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Dormant Season Burning Impacts to Migratory Bats

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Executive Summary

Day-roost selection and foraging habitat use by non-hibernating tree bats (Genus *Lasiurus*) during winter is poorly known throughout much of the Southeastern Coastal Plain. Of particular interest to natural resource managers is the response of these bats to dormant season (non-growing season) burning in the near- and long-term. For Part I, to assess dormant season tree bat day-roost selection in a pyric (frequent fire) landscape managed in part with dormant season burning, we mist-netted and radio-tracked Seminole bats (*Lasiurus seminolus*), hoary bats (*Lasiurus cinereus*) and eastern red bats (*Lasiurus borealis*) to day roosts in February-March and December 2019 at Camp Blanding Joint Training Center (CB) in northern Florida. For a subset of bats following day-roost location, we conducted a series of small prescribed burns surrounding occupied roosts to observe bat response to fire. Sample size of Seminole bats was sufficient to make inferences about dormant season day-roost selection. Generally, Seminole bats selected day-roosts in more mesic (higher moisture) forest stands with high mean fire return intervals. Roosts, primarily in longleaf pine (*Pinus palustris*), loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliotti*), tended to be larger, taller and in higher canopy dominance classes than surrounding trees. Of day-roosts subjected to prescribed burns, only one male Seminole bat and one male eastern red bat evacuated during the fire event. In both cases, these bats had roosted at heights lower and in trees smaller than the majority of other day-roosts in our study – and in both cases bats moved to nearby mesic forest types. Our results suggest tree bats choose winter day-roosts that both maximize solar exposure and minimize risks associated with fire. Nonetheless, at least for Seminole bats, because selected day-roosts largely were fire-dependent or fire-tolerant species, application of fire widely on the Coastal Plain landscape does need to periodically occur to promote recruitment and retention of selected tree species.

For Part II, to assess the impacts of fire and environmental factors on bat activity at CB, we deployed 34 zero-crossing/frequency division acoustic detectors across the installation from late February to early April 2019, and from mid-December 2019 to mid-January 2020 in a variety of habitat conditions. We acoustically identified eight bat species native to the region as present at CB: northern yellow bat (*Dasypterus intermedius*), big brown bat (*Eptesicus fuscus*), eastern red bat, hoary bat, Seminole bat, southeastern myotis (*Myotis austroriparius*), evening bat (*Nycticeius humeralis*), tri-colored bat (*Perimyotis subflavus*), and Brazilian free-tailed bat (*Tadarida brasiliensis*). Overall, bat activity was related to the proximity of mesic habitats as

well as the presence of pine or deciduous forest types, depending on species morphology, i.e., body size, wing-loading and echolocation call frequency. Overall bat activity was influenced positively by either time since fire or mean fire return interval. Our results suggest fire use provides a diverse landscape pattern at CB that maintains mesic, deciduous habitat within the larger pine forest matrix thereby supporting a diverse bat community during the dormant season. Both components of our study were regarded as a pilot “proof-of-concept” effort. Additional work at CB to better describe dormant season day-roosts of eastern red bats and hoary bats seems warranted. Moreover, replicating this work along a south to north gradient within the Coastal Plain from Florida to the mid-Atlantic that would encompass wider variation in dormant season weather and habitat conditions would be beneficial.

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PART I

Winter Roost Selection of Lasiurine Tree Bats in a Pyric Landscape

1.1 Abstract

Day-roost selection by tree bats during winter and their response to dormant season fires is poorly known throughout much of the southeastern United States. In the winter of 2019, we mist-netted and affixed radio-transmitters to 16 Lasiurine bats, primarily Seminole bats (*Lasiurus seminolus*) at Camp Blanding Joint Training Center in northern Florida. We then located day-roost sites to generally describe roost attributes. For five Seminole bats, one eastern red bat (*Lasiurus borealis*), and one hoary bat (*Lasiurus cinereus*), we applied prescribed burns in the roost area to observe bat response. Generally, Seminole bats selected day-roosts in mesic (moistedaphic conditions) forest stands with high mean fire return intervals. At the roost tree scale, Seminole day-roosts tended to be larger, taller and in higher canopy dominance classes than surrounding trees. Seminole bats day-roosted in longleaf (*Pinus palustris*), slash (*Pinus elliotii*) and loblolly pine (*Pinus taeda*) more than expected based on availability, whereas sweetbay (*Magnolia virginiana*), water oak (*Quercus nigra*) and turkey oak (*Quercus laevis*), were roosted in less than expected based on availability. Of the seven roosts subjected to prescribed burns, only one male Seminole bat and one male eastern red bat evacuated the day-roost during or after burning. In both cases, these bats had day-roosted at heights lower and in trees smaller than the majority of other day-roosts observed during our study. Although fires historically were predominantly growing season in timing, they now occur in the dormant season in this part of the Coastal Plain. Our results possibly suggest Seminole bats choose winter day-roosts that both maximize solar exposure and minimize risks associated with fire. Nonetheless, at least for Seminole bats, because selected day-roosts largely were fire-dependent or tolerant species, application of fire does need to periodically occur to promote recruitment and retention of these tree species.

