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Variation In Bat Activity Across Upland Embedded Wetlands In The Cumberland Ranger District Of The Daniel Boone National Forest

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VARIATION IN BAT ACTIVITY ACROSS UPLAND EMBEDDED WETLANDS IN THE CUMBERLAND RANGER DISTRICT OF THE DANIEL BOONE NATIONAL FOREST

BY

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BRITTANY RYAN

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ABSTRACT

Within the Daniel Boone National Forest (DBNF) in Kentucky, over 800 upland-embedded wetlands (UEWs) have been constructed in past decades to provide habitat for bats and other wildlife. This research focused on identifying differences in bat activity and occupancy across natural and constructed UEWs. Acoustic detectors were deployed at 9 natural and 31 constructed UEWs across the Cumberland Ranger District of the DBNF. Each UEW was surveyed across 3 intervals from May – August 2022, and each recording session spanned $\geq$3 consecutive nights, yielding a total of 413 detector nights. Occupancy modeling and AIC model selection were used to evaluate the influence of environmental covariates on species-specific detection probability and habitat characteristics of site-occupancy for of bats 5 species groups (based on echolocation similarities). Factors influencing bat detection and occupancy varied among species groups. Probability of detection was commonly and negatively affected by precipitation, but was also negatively influenced by windspeed, and survey month across species groups. Occupancy of *Myotis* ssp. was negatively associated with percent slope of the landscape, while no other habitat variables was significantly associated with occupancy of other species groups. Bat activity was positively associated with the presence of standing water across most species groups. These data suggest constructed UEWs that do not dry during the year provide more consistently-used habitat for a variety of bat species. The influence that slope may have on UEWs should be considered during future construction efforts to effectively manage for imperiled *Myotis* species. Results of this study will provide resource managers with insight as to what UEW conditions are most important for bat communities in the Appalachian region.

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Introduction

Wetlands comprise some of the most critical ecosystems on the planet due to their ecological functions, their role as an ecotone between aquatic and terrestrial habitats, and the provision of a wide range of organisms with high-quality habitat (Mitsch and Gosselink 2015). However, recent loss of wetland habitat due to human influence such as agriculture, development, and logging has been detrimental to biodiversity across the United States. Kentucky has experienced drastic wetland declines, losing more than 80% of its wetlands by 1980 (Dahl 1990). Preservation of remaining wetlands has subsequently become a high priority and strategies to restore or construct wetlands have become common practice (Denton and Richter 2013).

Aside from wetlands typically found in lowland conditions, Kentucky also has naturally occurring upland-embedded wetlands. Upland-embedded wetlands are found across the United States and are defined as “completely surrounded by uplands” (Cohen et al. 2016, Calhoun et al. 2017). In Kentucky, these wetlands are found on forested ridge-tops (Brown and Richter 2012). Natural upland-embedded wetlands are often smaller in size and shallower compared to lowland wetlands and have a shortened periods of inundation (here after referred to as hydroperiod) (Brown and Richter 2012). Typically, upland-embedded wetlands hold water from winter through spring and are dry in summer and fall (Brown and Richter 2012, Golden et al. 2017, Calhoun et al. 2017). The unique location of upland-embedded wetlands provides resources for a variety of species (Brown and Richter 2012). These wetlands are at risk of degradation and are not jurisdictional (Environmental Law Institute 2008), so replacement of lost wetlands is not mandatory (Brown and Richter 2012). Efforts to document the function and importance of these wetlands has become priority for both conservation and management (Golden et al. 2017, Calhoun et al. 2017).

In the Daniel Boone National Forest (DBNF), a large tract of federal forestland spanning over 28,6517 ha, upland-embedded wetlands are important for a variety of species (Daniel Boone National Forest - USDA). Natural upland-embedded wetlands are scattered throughout the Cumberland Ranger District in the DBNF, and have been subjects of previous amphibian and vegetative research (Brown and Richter 2012, Denton and Richter 2013, Drayer and Richter 2016, Fedders and Richter 2018). Upland-embedded wetlands in the DBNF are surrounded by dense deciduous forest vegetation and are characterized by hydrophytic trees, and shrubs (Denton and Richter 2013). These ephemeral pools provide breeding habitat for a number of amphibians adapted to drying pools such as wood frogs (*Lithobates sylvaticus*), marbled salamanders (*Ambystoma opacum*), spotted salamanders (*A. maculatum*), and American and Fowler's toads (*Anaxyrus americanus, An. fowleri*) (Brown and Richter 2012, Drayer and Richter 2016). Due to reliance on upland-embedded wetlands by ephemerally-adapted species, and the potential they have to provide other species resources due to their unique ridgetop location, stewards have attempted to recreate these keystone ecosystems (Brown and Richter 2012, Denton and Richter 2013).

Artificial upland-embedded wetlands were constructed throughout the DBNF starting in 1988 (Denton and Richter 2013). However, research has shown that constructed upland-embedded wetlands function differently than natural. Characteristics such as canopy closure, amount of course woody debris, wetland area, wetland depth, and hydroperiod differ between constructed and natural upland-embedded wetlands

(Brown and Richter 2012, Denton and Richter 2013, Drayer and Richter 2016). Constructed wetlands were designed to hold water year-round in an effort to provide a permanent water source for game species like deer and turkey (Brown and Richter 2012).

Changes in management focus led to two types of constructed upland-embedded wetlands in the DBNF, old construction method (built 1988–2003), and new construction method (built 2004–2007) (Denton and Richter 2013). Old constructions are typically larger and deeper, remain saturated year-round, and are surrounded by grass and herbaceous vegetation, resulting in a more open canopy (Brown and Richter 2012). New constructions were designed to better benefit non-game species, such as bats (Denton and Richter 2013). As such, new constructions are typically smaller, shallower, and have increased amounts of woody debris relative to old constructions. Management goals related to the construction of upland-embedded wetlands has promoted variation of wetland characteristics across constructed wetlands, including creating areas with open canopies to create bat flyways (Brown and Richter 2012). Although upland-embedded wetlands were, in part, constructed to aide in bat conservation, the extent to which bats use natural and constructed upland-embedded wetlands in Kentucky has not been thoroughly examined. Though data in Kentucky are lacking, Maslonek (2010) studied bat use of constructed and natural wetlands in Pennsylvania and found that wetland type and landscape variables (e.g., wetland size, origin, distance to highway, surrounding land use, etc.), in combination with wing morphology and habitat preferences across bat species, influenced bat activity across wetlands.

Of the 47 species of bats found in the United States, 44 are insectivorous, including the 16 species found in Kentucky (Taylor et al. 2020). Of these species, the gray bat (*Myotis grisescens*), Indiana bat (*M. sodalis*), northern long-eared bat (*M. septentrionalis*), and Virginia big-eared bat (*Corynorhinus townsendii virginianus*) are federally protected species (KDFWR 2023). The United States Fish and Wildlife Service (USFWS) is also currently considering federally listing the little brown bat (*M. lucifugus*) and the tri-colored bat (*Perimyotis subflavus*) (M. Armstrong, USFWS, pers. comm.). Previous research has shown that forested wetlands provide high-quality foraging habitat for insectivorous bats given the abundance of prey potentially present, which allows bats to productively forage at these sites (Brooks and Ford 2005, Francl 2008, Maslonek 2010, McNamara 2019, Mas 2020). Given this knowledge, upland-embedded wetlands in the DBNF may provide important habitat for bats and should be considered when creating management plans.

Managers must consider variation in habitat use among bat species when attempting to create or preserve critical habitats. Previous studies suggest variation in morphology and echolocation call structure contribute to differences in suitable foraging habitats across bat species (Ford et al. 2005, Maslonek 2010, McNamara 2019). Clutter, or dense vegetation, influences bat species' use of an area. High wing loading, large-bodied species tend to forage at forested wetlands with less clutter due to their lack of maneuverability, whereas smaller, more aerobatic species with lower wing loading tend to frequent more cluttered areas (Brooks and Ford 2005, Ford et al. 2005, Maslonek 2010). Larger species produce low frequency calls for long range detection, making them better adapted to foraging in open spaces. Conversely, smaller species produce high frequency calls that generate much higher detail and help to orient bats in more cluttered habitats (Schnitzler et al. 2003). Both call frequency and morphology make low wing loading bats better able to forage in more densely cluttered areas and restrict high wing loading bats to more open areas (McNamara 2019).

Understanding relationships between foraging ecology and habitat use are critical to bat conservation. Recovering populations from the impacts of white-nose syndrome (*Pseudogymnoascus destructans*, WNS) plays a major role in recent bat management plans in Kentucky (Thalken et al. 2018). Habitat with ample insect prey is critical to persistence of bat populations. Natural and constructed upland-embedded wetlands have the potential to provide high-quality habitat for bats by providing an abundance of prey in a more maneuverable area over the wetland. However, only one previous study has looked at comparing bat use at these wetlands in the DBNF.

Huie (2002) assessed bat activity at ten constructed wetlands in the Morehead Ranger District of the DBNF during summers of 1994 and 1995 using mist-netting surveys. Results from Huie (2002) suggests the presence of forested habitats, rather than clearcuts, and upland-embedded wetlands with intermediate tree density and an open corridor or road nearby has a positive effect on the number of bat species present. Since this study, WNS has caused changes in bat assemblages. Cave hibernating species most susceptible to WNS have experienced drastic declines in population numbers and have lowered reproductive success, causing slow population recovery for affected species (e.g. *Myotis septentrionalis*) (Thalken et al. 2018). Research that examined capture rates of both affected and less-affected species saw an increase in capture rates of less-affected species (e.g. *Nycticeius humeralis, Eptesicus fuscus, and Lasiurus borealis*)

(Thalken et al. 2018). This suggested that since the devastation of WNS, there has been a shift in bat species assemblages foraging in forested areas. Increased risks and loss of large numbers of bats have underscored focus on bat management and monitoring. Notably, Huie (2002) did not compare activity between natural and constructed wetlands in the DBNF; no data exist regarding potential differences in foraging activity between wetland types. Variation of habitat conditions at wetlands could contribute to potential differences in species utilization across wetland types. Further, insight as to what characteristics influence bat activity will inform management efforts of upland-embedded wetlands to better provide foraging habitat for bats.

The objectives of my study were to i) determine habitat parameters that drive potential differences in bat foraging at upland-embedded wetlands in the Cumberland Ranger District of the Daniel Boone National Forest and ii) investigate potential associations between bat activity and both hydroperiod and wetland type (i.e., natural or constructed). Specifically, I intended to determine differences across wetland types. I hypothesized that i) overall bat occupancy would be higher at constructed wetlands, ii) pool size will be directly related to overall activity and species diversity, iii) and overall use would decrease with the lack of or loss of water throughout the sampling timeframe, as reported in other studies (Brooks and Ford 2005, Francl 2008, Maslonek 2010, Thalken 2018).

Methods

Study Area

Research was conducted in the Cumberland Ranger District of the DBNF. This district is one of four on the DBNF and spans 286,517 ha. Natural and constructed upland-embedded wetlands are found on ridges across the DBNF, within mixed mesophytic forest in the Western Allegheny Plateau Ecoregion (Jones 2005, Woods et al. 2002). Upland-embedded wetlands were constructed by the U.S. Forest service, beginning in 1988, for wildlife habitat management (Drayer and Richter 2016). The Cumberland Ranger District possesses a high density and clustering of natural and constructed upland-embedded wetlands (ca. > 800 in total), providing a unique opportunity for monitoring across wetland conditions.

