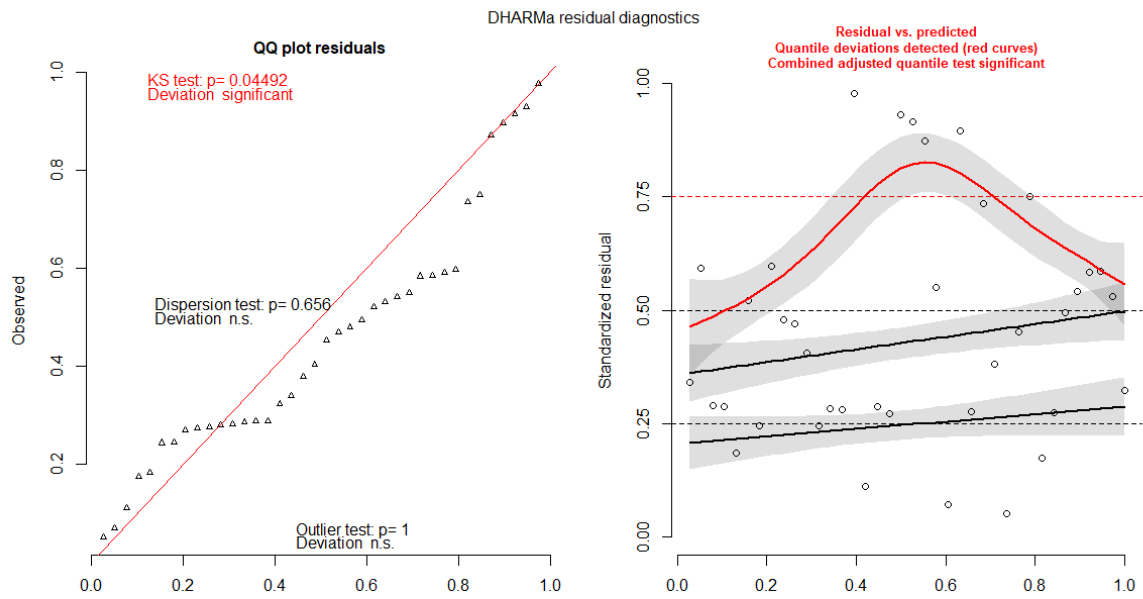
Figure 4. QQ plot and a plot of simulated residuals vs. predicted values for the top-ranked model in the model set. Plots produced using the DHARMa package.
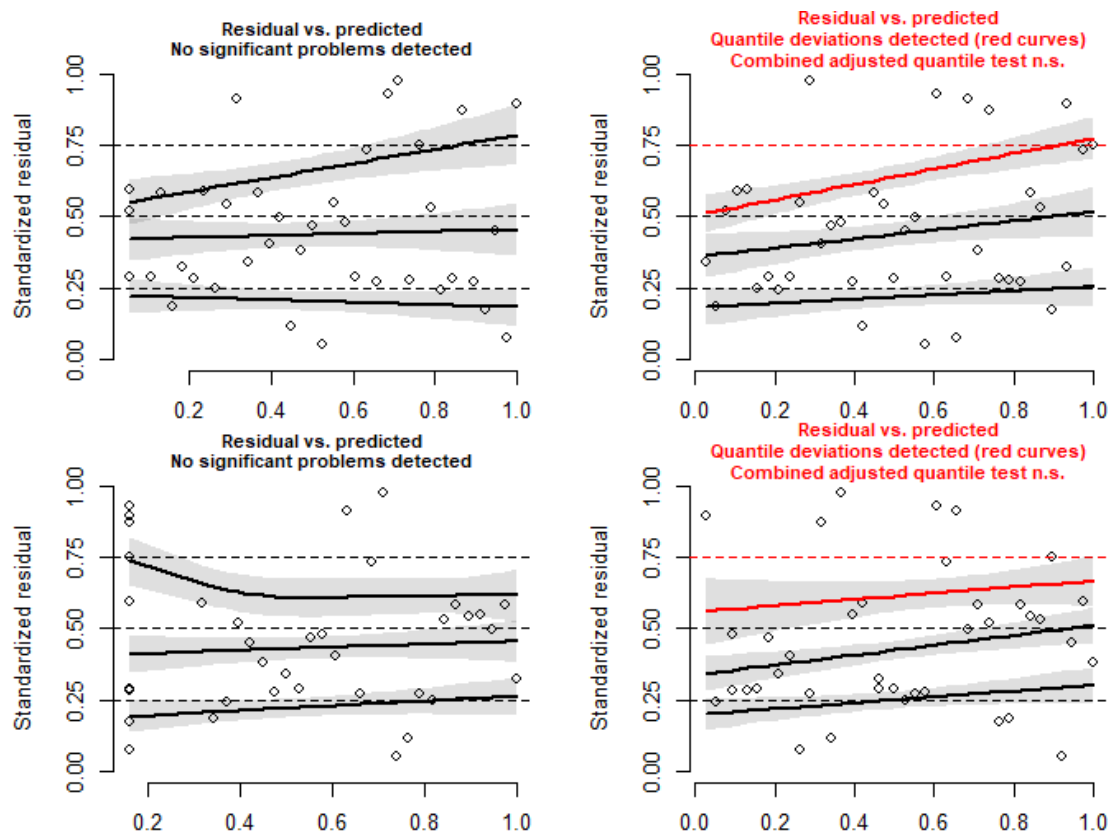

Figure 5. Simulated residuals plotted against each of the predictor variables appearing in the top-ranked model. Clockwise from top left, these plots pertain to *EvergreenClosure*, *RoostCanopyClosure*, *RoostTreeDBHAve*, and *RoostVineClosure*. Plots produced using the DHARMa package.