1.2 Introduction

Prescribed fire is used to restore historical disturbance regimes, alter vegetation structure, reduce fuel loads, and maintain wildlife habitat (Waldrop et al. 1992). In the southeastern United States, the longleaf pine (*Pinus palustris*) ecosystem is an archetypal, fire-mediated, ecosystem with one of the shortest fire return intervals of any system in North America (Christensen 1981; Waldrop et al. 1992). This ecosystem is characterized by structural attributes that facilitate frequent fires including fine-fuel inputs, such as pine needles with high resin content, along with

wire-grass (*Aristida* spp.) and other bunch grasses that provide micro-elevation for fuel desiccation and well-ventilated fires (Myers 1990; Hendricks et al. 2002). Conversion to plantation forestry and agriculture or development has reduced the longleaf pine ecosystem to < 5 percent of its historical range (Frost 1993; Brockway et al. 2005). Moreover, widespread fire suppression has led to forest “mesophication”, the process whereby shade-tolerant and fire-intolerant species replace shade-intolerant and fire-tolerant species (Nowacki and Abrams 2008). This often invokes a feedback loop that continually promotes hardwood invasion and further changes subsequent fire behavior when applied (Hiers et al. 2007). Consequently, two-thirds of all species of flora and fauna that are threatened, endangered, or in decline in the Southeast are associated with the longleaf pine ecosystem, making restoration a high priority for conservation (Kirkman and Mitchell 2006).

Longleaf pine ecosystem maintenance and restoration efforts include returning prescribed fire to the landscape at regular, frequent intervals (Landers and Mueller 1986; Landers et al. 1995) and mechanical (Provencher et al. 2002; Kush et al. 2004), as well as, chemical (Brockway and Outcalt 2000) removal of hardwoods within pine stands. In the Coastal Plain, longleaf pine communities naturally burned during the growing season (Frost 1990; Landers 1991). However, many land managers utilized dormant season burning for many decades because fires burn at lower intensities, to promote northern bobwhite (*Colinus virginianus*) habitat, to not disrupt spring or summer ground nesting herpetofauna and avifauna, or to minimize risk to endangered red-cockaded woodpecker (*Leuconotopicus borealis*) cavity trees (Stoddard 1931; Robbins and Myers 1992; Glitzenstein et al. 1995; Brockway and Lewis 1997; Brennan et al. 1998; Knapp et al. 2009).

Currently, bats are a taxa of high conservation concern in North America due to ongoing impacts of white-nose syndrome on hibernating species (Nocera et al. 2019) and wind-energy impacts to migratory, non-hibernating species (Muthersbaugh et al. 2019; hereafter “tree bats”). Depending on the bat species and habitat type therein, bat response to fire management practices generally is neutral to positive in the Southeast (Perry 2012; Austin et al. 2019). Repeatedly burned stands, with reduced overstory clutter and stocking, have increased foraging activity, relative to unburned stands particularly among less maneuverable, larger-bodied bats, or generalist foragers (Ford et al. 2006; Loeb and Waldrop 2008; Braun de Torrez et al. 2018). This occurs even though arthropod prey biomass, such as Lepidopterans, may decrease temporarily following burning (Armitage and Ober 2012). This highlights the importance of prey

availability, which is driven by forest structure, over actual prey abundance. For cavity and exfoliating bark day-roosting species, burning can both destroy potential roosts (Johnson et al. 2009) and create temporally improved day-roost conditions (Johnson et al. 2010). However, most research shows fire improves summer day-roosting habitat by increasing the number or relative availability of snags or improving the roosting characteristics of extant live-trees (Menzel et al. 2000; Menzel et al. 2001; Boyles and Aubrey 2006; St. Germain et al. 2017). Prescribed fire and improved day-roosting conditions also have been shown to increase the connectedness of bat social networks which is believed beneficial to reproductive success and subsequent juvenile recruitment (Ford et al. 2016).