Wetlands within the study area were divided into two groups, natural and constructed. Then a hierarchical agglomerative clustering analysis was used (PC-ORD v.7.09) to arrange 823 individual wetlands into nine groups (i.e., clusters), as a function of within and between cluster similarity distance metrics on landscape variables (McCune and Mefford 2016). Parameters used to discriminate clusters included the size (ha), distance from roads (ft), slope (%), wetland density, and elevation of wetlands. Wetlands were then randomly selected from within each of the resulting cluster groups to maximize sampling diversity across wetland types. From the cluster analysis, a total of 102 wetlands were randomly selected for potential sampling to account for variation. Final wetland selection was then prioritized from this list of candidates. Wetland accessibility was a consideration necessary to maximize sampling effort; natural wetlands were selected first because they were less abundant and accessible then most constructed wetlands in the DBNF. Constructed wetlands were then selected based on relative distance from selected natural wetlands to maintain feasibility of project goals. When accessing sites for the first time, if sites were unreachable within the necessary timeframe to achieve the project goals, then, a different wetland in the area was selected. These criteria resulted in selection of 40 wetlands total (Figure 1). Due to the rare and remote nature of natural upland-embedded wetlands, nine natural and 31 constructed wetlands were sampled in total.

Acoustic Deployment

Acoustic assessment of bat activity was conducted at 40 wetlands from May 22nd to August 14th of 2022. Each wetland was sampled during three separate sampling periods (May–June, June–July, July–August). Each week, single Song Meter 3 (Wildlife Acoustics, Maynard, MA) detectors were deployed at between four and nine wetlands at a time. Detectors recorded calls from 30 minutes prior to sunset through 30 minutes after sunrise across multiple nights (≥ 3) during each sampling period to account for nightly variation in bat activity (Menzel et al. 2005, McNamara 2019). After each deployment, memory cards and batteries of acoustic detectors were replaced. In total, these efforts yielded approximately 412 detector nights across the 40 wetlands sampled.

Detectors were placed at the edge of the wetland with the microphone directed toward the center of the wetland. Detector location was selected to maximize the airspace sampled over the wetland and avoid sources of vegetation clutter. External microphones were mounted 3-m above the ground and attached directly to detectors with a 3-m cable. Bats are known to forage during light rainfall and after heavy precipitation events (Andreassen et al. 2014); thus, detectors were deployed consistently regardless of weather conditions.

Habitat Characterization

Physical characteristics of each upland-embedded wetland were measured to assess potential relationships between habitat quality and bat activity. Landscape-level habitat variables were acquired from a geographic information system (GIS) and preexisting LiDAR data (ArcGIS V 10.5, ESRI, Redlands, CA). Wetland parameters examined included: elevation (m), wetland area (m^2), aspect (degrees), slope (%), density of wetlands (km^2), and proximity to closest road (m). Proximity measurements were derived using the ‘Point Distance Tool’ within the Proximity toolset. Kernel Density Analysis tool, within the Spatial Analyst toolset, was utilized to assess density of all wetlands. The Spatial Analyst toolset was also used to derive topographic elements. Data layers were used to determine other habitat variables at each site (National Landcover Database (U.S. Geological Survey 2011), National Hydrography Dataset (U.S. Geological Survey et al. 2008) and Kentucky State Road Dataset (Kentucky Transportation Cabinet 2018).

In addition to GIS-derived data, in-field habitat measurements were collected at each wetland (Figure 2). Measurements were collected across sampling periods. Five sampling points were selected, located at the wetland edge in each of the cardinal directions and the detector location. During the first sampling period (May-June), wetland depth (m) was recorded at each wetland. Wetland depth was measured with a meter stick at 1-m from the wetland edge at each sampling point during the first sampling period when wetlands were expected to be at their highest water level. During the second sampling period (June-July), basal area (ft^2/acre) and canopy closure (%) were measured at each wetland. Basal area was measured using a wedge prism, with a basal area factor (BAF) of 10, using all visible trees from the center of each sampling point (Huie 2002 and McNamara 2019). Measurements from all sampling points were averaged to determine basal area for each site. Canopy closure was estimated using a spherical densiometer. Canopy closure measurements were taken at each sampling point and averaged together for an estimate at each site. During the third sampling period (July-Aug), tree height (m), DBH (cm), and distance to closest wetland edge were assessed for five mid-story and five over-story trees at each wetland. The closest mid and overstory tree to each sampling point was determined, and distance from these trees to closest wetland edge was measured. DBH was measured with a logger's tape, and tree height was measured using an ultrasonic hypsometer (Haglöf Vertex 5). Average daily temperature, precipitation, and windspeed were derived from Kentucky Mesonet (www.kymesonet.org,accessed 20 November 2022) using the weather data from the closest gathering station (Bath, Morgan, and Rowan County).

Habitat parameters were examined to determine potential differences of wetland characteristics between natural and constructed upland-embedded wetlands. Parameters with a normal distribution were compared between wetland types using an ANVOA in the package car (Fox and Weisberg 2019), whereas those with a non-normal distribution were compared using a Wilcoxon test in the package coin in R (Hothorn et al. 2008). Emphasis was placed on habitat parameters associated with clutter and open forest gaps that could be used as potential foraging habitat for bats (i.e., size, basal area, canopy closure, distance to road, wetland density, tree height of mid- and overstory trees, and distance of mid- and overstory trees from the wetland edge).

Acoustic Data Processing

Data were downloaded from detectors following each deployment and Kaleidoscope Pro (V 3.1.7, Wildlife Acoustics, Maynard, MA) was used to process data. Each call file (each individual call recorded by detector) was assigned an automatic identification using the software's native reference library for bats found in Kentucky, using a high-sensitivity setting to increase accuracy of identification. Calls that were not conclusively identified by Kaleidoscope Pro were eliminated from all subsequent analyses. Call data were organized into a comprehensive nightly detection history composed of ones (detection) and zeros (no-detection). Bat species presence at each site was determined with identifications produced. The mean number of bat calls detected (per species group and total) at each wetland during each sampling period were then calculated. Following Burns et al. (2019), species with similar echolocation call morphology were grouped together to account for potential misidentification of calls, narrowing inferential analyses to six species groups; *Myotis* species (MYSP), big brown and silver-haired bats (EPFU/LANO), eastern red and evening bats (LABO/NYHU), hoary bats (LACI), and tri-colored bats (PESU).

Occupancy Modeling

Detection data were used in occupancy analyses to perform a likelihood-based, information-theoretical framework to estimate probability of detection (*p*) and the probability of site occupancy (Ψ) (MacKenzie et al. 2002). When using the terms "detection", "occupancy", and "occurrence", I refer to use, as bats are not constantly occupying a site. Detection probability was assessed using models with environmental covariates that may affect bat detection. Site occupancy was modeled using habitat variables (Table 1). All occupancy models were created in the package unmarked in R (Fiske 2011).

First, *p* was assessed while holding Ψ constant to determine which environmental and temporal covariates most influenced detection of each species group (Table 1). Models were ranked based on AICc scores using AICcmodavg (Mazerolle 2020). Models with a ΔAICc score of ≤ 2 were considered competing models. Models with the lowest AICc were considered to contain influential detection covariates, and were then incorporated into a suite of 16 *a priori* occupancy candidate models to examine the relationship between occupancy and these environmental factors (Burnham and Anderson 2002, MacKenzie et al. 2002). Models with an AICc score of < 2 were considered competing and covariates were considered influential. Model averaging of all models that included these covariates was used to determine parameter estimates and standard errors for each covariate. If the 85% confidence interval of these parameter estimations included zero, covariates were not considered significantly influential. Models were developed based on factors that may influence detection and occupancy of bat species found at sites and included various combinations of habitat covariates (Table 1). Pearson correlation coefficients (r), between all possible pairs of covariates were calculated to assess multicollinearity. Only predictor variables with a weak association to one another ($|r| < 0.70$) were used in models. Following Burns et al. (2019), given that species were grouped, the effects of species level covariates on false-positive and true-positive probabilities were not explored. Models that did not converge or produced nonsensical parameter estimates were eliminated. Elevation was eliminated as a covariate from all species group modeling due to the lack of convergence of any models including this parameter. Parameters included in competing models were averaged to determine significance and direction of influence using AICcmodavg (Mazerolle 2020).

Wald Chi-Square test

Generalized linear mixed models were also developed to examine differences in bat activity with respect to wetland type (i.e., natural or constructed) and the presence of water (i.e., standing water, saturated soil, or dry basin). Response variables in these models were average calls per night for each species group. Two models were developed for each species group, one assessing the effect of wetland type on species group specific bat activity, the other investigating the effect of water presence on species group specific bat activity. Both models included sampling period as a random effect to avoid issues associated with pseudoreplication. Negative binomial distributions were used for all species group models due to data overdispersion. Models were created in R using the lme4 package and the function *glmer.nb* (Bates et al. 2015). The model with the lowest AICc score was considered the best model. A Wald test, using the package car (Fox and Weisberg 2019) and the function *Anova*, was performed using the single top model to determine if there was a significant association between predictor variables and bat activity. If a significant association was detected, a Tukey's post hoc comparison was then performed, using the package multcomp and function *glht* (Hothorn et al. 2008), to identify which levels of predictor variables differed significantly in bat activity.

Results

Among the 40 sites sampled, 12 bat species were identified: big brown bats (*Eptesicus fuscus*), eastern red bats (*Lasiurus borealis*), eastern small-footed bats

(*Myotis leibii*), evening bats (*Nycticeius humeralis*), gray bats, hoary bats (*Lasiurus cinereus*), little brown bats, northern long-eared bats, silver-haired bats (*Lasionycteris noctivagans*), southeastern myotis (*Myotis austroriparius*), tri-colored bats, and Virginia big-eared bats. A total of 12,128 bat calls were positively identified at 31 constructed wetlands across 315 detector nights (mean ± SE = 39 + 3.6 calls/night). A total of 3,088 bat calls were positively identified at nine natural wetlands across 97 detector nights (mean ± SE = 32 ± 7.3 calls/night). Generally, the total number of identified bat calls mirrored the disproportionate sampling efforts between wetland types (i.e., 31 constructed vs. 9 natural wetlands); even so, species detection rates were quite high and balanced across both wetland types (Table 2).

Median calls per night for all bat species identified across sampling periods indicated a trend of higher overall activity at constructed upland-embedded wetlands in the first and second sampling periods (Figure 3). During the third sampling period, activity was higher at natural upland-embedded wetlands. Activity varied across species groups during the three sampling periods (Figure 4). Across sampling periods at constructed wetlands, MYSP and PESU activity was relatively consistent, whereas EPFU/LANO activity progressively decreased and activity for other species groups was more variable. Regarding natural wetlands, MYSP, EPFU/LANO, and LABO/NYHU all had higher activity in the first and third sampling periods, whereas LACI activity was relatively consistent and PESU activity peaked in the third sampling period. Overall activity varied greatly according to wetland size (Figure 5), but activity generally increased as the size of constructed wetlands increased whereas activity generally decreased as size of natural wetlands increased (Figure 5). More clearly, bat activity generally decreased for both wetland types as the distance to nearest road increased (Figure 6).