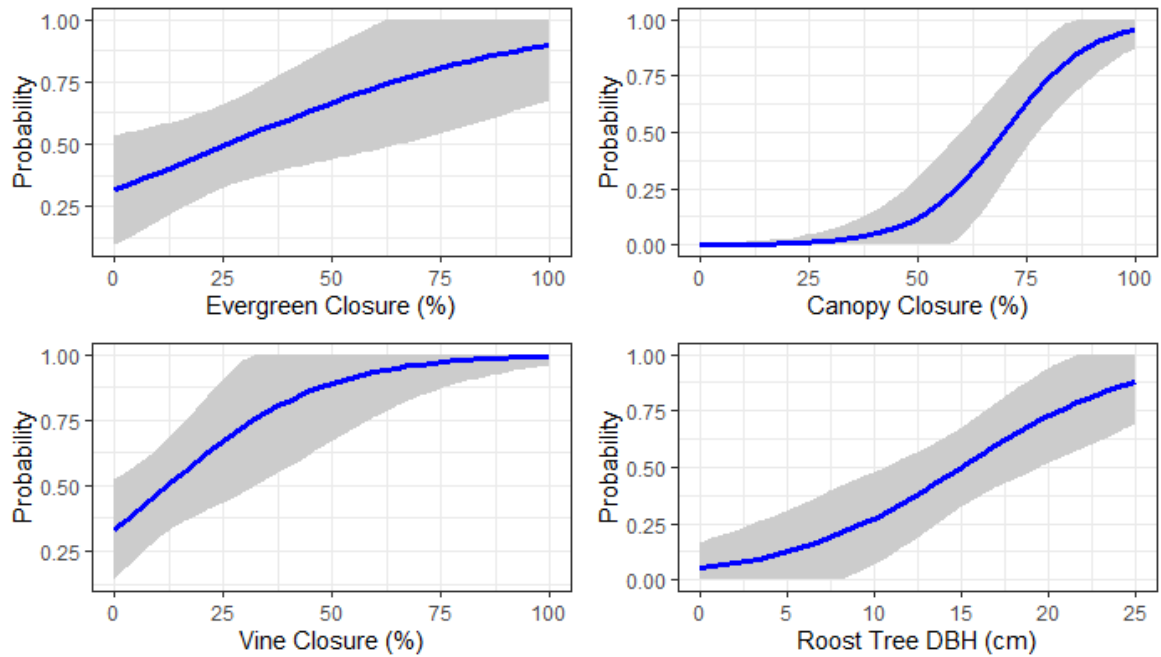
Figure 6. Estimated probabilities that a given survey plot contained a Long-eared Owl roost. Graphs are based on bivariate glms of roost status and each of the four predictor variables appearing in the top-ranked model.
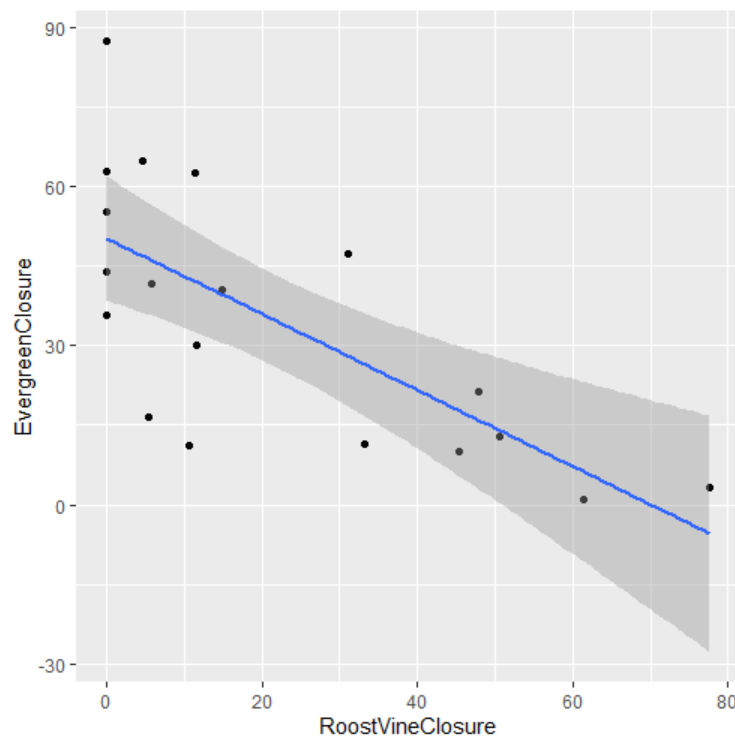

Figure 7. Inverse relationship between vine closure and evergreen closure in the canopies at Long-eared Owl roosts