Although prescribed fire may improve bat foraging and day-roost habitat conditions in the medium- to long-term, little work has examined the direct effects of fire *in situ* (Perry 2012). Dickenson et al. (2010) cautioned that fires with taller flame heights and intense heat could stress tree-roosting bats due to high carbon monoxide in the smoke plume and/or thermal damage to heat-sensitive tissue such as the patagium and pinna. For dormant season prescribed fires in upland portions of the southeastern United States, i.e., the upper Piedmont and Southern Appalachians physiographic provinces, most hibernating species are presumed to not yet be on the landscape, nor would the migratory tree bats be present in appreciable numbers before the advent of warmer weather (Carter et al. 2002). However, this may not be true in the Coastal Plain where current and past legacies of dormant season burning occur when both resident and migratory tree bats are present.

During the dormant season in the Southeast, members of the tree bat clade, specifically eastern red bats (*Lasiurus borealis*) and Seminole bats (*Lasiurus seminolus*) day-roost in the foliage of trees, but will occasionally ground-roost within the leaf litter during colder weather where they enter short to medium duration bouts of torpor to reduce energetic demands (Saugey et al. 1998; Cryan 2003; Hein et al. 2005; Mormann and Robbins 2007). Anecdotal observations of bats abandoning day-roosts in trees or on the ground ahead of advancing flames during dormant season burning are known (Saugey et al. 1998; Moorman et al. 1999; Rodrigue et al. 2001). Regionally, tree-bat ground-roosting in leaf litter occurs when nighttime temperatures approach or fall below freezing and day temperatures fail to exceed 15°C (Mormann and Robbins 2007; Hein et al. 2008). Experimental trials have shown that eastern red bats will arouse from torpor when exposed to smoke or audible fire stimuli, however arousal time was negatively correlated with temperature, suggesting vulnerability or potential mortality from fire

during lower ambient temperatures (Scesny 2006, Layne 2009; Perry and McDaniel 2015). Paradoxically, eastern red bats will raise their metabolism when temperatures approach freezing but do not when ambient temperatures are $\geq 5^{\circ}\text{C}$. This means arousal times and risk to fire might be high at low, but still non-freezing, temperatures when managers choose to burn (Dunbar and Tomasi 2006). Although believed to be less impactful than to ground-roosting bats, the consequences of dormant season fire from smoke and flames to bats day-roosting in canopy foliage during warmer temperatures are also largely unknown (Perry 2012).

The Seminole bat is a North American tree bat that typically roosts in foliage in pine (*Pinus* spp.) canopies throughout its range in the southeastern United States (Menzel et al. 1998; Hein et al. 2005; Perry and Thill 2007). Though widespread during the maternity season in winter, the species' eastern distribution is concentrated to lower Coastal Plain in South Carolina south throughout the Florida peninsula (Perry 2018). Limited data exist on dormant season day-roosting for the Seminole bat, but Hein et al. (2005) observed both tree/foliage use as well as ground-roosting during colder weather in coastal South Carolina. Concerns have long existed about the immediate impact to wildlife from prescribed burning, particularly for less-studied taxa and that dormant season burning, though widespread in application, is an ecological "mis-match" with natural fire disturbance processes and regimes in the southeastern United States (Knapp et al. 2009). With bats facing numerous novel stressors, managers need better information about the full array of both the positive and potentially negative aspects of dormant season burning in longleaf pine as a stewardship practice. Herein, we assessed the winter day-roost selection of tree bats in a frequently burned longleaf pine ecosystem to identify what vegetation characteristics influence the distribution of roosting bats during the dormant season. To examine how roost selection influences susceptibility to fire effects, we also assessed direct response of tree bats in this system to dormant season prescribed fire by exposing marked individual tree bats in their day-roosts to prescribed fire and describing their response and subsequent roost selection.