Virginia big-eared bats were excluded from analyses due to low detection rates (<200 calls recorded across all sites). EPFU/LANO and LACI were the most commonly detected species groups and were cumulatively detected at 97.5% of sites (Table 3). LABO/NYHU were cumulatively detected at 92.5% of sites, PESU at 90% of sites, and MYSP at 85% of sites (Table 3).

MYSP Occupancy

Detection of MYSP was best explained by windspeed (ΔAICc = 0, AICc weight = 0.577), with competition from precipitation (ΔAICc = 1.14, AICc weight = 0.326). Model-averaged effect sizes indicated significant association between probability of detection of MYSP and windspeed (β = -0.21, 85% CI: -0.32, -0.09), and precipitation (β=-0.75, 85% CI: -1.21, -0.29). Both models indicated a negative influence of windspeed and rainfall on MYSP detection. Windspeed and precipitation were thus included as detection covariates in all *a priori* occupancy models. A single model containing slope best predicted occupancy (Table 4). The next highest-ranking model had an AICc score >2, therefore occupancy models were not averaged. The 85% confidence intervals for slope (β = -0.05, 85% CI: -0.08, -0.01) did not include zero, indicating increasing slope has a significant effect on MYSP occupancy across my sites (Figure 7). Although MYSP was the only species group that included slope as a significant occupancy covariate, overall bat activity tended to decrease as slope of the landscape increased among both natural and constructed upland-embedded wetlands (Figure 8).

EPFU/LANO Occupancy

Detection of EPFU/LANO was best explained by month (ΔAICc = 0, AICc weight = 0.649), with competition from precipitation (ΔAICc = 1.477, AICc weight = 0.310). Model-averaged effect sizes indicated significant associations of the probability of detection of EPFU/LANO with month (β = -0.35, 85% CI: -0.55, -0.14) and precipitation (β = -0.55, 85% CI: -0.92, -0.19). Both models indicated a negative influence of month and precipitation on detection. Thus, month and precipitation were included in all *a priori* occupancy models. Occupancy of EPFU/LANO was best explained by aspect, with competition from month and basal area (Table 4). All confidence intervals of model averaged parameter estimates included zero, indicating that occupancy of EPFU/LANO was not significantly explained by any occupancy covariates (Table 5).

LABO/NYHU Occupancy

Detection of LABO/NYHU was best explained by precipitation (ΔAICc = 0, AICc weight = 0.856). Model-averaged effect sizes indicated significant associations of the probability of detection of LABO/NYHU with precipitation (β = -0.85, 85% CI: -1.23, -0.47). Based on AICc score and *wi*, there were no other competing models; thus, precipitation was included in all *a priori* models predicting occupancy for LABO/NYHU. The model containing only wetland depth best predicted occupancy based on AICc score and *wi* (Table 4). The next highest-ranking model had an AICc score >2, therefore occupancy models were not averaged. The covariate 85% confidence interval that did not include zero, indicating wetland depth had no significant effect of occupancy (Table 5) (β = 1, 85% CI: -0.41, 2.41).

LACI Occupancy

Detection of LACI was best explained by month (ΔAICc = 0, AICc weight = 0.996). Model-averaged effect sizes indicated significant associations of the probability of detection of LACI with month (β = -0.5, 85% CI: -0.68, -0.31). Estimates of detection were highest in the month of May (0.573), followed by June (0.507), July (0.441), and August (0.110). Month was included in all *a priori* models predicting occupancy. The model containing only month was the top model according to AICc score and *wi* (Table 4). The next closest model had a ΔAICc >2, so models were not averaged, and month was considered the best fit.

PESU Occupancy

Detection of PESU was best explained by precipitation (ΔAICc = 0, AICc weight = 0.993). Model-averaged effect sizes indicated significant association of the probability of detection of PESU with precipitation (β=-0.85, 85% CI: -1.23, -0.47); thus, precipitation was included in all *a priori* models predicting occupancy. The model that best explained occupancy included wetland density (Table 4). A total of eight models predicting occurrence of PESU had a ΔAICc of < 2, and were considered competing (Table 4). All covariate confidence intervals included zero, indicating that none of the covariates had a significant effect on PESU occupancy (Table 5).

Activity Models

Average calls per night for each species group were used to visualize differences in activity among wetland types and according to water presence at wetlands (Figure 9). AIC model selection identified presence of water as the better explanatory model for all species groups except EPFU/LANO. No significant difference in MYSP activity was detected among wetland conditions (Table 6). However, there was a significant difference in LABO/NYHU (χ^2 = 15.66 p=<0.001), LACI (χ^2 = 18.99, p=<0.001), and PESU (χ^2 = 12.44, p=0.002) activity among wetland conditions. There was significantly more LABO/NYHU activity at wetlands with saturated soil (p=0.044), and standing water (p=<0.001), than dry basins. There was significantly more LACI activity at wetlands with saturated soil than wetlands with either standing water present ($p \leq 0.001$) or dry basins ($p \leq 0.001$). There was significantly more PESU activity at wetlands with standing water (p=0.001), than dry. Wetland type was identified as the better predictor of EPFU/LANO activity by AIC, and activity was significantly higher at constructed wetlands (Table 6).

Habitat Characteristics

Results from habitat comparisons indicated there was a significant difference in distance to nearest road and the average distance of mid- and over-story trees from wetland edge between natural and constructed upland-embedded wetlands (Table 7). There was a significantly greater distance from natural upland-embedded wetlands to the nearest road. The average distance of the closest mid- and over-story tree from the wetland edge was significantly greater at constructed upland-embedded wetlands (Figure 10). There was no significant difference in other habitat variables, despite variation between wetland types (Figure 11).

Discussion

Contrary to my expectations, bat occupancy did not differ between natural and constructed upland-embedded wetlands. Rather, I found the presence of water at wetlands as a driving feature that determined bat use of these habitats. While the association of bats with wetlands that are ‘wet’ superficially seems a simple and expected outcome, these results should be rationalized in terms of bat conservation, as well as wetland restoration efforts. My results suggest constructed upland-embedded wetlands are as important habitat for the same community of bat species as natural upland-embedded wetlands and, further, bats used wetlands in my study on the basis of water presence. This may reflect habitat selection by bats due to differences in prey availability and less so on the basis of wetlands functioning as simple canopy gaps in a forested environment.

My findings support existing literature concerning the importance of water presence for bat activity (Brooks and Ford 2005, Menzel et al. 2005). For many species groups, activity increased with the presence of standing water. During sampling, most natural wetlands that dried were holding water during the first sampling period, and this was the highest water level for most of those wetlands. During the final sampling period, specifically during the month of August, there were substantial rain events, causing wetlands that were not previously dry or saturated, to hold water. I suspect fluctuations of average activity at sampled wetlands corresponds with this trend in water presence at some sites. Sites with saturated soils during sampling were typically holding water prior to sampling events. While constructed upland-embedded wetlands in the DBNF were designed to hold water year-round, natural upland-embedded wetlands are ephemeral. This causes water levels of natural upland-embedded wetlands to be dependent on weather conditions (Brown and Richter 2012), potentially making them more unreliable foraging habitat. Water presence influences many insects consumed by bats, which are often aquatic for part of their lifecycle (Lacki et al. 2007). Given this reliance on water, drying conditions may reduce the number of insects emerging from these areas or alter the timing of emergence (Imes 1992). This suggests decreased activity at dry wetlands could be related to the lack of readily available and abundant food resources. Insect abundance is expected to be higher at constructed upland-embedded wetlands in the DBNF because they often hold water permanently, whereas natural upland-embedded wetlands tend to be ephemeral (Brown and Richter 2012). Despite the positive association between bat activity and standing water, bats were not absent when upland-embedded wetlands were not holding water, suggesting that these wetlands' canopy gaps may still be important foraging habitat for bats. Results of this study suggest constructed upland-embedded wetlands may provide important habitats for bats and their prey due to an extended hydroperiod.

Wetland type was not associated with bat occupancy, indicating that both constructed and natural upland-embedded wetlands are important foraging habitat for bats. This finding is similar to that of others which have found that both constructed wetlands and woodland ponds provide valuable habitat for a variety of bat species (Huie 2002, Brooks and Ford 2005, Francl 2008). However, EPFU/LANO activity was significantly higher at constructed upland-embedded wetlands. Although there was not a significant difference in average size of natural and constructed upland-embedded wetlands, constructed wetlands were more variable in size. Thus, the presence of larger constructed wetlands could have influenced EPFU/LANO activity. Big brown bats are high-wing loading and silver-haired bats are intermediate-wing loading species (Reimer et al. 2010), and the larger constructed upland-embedded wetlands could have allowed these species to maneuver more efficiently while foraging. There was no significant association between activity of other species groups and wetland type. Although there was no significant association, MYSP and PESU activity was more evenly distributed across wetland type than the other species groups. These groups are smaller-bodied more maneuverable species that are better able to utilize foraging habitat with a smaller canopy gap and more clutter, which is typically associated with natural upland-embedded wetlands. In contrast, the other species groups that included larger bodied species had higher activity at constructed upland-embedded wetlands. This lack of significant differences in activity levels could indicate that wetlands of all sizes provide valuable habitat to bats. Lack of preference for pool size could indicate all canopy gaps in a forested environment are important foraging habitat for bats (Francl 2008, Barbour and Davis 1969). Our results indicate a lack of influence of basal area and canopy closure, contrary to findings of Huie (2002). Although natural upland-embedded wetlands had greater canopy closure and basal area, this may indicate the lack of variability across constructed and natural upland-embedded wetlands due to regrowth at constructed sites. Constructed upland-embedded wetlands were developed between 1988-2007, and may have had up to 35 years of regrowth following the initial clearing for construction purposes. This would allow the forest structure to be more similar to those of natural wetlands. Huie (2002) also found that wetlands in area with older-growth forest, rather than clear-cuts, had high activity. This further supports lack of variation across wetland types due to the forest regeneration that has occurred since construction. Basal area and canopy closure have increased in the year since construction, creating less variety across constructed upland-embedded wetlands. However, the upland-embedded wetlands I sampled may not have had enough variation to see influential differences from other aspects on the landscape. Huie (2002) found that distance to roads and other open corridors had a positive influence on bat activity. These characteristics provide other canopy gaps to foraging bats. These features will not change overtime (unless access roads are no longer maintained), and therefore continue to provide increased foraging habitat at constructed upland-embedded wetlands. Despite sampled natural upland-embedded wetlands being, on average, further from roads then constructed upland-embedded wetlands, this did not have a significant effect on bat occupancy. Additionally, the distance of trees to wetland edges in this study will likely not change over time, thus my habitat data suggest constructed wetlands afford persistent tree gaps for foraging bats. This is typically a larger area for constructed wetlands than natural, due to the process of clearing trees during construction, creating a foraging space conducive to more bat species then those with shorter distances from wetland edge to nearest trees, such as in naturals. This could explain why, although I observed species at most constructed and natural upland-embedded wetlands, most species activity was greater at constructed wetlands.