1.3 Methods

We conducted our study at Camp Blanding Joint Training Center and Wildlife Management Area (CB), a 227 km² site managed by the Florida Department of Military Affairs and Florida Fish and Wildlife Conservation Commission. Elevations on CB range from 15 m to 74 m. Mean annual temperature is 20.5°C and mean annual precipitation is 123.5 cm. Camp Blanding has a subtropical climate characterized by hot humid summers and mild winters. Land use at CB includes military training, forest management, sand mining, and wildlife habitat

management. Major forest types included mesic flatwoods dominated by uneven-aged longleaf pine woodlands, slash pine (*Pinus elliotii*) plantations, xeric (dry edaphic conditions) sandhills, and riparian hardwood forests. Prescribed burning is used for habitat restoration on a three to five-year rotation depending on forest stand composition and installation training needs.

To capture bats, we mist-netted for two nights in February of 2019 and four nights in December of 2019. We erected mist-nets (Avinet, Inc., Dryden, New York) over single-track, unimproved roads, trails, and two retention ponds on CB (Figure 1.1). Mist-netting was conducted for three to five hours following sunset. For every bat captured, we recorded species, age (by degree of epiphyseal fusion), sex, mass (grams), right forearm length, and reproductive condition (Anthony 1988, Menzel et al. 2002). We attached uniquely serialized, lipped



aluminum bands to the right forearm of all male and the left forearm of all female Lasiurine bats (i.e. *Lasiurus cinereus*, *L. seminolus*, and *L. borealis*). We affixed a 0.27-gram VHF radio-transmitter (Model LB-2X; Holohil Systems Ltd., Carp, Ontario, Canada) between the scapulae of captured Lasiurine bats using Nu-Hope© (Nu-Hope Laboratories, Inc., Pacoima, California,) or Perma-Type© (The Perma-

Type Company, Inc., Plainville, Connecticut) surgical cement. Weight of the transmitter plus glue was < 5 percent of the body mass of radio-tagged bats, as recommended by Aldridge and Brigham (1988). Bat capture and handling protocols were approved by the Animal Care and Use Committee of Virginia Polytechnic Institute and State University (Protocol Number 16-240) and Florida Fish and Wildlife Conservation Commission Scientific Collecting Permit # LSSC-19-00004.



Seminole bat with radio-transmitter
(Photo by A. Hallman, Florida Fish
and Wildlife Conservation
Commission)

We used TRX-2000 radio telemetry receivers and 3-element Yagi antennas (Wildlife Materials Inc., Murphysboro, Illinois) to locate day-roosts. Tracking was conducted beginning at sunrise from vehicles and then on foot by multiple teams simultaneously and continued for nine days in late February through early March 2019 and then again

in early December 2019 until a transmitter dropped from a bat. Once we located a roost, the GPS coordinates were recorded along with a suite of measurements. Following the methods of Silvis et al. (2012), for each day-roost located, we recorded roost species, diameter at breast height (DBH), tree height, overstory canopy cover at the day-roost, crown class (Nyland 1996; i.e., 1 = suppressed, 2 = intermediate, 3 = codominant, 4 = dominant), decay class (Cline et. al. 1980; 1 = live, 2 = declining, 3 = recent dead, 4 = loose bark, 5 = no bark, 6 = broken top, 7 = broken bole) and whether roost was in live or dead foliage. We measured the closest four trees, (hereafter, quadrant trees) in each quadrant around the roost tree using the point-quarter method (Brower and Zar 1984). For each of the quadrant trees, we also recorded species, distance to roost, DBH, tree height, canopy cover, decay class, and crown class. After tracking each morning, roost tree locations were conveyed to the CB natural resource staff who then decided which roost locations (7) were feasible to burn based on current and expected weather conditions, military training schedules, and installation land-management goals.

Prescribed burns were then conducted around selected roost trees in the late afternoon. Because holding lines were created near day-roosts with a bulldozer, we monitored bats at day-roosts prior to burning to ensure evacuation was not part of the burning preparation process. Once lines were completed, we used either a strip-head or ring firing techniques depending on the size and shape of the burn unit along with wind direction and speed. During burns, two research team members actively monitored the roost tree(s) using binoculars and telemetry



receivers to determine if tagged bats flushed during burns and to record fire behavior. For each burn, we recorded start and end time, bat flush time (when applicable), burn area, and approximations of average flame height, maximum flame height, flame height under the roost, overall smoke production time, and smoke impact time at the roost. If a bat flushed during the burn, we then tracked it to its escape day-roost that afternoon and recorded the same suite of roost measurements described previously. If a bat did not move during a burn, survival was assessed by tracking it to day-roosts on subsequent days.

To assess the impact of fire and land cover on bat roost area and tree selection (Johnson 1980), we assembled fire history and environmental data from CB historical fire data since 2001 and vegetative cover data to create spatially explicit variables using ArcMap 10.2 (Environmental Systems Research Institute, Inc. Redlands, California). We calculated mean fire return interval by averaging the time between burns in years since 2001, which was therefore a surrogate for the overall fire frequency for any given portion on CB. We created a raster layer contrasting mesic and xeric vegetation by designating forest stands and vegetative communities based on their vegetative alliances. For example, the slash pine saturated temperate woodland alliance or deciduous bottomland hardwoods were categorized as mesic whereas the sandhill longleaf pine-turkey oak (*Quercus laevis*) was considered xeric. We reclassified land cover based on vegetative alliances and dominant tree species into deciduous, pine, swamp, shrub/open and the presence of human structures as urban. Lastly, to understand the real-time effects of prescribed fire on roosting bats we noted the species of bat roosting, whether the bat evacuated

or remained during the fire, the average daily temperature during the day of the fire, time to flush since ignition, tree height and tree species.

To estimate the effects of fire and mesic versus xeric vegetation on roost area selection, we utilized generalized linear models in program R (GLM; Faraway 2016; R Core Team 2019). We randomly selected 200 points within the northern portion of CB that was within the plausible area where tagged bats might day-roost and contained a wide array of forest and burn conditions using the sample stratified function in the raster package in program R (R Core Team 2019; Hijmans 2020). We hypothesized that mean fire return interval, mesic versus xeric vegetation, and land cover would differ between roost points and random points. To assess this, we created seven models with the binomial family and a probit regression link representing all possible combinations of those variables as well as a null model. We fit the models with the GLM function in the stats package in program R and used Akaike Information Criterion (AIC) to compare model weights and determine the top model (Akaike 1974).

To estimate the effects of DBH, tree height, crown class and decay class on roost selection, we utilized two-sample *t*-tests to compare characteristics of roost trees relative to available surrounding trees and used Pearson's chi-squared tests (Zar 2010) to determine if the distribution was equitable among roost tree species to surrounding tree species. To discern the available trees surrounding the roost trees, we used the characteristics of the nearest tree in each of the surrounding quadrants. Analyses were performed using program R (R Core Team 2019) and we assigned significance at $\alpha = 0.05$.

Because there were too few samples to statistically analyze the impact prescribed fire had on day-roost evacuation, we provide qualitative descriptions of the fire conditions, weather conditions, and bat responses. However, if a bat evacuated the roost, we further described the characteristics of the escape roost chosen by the bat. Layne (2009) examined response of eastern red bats caught and experimentally placed on a burn site in Missouri and Dickenson et al. (2009) recorded responses of two roosting northern long-eared bats (*Myotis septentrionalis*) to prescribed fire. However, as far as we are aware, our study was the first of its kind that attempted to document the real-time response of non-hibernating, tree bats in day-roosts of their choosing in a natural setting during prescribed burns. As such, we also provide recommendations for future research attempting to replicate this experiment.