Due to their scarcity and the need to navigate difficult terrain to reach them, fewer natural upland-embedded wetlands were sampled than constructed upland-embedded wetlands. In the future, more comprehensive assessment of natural upland-embedded wetlands would improve our understanding of how bat activity might vary across wetland types. Of the 31 wetlands sampled, only eight had dry periods during sampling (five natural and three constructed). Wetlands that underwent dry periods had less overall activity during those times than when standing water or saturated soils were present. Increased sampling of dry wetlands will further elucidate the importance of water presence.

Results indicated that environmental factors were the most influential variables predicting probability of detection. Precipitation was associated with decreased detection probability of most species groups. Relatedly, windspeed was also negatively associated with detection probability of MYSP. Bats are endothermic mammals that are sensitive to changes in weather conditions (Erickson and West 2002). Increased amounts of precipitation and windspeed are known to impose additional energetic demands related to thermoregulation, potentially causing a decrease in bat activity and thus lowering the probability of detection (Austin et al. 2020, Hyzy et al. 2020). Precipitation may also cause a decrease in arthropod prey availability for bats, which likely also contributes to less activity during precipitation events (Grindal et al. 1992, Erickson and West 2002). Due to their smaller body size, I speculate windspeed could have a more of an impact of MYSP than other larger-bodied species.

EPFU/LANO and LACI detection was significantly affected by month of sampling. This finding aligns with a previous study that observed decreases in bat activity patterns throughout summer (Brooks 2009). Detection estimates of both species groups in my study was highest in May and decreased sequentially in each of the following months. Early in the summer, some females lactate, which causes an increase in foraging activity to combat the energy cost associated with feeding young (Anthony et al. 1981). As summer progresses and young bats begin to feed on their own, foraging activity of post-lactating females may decrease, which could explain decreases in probability of detection. Notably, the number of sites that I sampled without standing water increased from May-July, before declining to none in August. The decrease in detection of EPFU/LANO and LACI could coincide with the increase in number of sampling nights without standing water present, which I found to be a significant predictor for activity of these species groups. Insect availability most likely decreases as the summer progresses as insects that have an aquatic life stage have emerged before wetlands dry. Other studies have found that insect emergence is highest in wetlands with intermediate hydroperiods (Whiles and Goldowitz 2001). Wetlands with short hydroperiods typically dry before insects can compete metamorphosis and wetlands with longer hydroperiods may have more predators, which may lower overall abundance (Wellborn et al. 1996). Drying of wetlands later in the summer could decrease the abundance of prey available at upland-embedded wetlands, which may also decrease bat activity as the summer progresses. Because both LANO and LACI are migratory species, declines in detection probability throughout the summer may be due to these species returning to winter roosting sites near the end of summer (Lacki et al. 2007).

MYSP occupancy was negatively related to percent slope of the landscape. Grouping all MYSP calls limited the ability to determine which individual species were negatively affected by slope. Jachowski et al. (2014) found varying results in the effects of slope on Indiana bat activity. Other studies have found that steep slopes had a significant negative impact on eastern small-footed bats, and northern long-eared bats and was included in the top models for Indiana bats, and little brown bats (Austin et al. 2020). This finding agrees with those of other studies of MYSP activity (Jachowski et al. 2014, Austin et al. 2020). Steeper slopes are associated with cold-air drainage events that have the potential to force prey sources uphill (Whiteman 2000). This could cause bats to move up to higher elevations to forage. MYSP may also avoid landscapes with steeper slopes due to the energetic demand required to maneuver in these areas, as foraging along steep elevation requires bats to devote energy to gaining the correct amount of lift to effectively maneuver (MacAyeal et al. 2011, Austin et al. 2020).

In summary, results reflected water presence as the driving factor for bat activity across upland-embedded wetlands. Given that constructed upland-embedded wetlands typically hold water longer than natural wetlands, these structures are important habitat for bats in the DBNF. This research provides a base for future research to dive deeper into long-term studies on the variation of water presence and prey abundance at these sites.

Management Implications

The lack of difference in bat occupancy between natural and constructed upland-embedded wetlands indicates that all upland-embedded wetlands are suitable habitat for bats in the DBNF. Further, the importance of standing water for bat activity suggests that creating upland-embedded wetlands that follow existing design protocols and that hold water for an extended period of time provides habitat beneficial for many (if not all) bat species in Kentucky. Given my habitat data, I suspect this is likely because extended water presence may increase prey availability. A persistent, full-season assessment of insect assemblages at natural and constructed wetlands would provide critical insight on the variation in insect species composition and abundance between natural and constructed upland-embedded wetlands. This would allow for informed management efforts to target specific wetland type and characteristics to increase presence and abundance of prey preferences of specific species groups. In-depth assessment insect of emergence patterns could provide further context for observed patterns of bat activity at natural and constructed upland-embedded wetlands across the year. Similarly, long term monitoring could summarize how precipitation levels vary and determine whether differences between hydroperiods of natural and constructed wetlands differ consistently. Intensive monitoring of bat activity after future construction of new upland-embedded wetlands is critical to understanding site selection determinants. Increased gap size during construction of these wetlands may positively influence bat activity, but no research has yet assessed this potential relationship, and other effects may exist. None of the sampled wetlands had managed wildlife openings adjacent. Monitoring wetlands with adjacent managed wildlife openings or other natural canopy gaps would provide further insight to the potential effects of larger forested canopy gaps on bat activity.

Regardless of the benefits of constructed wetlands for bats, managers must consider potential impacts of permeant water sources on other species, such as amphibians (Brown and Richter 2012, Drayer and Richter 2016). Considering impacts on other species and further examination of the importance of upland-embedded wetlands for various species will aid in multispecies management in the future.

When managing for *Myotis* bats, consideration of the slope of the landscape of proposed construction is crucial. Across sampled sites, there was a greater variation in slope across constructed upland-embedded wetlands. Constructed wetlands located on a steeper slope could potentially be modified to level the ground surrounding the wetland. Future construction efforts should select areas with gentle slopes in order to maximize

Myotis bat occupancy. This species group includes federally endangered bats, so special consideration for management plans for this species group is critical. Management plans for tri-colored bats should consider the presence of standing water. Constructed upland-embedded wetlands tend to have standing water for longer periods of time than natural upland-embedded wetlands. Construction of new upland-embedded wetlands or modification of existing constructed upland-embedded wetlands to ensure standing water for longer should be considered to maximize tri-colored bat activity.

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APPENDICES

Appendix A: Figures

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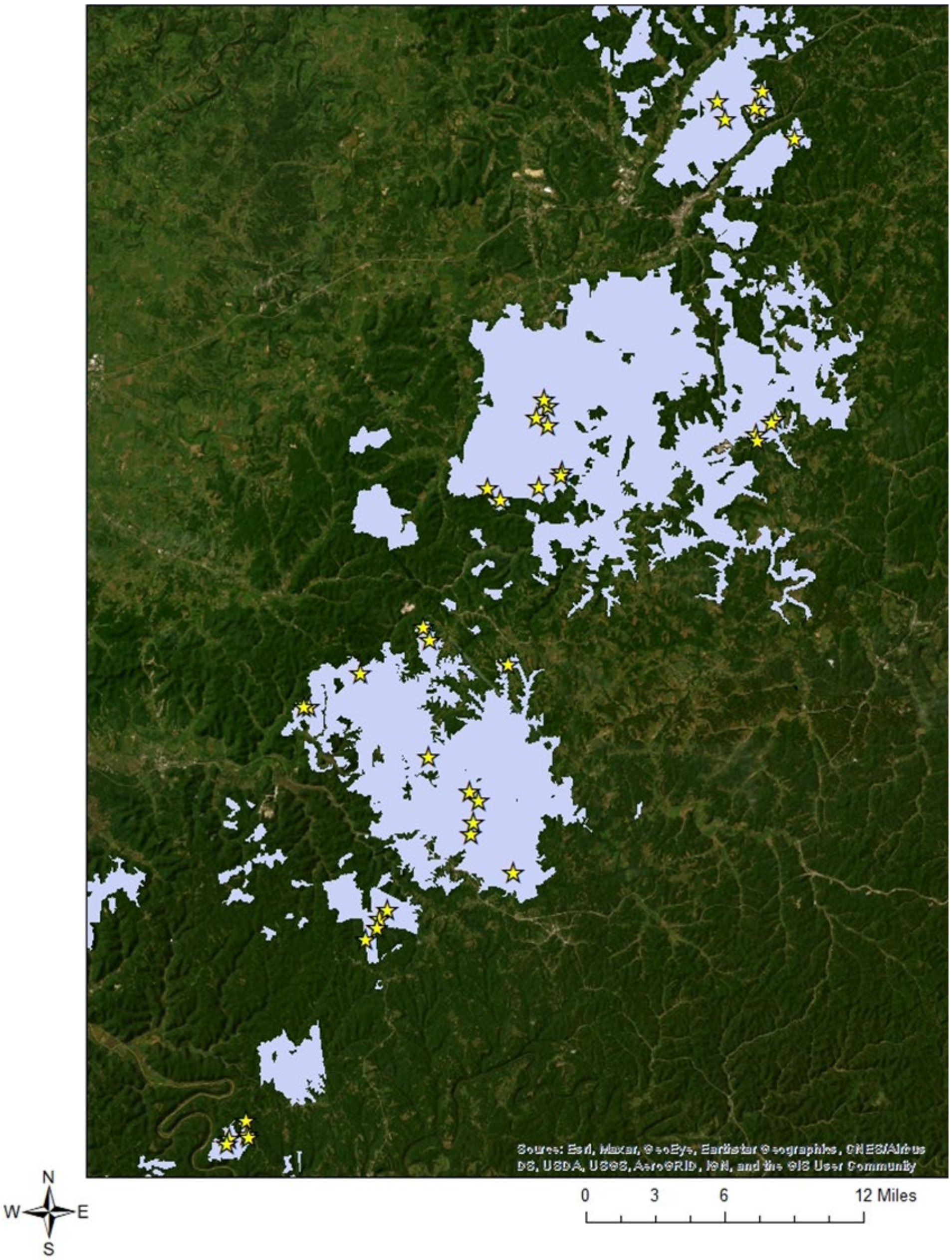
Sources: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 1. Locations of 40 upland-embedded wetlands where acoustic surveys for bats were conducted from May-August 2022 in the Cumberland Ranger District of the Daniel Boone National Forest, Kentucky.