1.4 Results

Over the two sessions, we captured 41 bats [eastern red bat = 1, hoary bat = 2, Seminole bat = 13, Southeastern myotis (*Myotis austroriparius*) = 13, evening bat (*Nycticeius humeralis*) = 3, and tri-colored bat (*Perimyotis subflavus*) = 9]. Of these, we affixed radio-transmitters to 13 Seminole bats, one red bat and two hoary bats. We located 49 Seminole bat roosts thereby allowing for statistical analysis thereof, whereas the low sample sizes of three red bat roosts and four hoary bat roosts from only one individual of each of these species precluded that. These locations accounted for approximately 88% of the possible tagged bat/day combinations during our tracking effort. Dormant-season Seminole bat roosts at CB had a mean DBH of $46.61 \text{ cm} + 7.12$, tree height of $21.60 \text{ m} + 2.68$, crown class of $1.7 + 0.20$, and decay class of $1.2 + 0.21$ (Table 1.1). Seminole bats selected dormant season day-roost with larger DBH, greater height, and in higher crown classes than surrounding available trees (Table 1.1). At the tree scale, Seminole bats day-roosted in loblolly bay (*Gordonia lasianthus*; $n = 1$), red bay (*Persea borbonia*; $n = 7$), longleaf pine ($n = 15$), slash pine ($n = 8$), and loblolly pine (*Pinus taeda*; $n = 12$), more than expected based on availability (Table 1.2). Sweetbay magnolia (*Magnolia virginiana*; $n = 1$), water oak (*Quercus nigra*; $n = 4$) and turkey oak ($n = 1$), were roosted in less than expected based on availability (Table 1.2). Tree species that were available but never used based on our point-quarter data included bald cypress (*Taxodium distichum*), boxelder (*Acer negundo*), red maple (*Acer rubrum*), American hornbeam (*Carpinus caroliniana*), common persimmon (*Diospyros virginiana*), Carolina holly (*Ilex ambigua*), sweetgum (*Liquidambar styraciflua*), yellow-poplar (*Liriodendron tulipifera*), rusty staggerbush (*Lyonia ferruginea*), Southern magnolia (*Magnolia grandiflora*), black cherry (*Prunus serotina*), swamp white oak (*Quercus bicolor*), turkey oak (*Quercus cerris*), Shumard oak (*Quercus shumardii*), post oak (*Quercus stellata*), live oak (*Quercus virginiana*), winged elm (*Ulmus alata*), and American elm (*Ulmus americana*). For roost area selection, our top (selected) model based on ΔAIC units and weight (Table 1.3) included mean fire return interval and mesic versus xeric vegetation. Seminole bats selected more mesic forest habitat and sites with longer mean fire return intervals for day-roosting (Table 1.4; Figure 1.2). Although there were too few roost sites to analyze for hoary bats, this is the first documentation of hoary bat day-roost sites in Florida during the winter. Of the four hoary bat roost sites we located, one was in loblolly pine whereas the remaining three were in water oak, all roosts were located in less fire prone mesic habitat on an alluvial terrace.

Despite our success in locating most day-roosts, the majority of roosts were located in mesic areas that could not be ignited under the weather conditions during either session. Nonetheless, we were able to apply six individual prescribed burns that encompassed five Seminole bat, two hoary bat and one eastern red bat day-roosts. From these fires, only one male Seminole bat and one male eastern red bat evacuated their roosts. Both bats flushed approximately ten minutes after the fire was ignited and evacuated only when the fire was near the roost tree, despite smoke reaching the roost prior to that. We observed that both bats flew directly to new day-roosts in adjacent mesic forests, with the Seminole bat moving 147 m and the eastern red bat moving 378 m from the day-roosts within the burns. Both fires that elicited evacuations were the highest intensity of our six burns (max flame heights of 2.43m and 3.05m, Table 1.5). Despite the mean area burned ($0.28 \text{ ha} \pm 0.13$) per fire being less than what occurs operationally, the smallest area burned (0.09 ha) was one in which a bat evacuated, likely due to a low tree height of 7.3m (Table 1.5). As for the bats that did not evacuate during the prescribed burns, their trees had a greater mean height ($16.42\text{m} \pm 5.03$) and were subjected to relatively low fire intensity with lower mean maximum flame heights ($1.32\text{m} \pm 0.43$). Additionally, one Seminole bat roosted within the burn boundaries of the area which had received a prescribed burn the day prior and two other bats (one Seminole and one hoary) switched roosts into areas which were burned the day prior. Another Seminole bat that received two prescribed burns four days apart did not evacuate from either burn despite moving to different roosts at night throughout our study.

1.5 Discussion

Overall, our analysis of Seminole bat day-roosts during the dormant season did not substantively differ from earlier findings in the Coastal Plain during the growing (Menzel et al. 1998, 1999, 2000). For the most part, Seminole bats tended to select larger trees in higher crown classes than surrounding trees, attributable to increased solar exposure to meet thermoregulatory requirements – a factor critical during the dormant season to maintain homeostasis. We did observe some exceptions with two Seminole bats day-roosting relatively low to the ground in red bay shrubs in open, riparian areas. Unlike Hein et al. (2008), our work did not coincide with temperatures low enough to induce bats to use ground-roosts for thermoregulatory benefit.