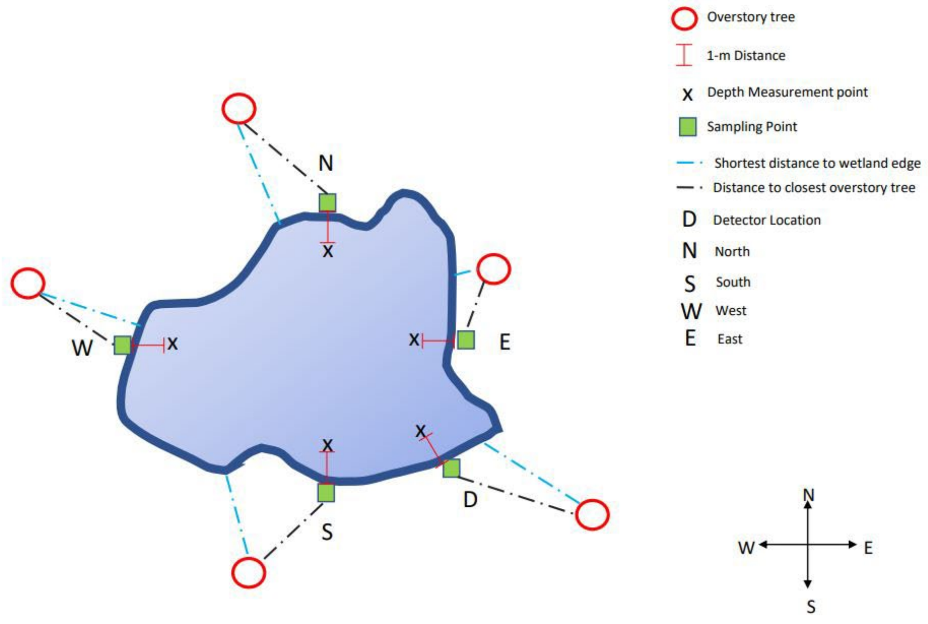

Figure 2. Example of wetland site and locations of each of sampling points. Measurements such as canopy cover and closure were taken at "Sampling Point". Wetland depth, distance to nearest overstory tree, and distance from overstory tree to wetland edge are all outlined in the diagram.

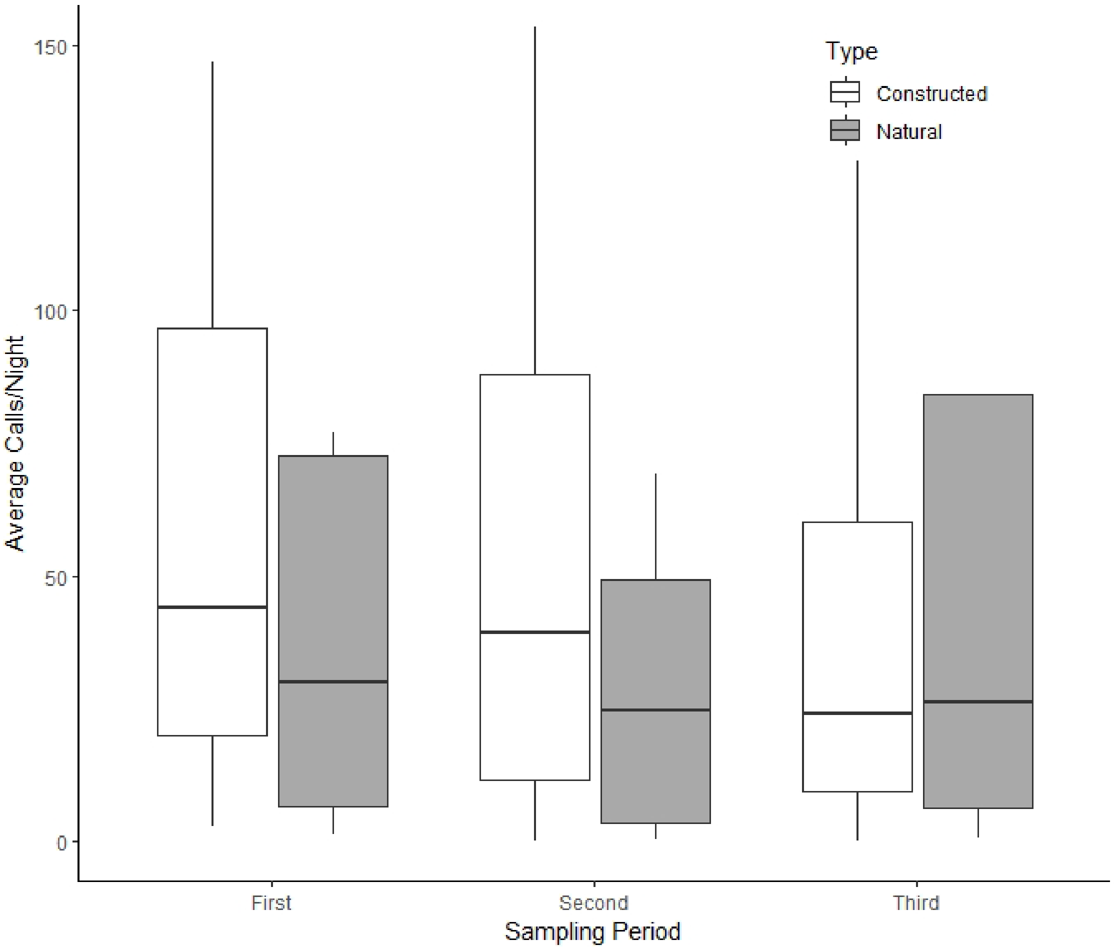

Figure 3. Box and whisker plot showing the median and interquartile ranges of variation in average bat calls per night recorded across upland-embedded wetlands during each sampling period during 2022 in the Cumberland Ranger District of the Daniel Boone National Forest, Kentucky.

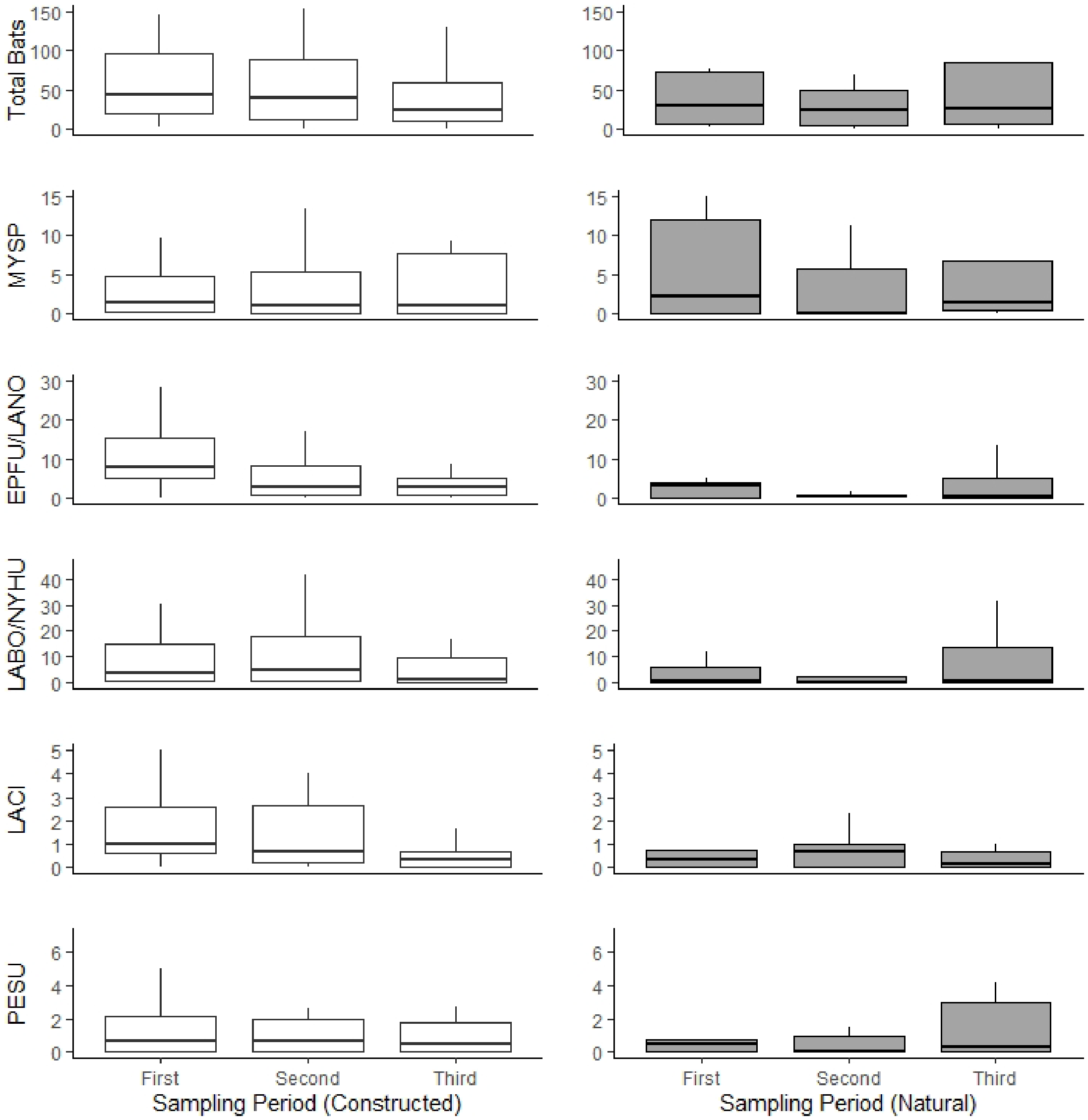

Figure 4. Boxplots showing median and interquartile ranges of variation in average number of bat calls per night across species groups during each sampling period at natural and constructed upland-embedded wetlands surveyed from May-August 2022 in the Cumberland Ranger District of the Daniel Boone National Forest, Kentucky.

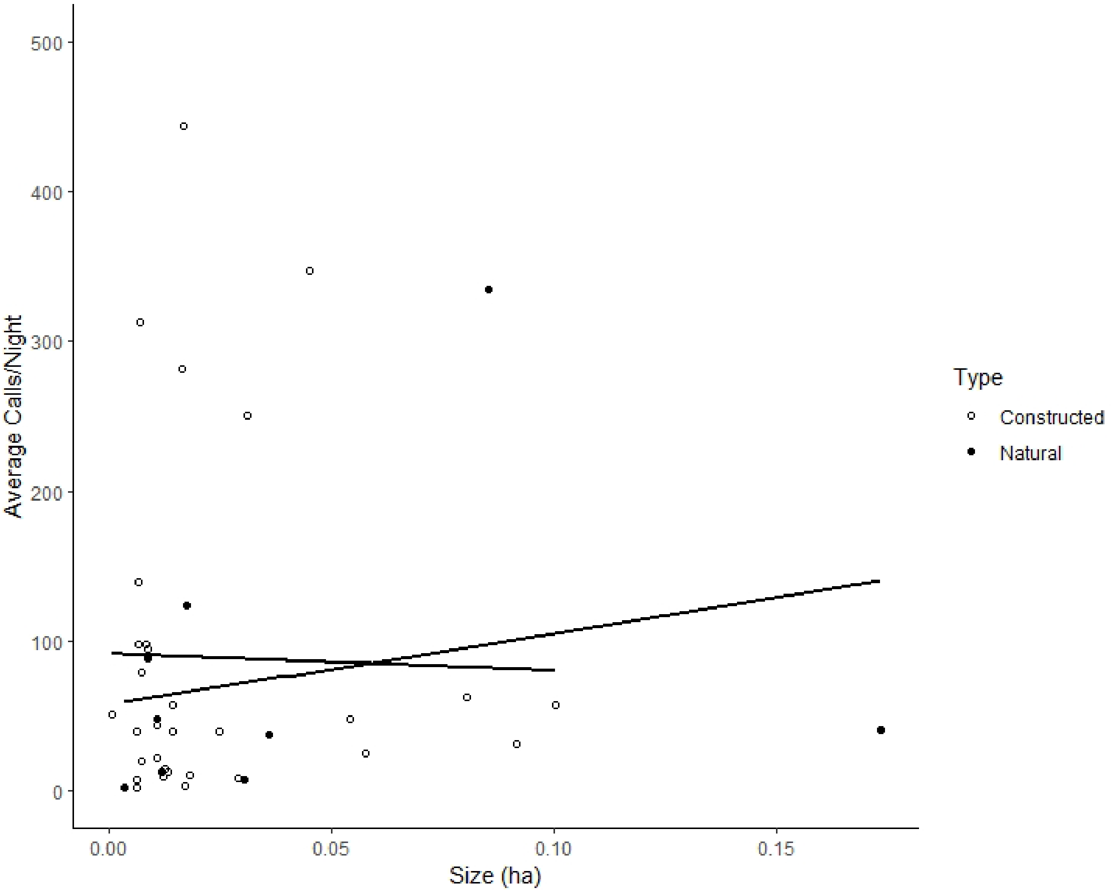

Figure 5. Scatterplot showing relationships between average bat calls per night and size (ha) across upland-embedded wetlands surveyed from May-August 2022 in the Cumberland Ranger District of the Daniel Boone National Forest, Kentucky.

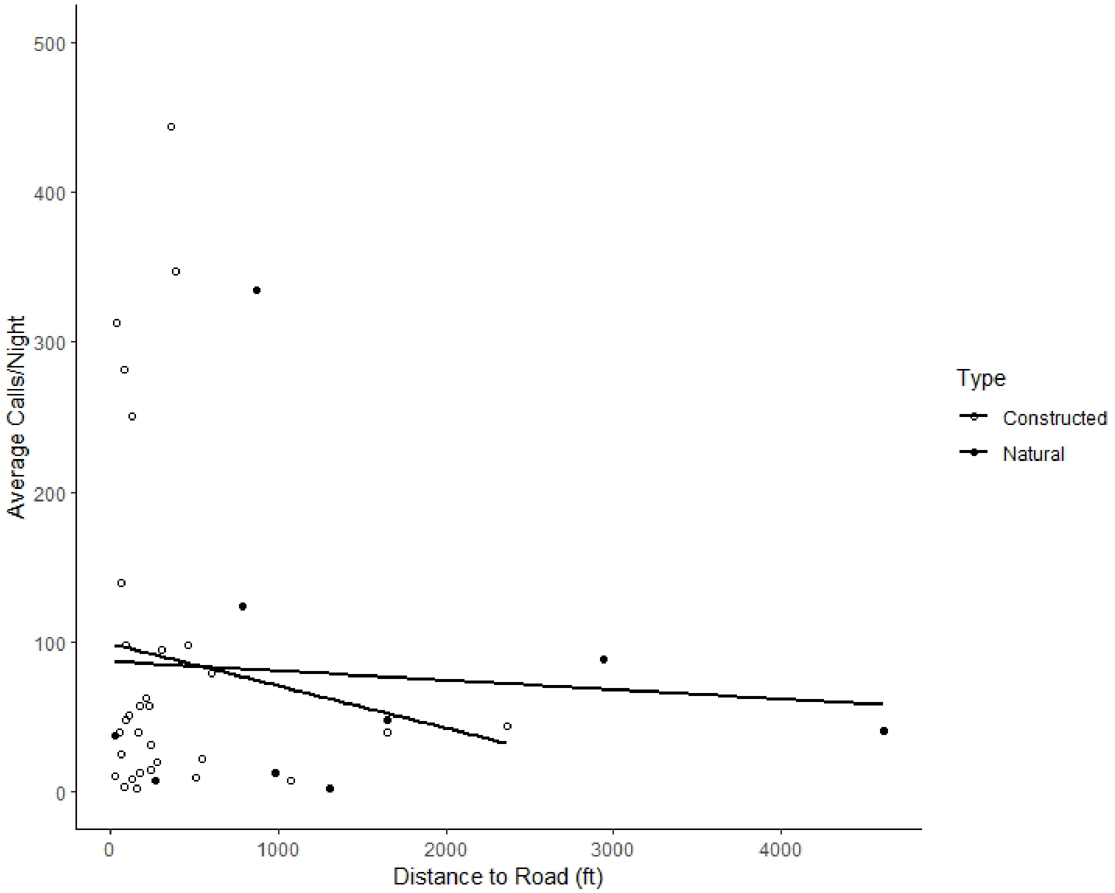

Figure 6. Scatterplot showing relationships between average bat calls per night and distance from the center of surveyed upland-embedded wetlands to the nearest road from May-August 2022in the Cumberland Ranger District of the Daniel Boone National Forest, Kentucky.

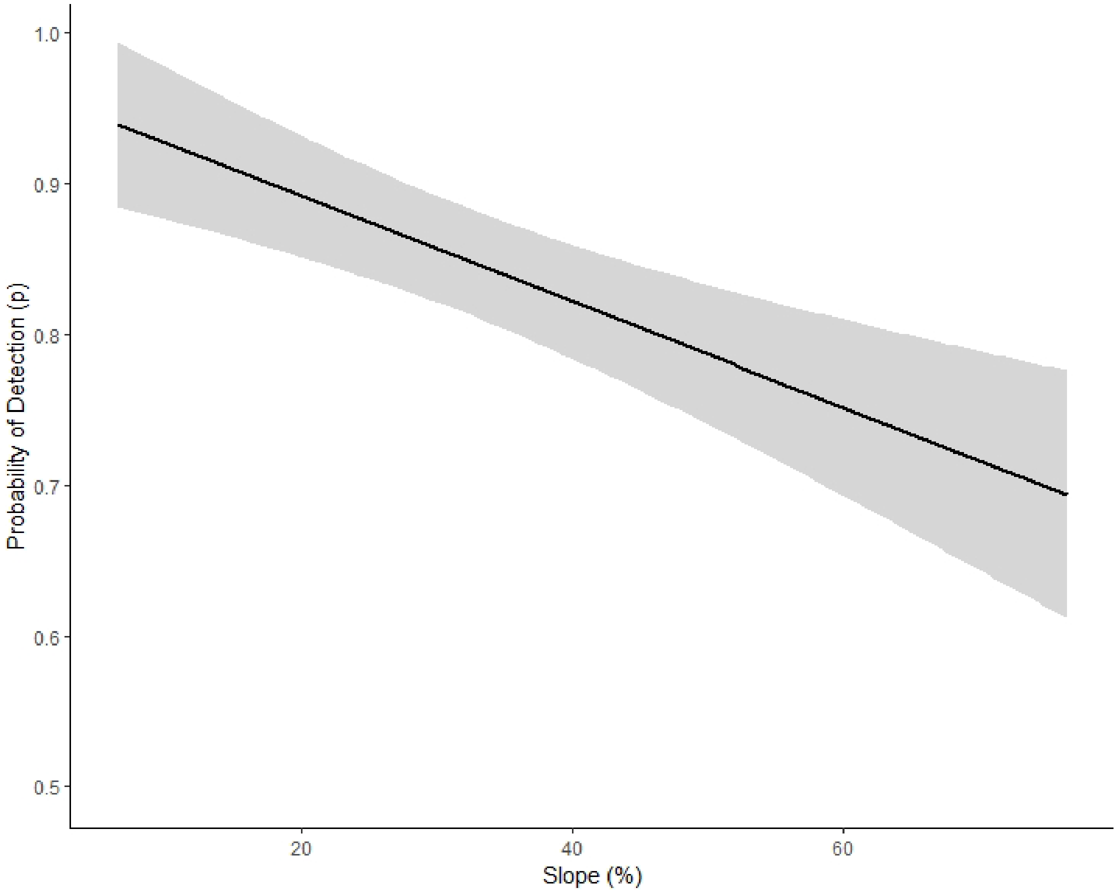

Figure 7. Probability of detection (± SE) of MYSP as a function of percent slope across upland-embedded wetlands surveyed from May-August 2022 in the Daniel Bone National Forest, Kentucky. Estimated probability derived for the most supported occupancy model.

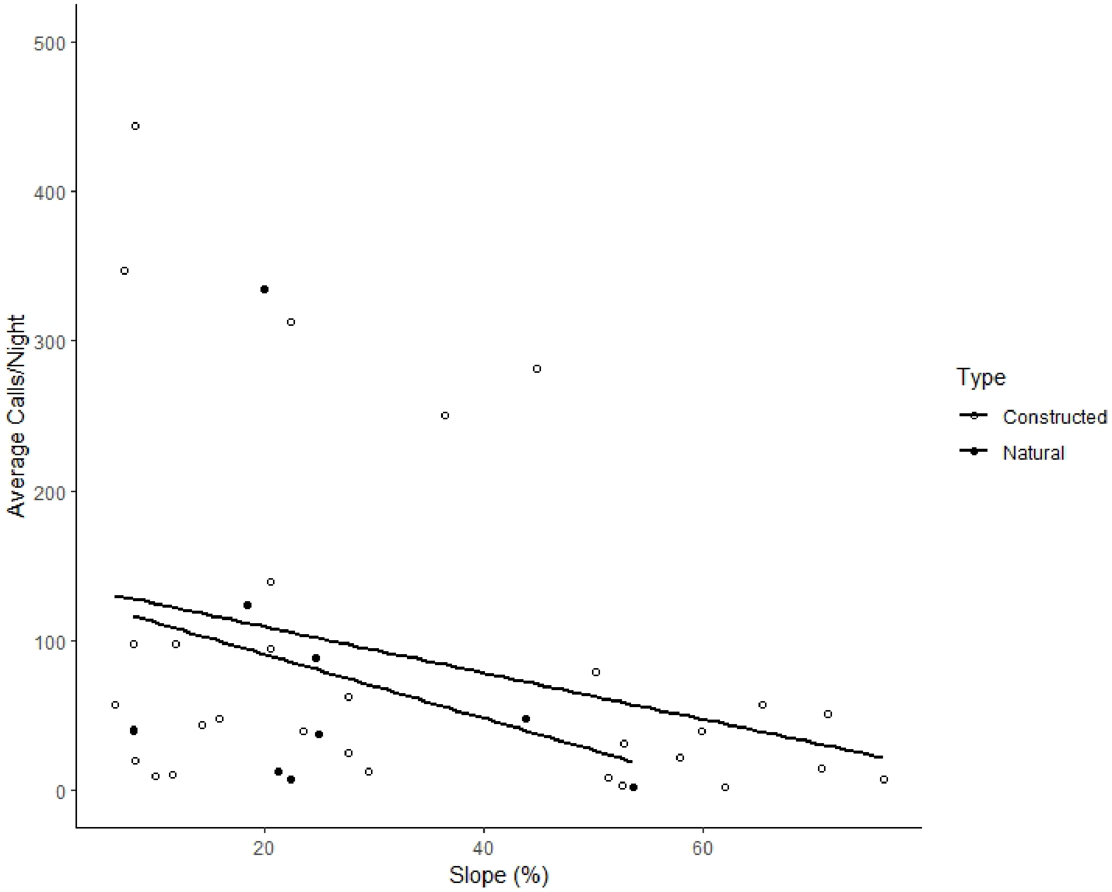

Figure 8. Scatterplot showing relationships between average bat calls per night and slope (%) across upland-embedded wetlands surveyed from May-August 2022 in the Cumberland Ranger District of the Daniel Boone National Forest, Kentucky.