With the exception of Spanish moss (*Tillandsia usneoides*) use by Seminole bats, our results align with those of Hein et al. (2005) whereby bats day-roosted mostly in large pines. Historical records suggest Seminole bats exclusively roost in Spanish moss during winter

(Constantine 1958; Jennings 1958), but we found no bats roosting therein, despite being readily available throughout CB. Despite providing insulating properties during the winter (Menzel et al. 1999), bats in our study likely did not need to use Spanish moss for insulation because minimum temperatures during our study (15°C) never fell as low as Hein et al. (2005) observed in coastal South Carolina (-6.8°C to 3.7°C). Our results are more similar to summer study results whereby Seminole bats tended to roost in the terminal branches in the crown of large overstory pine trees (Menzel et al. 1998, 1999, 2000). Because Florida experiences relatively mild winters, it is not surprising that winter roost selection would more closely resemble summer day-roost selection, compared to the greater seasonal differences in roost selection in more northern extents of their range.

The bat species we tracked used day-roosts of fire-adapted tree species, i.e., longleaf pine, slash pine and to a lesser degree, loblolly pine consistent with previous work (Menzel et al. 1998, 1999, 2000; Hein et al. 2008). Nonetheless, the majority of Seminole bat, and all of the hoary bat day-roosts we found were located in mesic areas with longer fire return intervals rather than in the larger xeric landscape with plantations or natural pine. The importance of these mesic areas and pine-hardwood mixed forests, as well as fire regimes, have been previously noted across a suite of different taxa (Kirby et al. 2017, Deuel et al. 2017), including at CB (Jorge et al. 2020). Our result of bats selecting more mesic habitat in areas of less frequent fires supports the hypothesis that roost selection may be a function of them seeking to minimize mortality risk from fire caused evacuations. Nevertheless, whether this substantively decreases overall risk is still an open question.

Alternatively, day-roost selection in mesic stands could also be the result of various combined factors such as proximity to water, decreased chance of fire, and increased ability to thermoregulate in colder weather. In other words, roosting in large trees in these mesic locations likely provides a greater range of thermoregulatory options both in terms of solar exposure and abundant mid-story clutter (a result of longer fire-return intervals and lower fire intensity) providing insulation from wind compared to the more open pine savannas in xeric areas, with the added benefit of a lower probability of needing to evacuate during burns which lowers the predator risk associated with moving during the day. Typically, the proximity of these mesic area pines was also closer to riparian areas, i.e., bottomland hardwood communities on CB. These areas provide a water resource and foraging habitat for Seminole bats and probably other tree bats in the Coastal Plain (Menzel et al. 2000). Given our observations, maintaining areas

with longer return interval within the longleaf pine ecosystem can create elements of forest structure and composition used by tree bats (Menzel et al. 1998, 1999, 2000; Hein et al. 2008). Our results provide another example of the benefits of heterogeneity in fire prescriptions for wildlife in longleaf pine systems (Lashley et al. 2015) whereby still providing somewhat for fire-adapted species therein (Brown and Smith 2000).

Across three foliage-roosting species we tracked to day-roosts at CB during the dormant season, only two out of seven bats subjected to a prescribed fire evacuated their roosts during prescribed burns. In both cases, the roost conditions might have influenced the need to evacuate, as the bats were in relatively lower roosts than we observed for other tagged bats and were exposed to higher fire intensities. Interestingly, when these two individuals evacuated they did so to mesic locations despite flying over suitable day-roost conditions in surrounding unburned xeric habitat – perhaps indicating an ability to assess the vulnerability of the site to continue to carry the fire. Despite dormant season burning being outside the natural historical norm, it did occasionally occur and this may have allowed bats to adapt to fire across both growing and dormant seasons. As such, an adaptation to find a low fire risk site makes evolutionary sense regardless of season. Bats that roosted in more fire-prone areas risk expending energy for evacuation or are more likely to be depredated on during diurnal movement (Lima and O’Keefe 2013; Mikula et al. 2016).