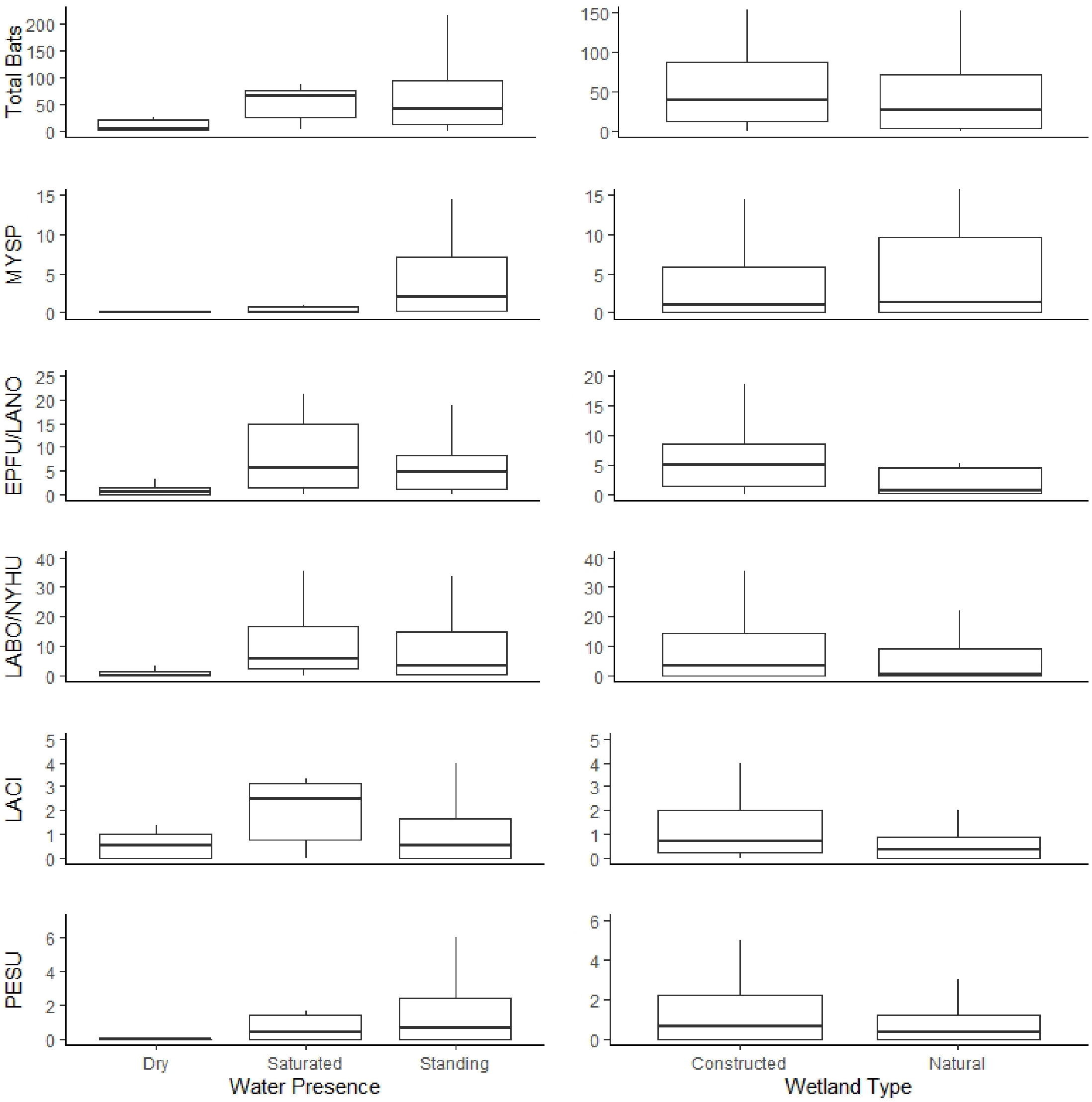

Figure 9. Boxplots showing the median and interquartile ranges of variation in average number of bat calls per night for each species group at various stages of water presence across upland-embedded wetlands surveyed from May-August 2022 in the Cumberland Ranger District of the Daniel Boone National Forest, Kentucky.

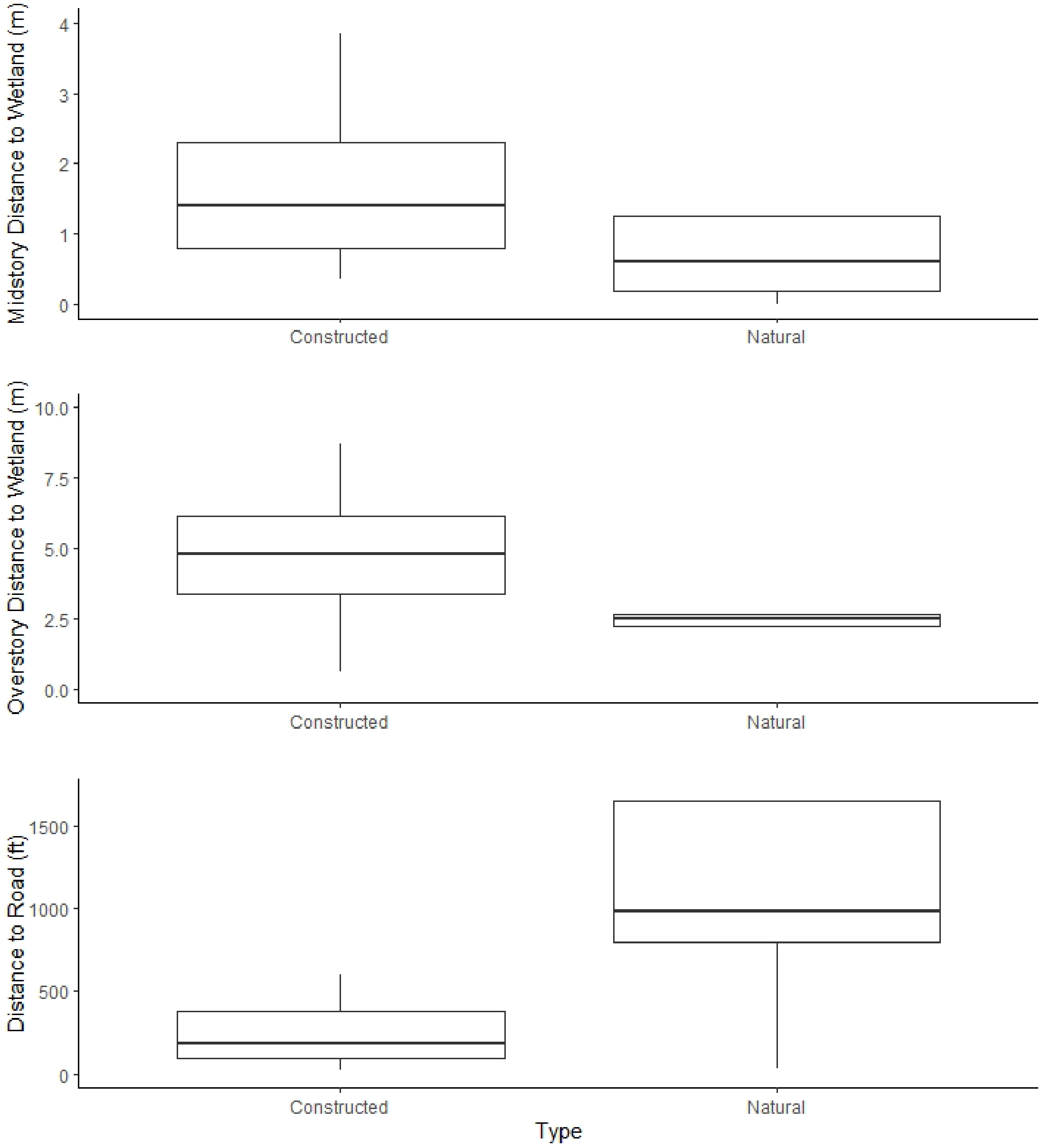

Figure 10. Boxplots showing the median and interquartile ranges of variation in distance of mid- and overstory trees to wetland across upland-embedded wetlands surveyed from May-August 2022 in the Cumberland Ranger District of the Daniel Boone National Forest, Kentucky.

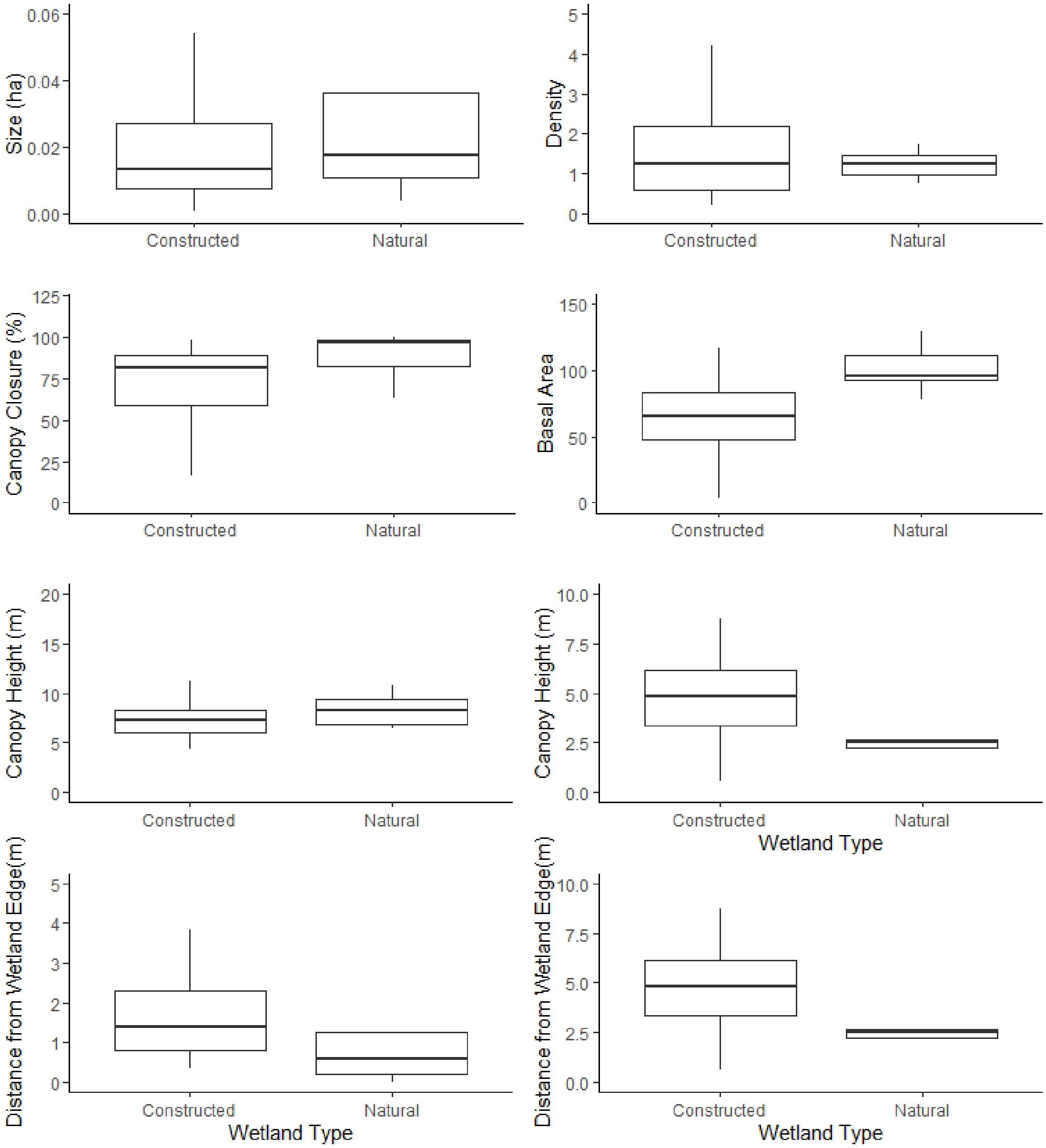

Figure 11. Boxplots showing the median and interquartile ranges of variation in habitat parameters across upland-embedded wetlands surveyed from May-August 2022 in the Cumberland Ranger District of the Daniel Boone National Forest, Kentucky.

Appendix B: Tables

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Table 1. Candidate set of models, and description of covariates used. Occupancy was held constant in all detection models.

Model (p/Ψ)	Description
Month (*p*)	Variable indicating month of data collection
Date (*p*)	Variable indicating days of data collection
Temp (*p*)	Average daily temperature (°F)
Precip (*p*)	Average daily precipitation (in)
Windspeed (*p*)	Average daily windspeed (mph)
Wetland (Ψ)	Indicating natural or constructed wetland
Size (Ψ)	Area of wetland (ha)
Density (Ψ)	Density of wetlands within 1-km^2 buffer
Aspect (Ψ)	Aspect northness (°)
Slope (Ψ)	Slope of wetland (%)
Road (Ψ)	Distance to nearest road (ft)
BA (Ψ)	Basal area (ft^2/acre)
Closure (Ψ)	Canopy Closure (%)
Wetland + Size + Depth (Ψ)	
Wetland + Density (Ψ)	
Aspect + Slope (Ψ)	
Basal Area + Closure (Ψ)	
Road + Density (Ψ)	
Road + Density + Wetland (Ψ)	
Aspect + Slope + Basal Area + Closure (Ψ)	

Table 2. Summary of bat species identification from acoustic surveys at upland-embedded wetlands in the Cumberland Ranger District of the Daniel Boone National Forest from May-August 2022. Kaleidoscope Pro V. 3.1.7 was used to determine species level identifications.

Species	# Calls Recorded (%)		# UEWs Detected (%)	
	Constructed	Natural	Constructed	Natural
COTO	140 (79)	37 (21)	17 (55)	6 (67)
EPFU	2,472 (94)	164 (6)	29 (94)	7 (78)
LABO	1,715 (84)	315 (16)	29 (94)	7 (78)
LACI	499 (88)	66 (12)	31 (100)	8 (89)
LANO	770 (86)	121 (14)	31 (100)	8 (89)
MYAU	532 (47)	595 (53)	24 (77)	7 (78)
MYGR	23 (31)	51 (69)	10 (32)	4 (44)
MYLE	406 (77)	121 (23)	13 (42)	5 (56)
MYLU	771 (73)	289 (27)	23 (74)	8 (89)
MYSE	770 (87)	115 (13)	20 (65)	6 (67)
NYHU	2,899 (90)	325 (10)	28 (90)	6 (67)
PESU	1,116 (56)	889 (44)	29 (94)	7 (78)

Table 3. Summary of bat species groups from acoustic surveys at upland-embedded wetlands in the Cumberland Ranger District of the Daniel Boone National Forest from May-August 2022. Kaleidoscope Pro V. 3.1.7 was used to determine species level identifications.

Species Group	# Calls Recorded (%)		# UEWs Detected (%)	
	Constructed	Natural	Constructed	Natural
MYSP	2,502 (68)	1,171 (32)	26 (84)	8 (89)
EPFU/LANO	3,242 (92)	285 (8)	31 (100)	8 (89)
LABO/NYHU	4,614 (88)	640 (12)	30 (97)	7 (78)
LACI	499 (88)	66 (12)	31 (100)	8 (89)
PESU	1,116 (56)	889 (44)	29 (94)	7 (78)

Table 4. Model, number of parameters, Akaike's Criterion (adjusted for small sample size; AICc), difference between the top model and that model (ΔAICc), and model weights (wi) for the confidence set of models with ΔAICc ≤ 4.0 to predict occupancy of species/species groups in Daniel Boone National Forest, Kentucky in May-August 2022.

Model	K	AICc	ΔAICc	*wi*
MYSP				
Ψ(Slope), *p*(WindSpeed + Precip)	5	492.93	0	0.32
Ψ(Depth), *p*(WindSpeed + Precip)	5	495.08	2.14	0.11
Ψ(Aspect), *p*(WindSpeed + Precip)	5	495.28	2.35	0.10
Ψ(Size), *p*(WindSpeed + Precip)	5	495.43	2.50	0.09
Ψ(Type + Density), *p*(WindSpeed + Precip)	6	495.59	2.66	0.08
Ψ(Road + Density), *p*(WindSpeed + Precip)	6	495.86	2.93	0.07
Ψ(Aspect + Slope), *p*(WindSpeed + Precip)	6	496.83	3.90	0.04
EPFU/LANO				
Ψ(Aspect), *p*(Month + Precip)	5	484.04	0	0.45
Ψ(.), *p*(Month)	3	485.43	1.38	0.22
Ψ(Basal area), *p*(Month + Precip)	5	485.80	1.76	0.18
Ψ(.), *p*(Precip)	3	486.91	2.86	0.10
LABO/NYHU				
Ψ(Depth), *p*(Precip)	4	502.87	0	0.51
Ψ(Basal area), *p*(Precip)	4	505.49	2.62	0.13
Ψ(Closure), *p*(Precip)	4	505.88	3.01	0.11
Ψ(Type), *p*(Precip)	4	506.38	3.51	0.08
Ψ(.), *p*(Precip)	3	506.84	3.97	0.07
LACI				
Ψ(.), *p*(Month)	3	553.68	0	0.52
Ψ(Basal area), *p*(Month)	4	556.11	2.42	0.15
Ψ(Closure), *p*(Month)	4	556.12	2.43	0.15
Ψ(Apsect), *p*(Month)	4	556.16	2.47	0.15
PESU				
Ψ(.), *p*(Precip)	3	529.01	0	0.21
Ψ(Density), *p*(Precip)	4	529.58	0.56	0.15
Ψ(Wetland), *p*(Precip)	4	529.82	0.80	0.14
Ψ(Aspect), *p*(Precip)	4	530.44	1.42	0.10
Ψ(Depth), *p*(Precip)	4	530.51	1.49	0.09
Ψ(Type + Density), *p*(Precip)	5	530.53	1.51	0.09
Ψ(Closure), *p*(Precip)	4	530.58	1.56	0.09
Ψ(Basal area), *p*(Precip)	4	530.65	1.63	0.09

Table 5. Model-averaged parameter estimates and standard errors (SE), and lower and upper 85% confidence intervals (CI) on parameter estimates included in the confidence set of models used to predict bat occupancy in Daniel Boone National Forest, Kentucky in May-August 2022. Values in **bold** indicate significant parameters (i.e., not overlapping zero).

Parameter	Estimate ± SE	Lower 85% CI	Upper 85% CI
MYSP			
Precipitation (*p*)	-0.75 ± 0.32	**-1.21**	**-0.29**
Windspeed (*p*)	-0.21 ± 0.08	**-0.32**	**-0.09**
Slope (Ψ)	-0.05 ± 0.02	**-0.08**	**-0.01**
EPFU/LANO			
Month (*p*)	-0.35 ± 0.14	**-0.55**	**-0.14**
Precipitation (*p*)	-0.55 ± 0.25	**-0.92**	**-0.19**
Aspect (Ψ)	5.73 ± 7.72	-5.39	16.85
Basal area (Ψ)	-5.51 ± 5.18	-12.96	1.95
LABO/NYHU			
Precipitation (*p*)	-0.85 ± 0.26	**-1.23**	**-0.47**
Depth (Ψ)	1.00 ± 0.98	-0.41	2.41
LACI			
Month (*p*)	-0.5 ± 0.13	**-0.68**	**-0.31**
PESU			
Precipitation (*p*)	-0.85 ± 0.26	**-1.72**	**-0.7**
Density (Ψ)	0.99 ± 0.85	-0.23	2.22
Type (Ψ)	-1.49 ± 1.14	-3.12	0.15
Aspect (Ψ)	-1.04 ± 1.17	-2.73	0.65
Depth (Ψ)	1.00 ± 0.98	-0.41	2.41
Closure (Ψ)	-2.64 ± 3.29	-7.37	2.1
Basal area (Ψ)	-1.74 ± 1.98	-4.59	1.11

Table 6. Parameters of best model, contrasts examined, estimates, and p-values resulting from a Wald test and Tuckey's post hoc comparison for each species/species group detected in the Cumberland Ranger District of the Daniel Boone National Forest, Kentucky. Values in **bold** indicate significant parameters (i.e., not overlapping zero).

Species	Parameter	Contrasts	Estimate	p-value
MYSP	Condition	Saturated – Dry	0.07	0.99
		Standing – Dry	1.03	0.14
		Standing – Saturated	0.95	0.38
EPFU/LANO	Type	Natural – Constructed	-1.28	**<0.001**
LABO/NYHU	Condition	Saturated – Dry	1.79	**0.03**
		Standing – Dry	1.99	**<0.001**
		Standing – Saturated	0.20	0.93
LACI	Condition	Saturated – Dry	1.81	**<0.001**
		Standing – Dry	0.39	0.56
		Standing – Saturated	-1.41	**<0.001**
PESU	Condition	Saturated – Dry	1.69	0.18
		Standing – Dry	2.56	**0.001**
		Standing – Saturated	0.86	0.47

Table 7. Test statistics and p-values for differences in habitat parameters between natural and constructed upland-embedded wetlands in the Cumberland Ranger District in the Daniel Boone National Forest, Kentucky. Values in **bold** indicate significant results.

Habitat Parameter (units)	Test	Test statistic	p-value
Size (ha)	Wilcoxon	Z = -0.89	0.37
Basal Area (ft²/acre)	ANOVA	F = 1.89	0.17
Canopy Closure (%)	Wilcoxon	Z = -1.08	0.27
Distance to road (ft)	ANOVA	F = 10.2	**0.002***
Wetland Density (within 1-km^2 buffer)	ANOVA	F = 0.10	0.74
Mid-story tree height (m)	ANOVA	F = 2.46	0.12
Over-story tree height (m)	Wilcoxon	Z = -1.24	0.21
Mid-story tree distance (m)	ANOVA	F = 4.71	**0.03***
Over-story tree distance (m)	ANOVA	F = 12.06	**0.001***