As for the five bats that did not evacuate during the prescribed burns, all roosted in taller trees and experienced less intense fire effects than surrounding areas lower in the canopy. Beside heat and fire, smoke has also been suggested to be detrimental to bats (Dickinson et al. 2009; Dickinson et al. 2010), but we observed that smoke quickly dissipated and it may have been cooler than growing season smoke. Furthermore, smoke has been suggested to be an indicator of fire threat (Doty et al. 2018) and in our study may have indicated low threat due to poor combustion and cooler smoke. Additionally, some bats switched roosts into areas that were burned the day prior, and one bat never evacuated even after receiving multiple burns. We suggest that fire not only has minimal negative consequences during a burn in this setting, but that the short-term post-fire conditions created may be also be beneficial for roosting bats (Harper et al. 2016; Ford et al. 2016). Smoldering embers as well as the decreased albedo, the percent of solar radiation reflected at the soil surface, generate higher temperatures than unburned areas (Neal et al. 1965) which could benefit bat thermoregulation during the winter. Furthermore, these sites provide roost areas with minimal risk of fire. Given our results, we

posit that the probability of evacuation is likely driven by the interaction of roost height and fire intensity with an increasing probability of evacuation with increasing fire intensity and decreasing roost height, which may be ultimately driven by the amount of heat reaching the roost. Despite previous studies recording bats roosting in the leaf litter (Saugey et al. 1998; Hein et al. 2005, 2008), we found no bats roosting in the leaf litter, which may have been due to temperatures not reaching the low threshold that triggers leaf litter roosting suggested by Hein et al. (2005).

The complex nature of this study required scientific research protocols, prescribed fire regulations and requirements, as well as optimal weather conditions to all be attained for data collection to occur. As such, many of our efforts were focused on proof of concept for the methods to expand this type of research more broadly; thus, resulting in meaningful, but coarse, data collection. With our observations, future studies attempting to replicate this study should attempt to increase sample sizes of radio-tagged bats particularly across areas more suitable to operational burning, and to more accurately measure fire and weather conditions and assess the effects across a latitudinal gradient to understand differences across temperatures and ecoregions. For example, moving farther north, where bats are more likely to roost in leaf litter due to colder temperatures, could provide more opportunities for this type of research and allow for a better understanding of the evacuation probabilities and mortality risks associated with leaf litter roosting when subjected to burning (Hein et al. 2005, 2008; Layne 2009). Furthermore, conducting experimentation in less fire-prone ecosystems, but where fire is still applied, such as the Piedmont portion of the Southeast, would increase our understanding of bat adaptation to fire across the spectrum of current fire regimes and ecosystems to more accurately represent bat responses to fire. Nevertheless, our data provide a valuable case study that begins to elucidate the function of vegetation attributes selected by tree bats for roost sites and highlights the importance of minimizing fire susceptibility in this selection process.

1.6 Conclusion

Bats in fire-dominated landscapes have evolved with fire and our results suggest minimal negative responses to dormant season fire and that any additive mortality from such seems unlikely. As such, we suggest the continued use of fire during the dormant season to support the military mission from a necessary training range perspective, benefit broader habitat restoration goals and provide long-term positive effects of bats. Furthermore, due to the majority of roosts occurring in fire-facilitated pine trees, we suggest a consistent but infrequent prescription of fire

be maintained in mesic locations to promote some pine regeneration while maintaining the longer fire intervals selected by Seminole bats and perhaps other tree bats. Nonetheless, when fire intensity is great or when roost height is low evacuations may occur. Collectively, our results may suggest a behavioral mechanism for roosting bats to mitigate the negative responses to fire in a fire-prone landscape by generally roosting in mesic areas in this part of the Coastal Plain. However, when the sites do burn, as in our case study, roosts were situated high enough to not be affected by fire. When that was not the case, as we observed in two xeric sites, bats evacuated to taller roosts in mesic areas.

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1.8 Tables

Table 1.1. Seminole bat (*Lasiurus seminolus*) comparison of dormant season day-roosts with surrounding point-quarter trees (Q TREE) for diameter breast height (DBH) height, crown class, and decay class, Camp Blanding, Clay County, Florida, February-March 2019 and December-January 2019-2020. SEM = Standard Mean Error. Class (Nyland 1996; i.e., 1 = suppressed, 2 = intermediate, 3 = codominant, 4 = dominant). Decay class (Cline et. al. 1980; 1 = live, 2 = declining, 3 = recent dead, 4 = loose bark, 5 = no bark, 6 = broken top, 7 = broken bole).

	DBH (cm)		Height (m)		Class (1-4)		Decay (1-4)	
Summary	Roost	Q TREE	Roost	Q TREE	Roost	Q TREE	Roost	Q TREE
Mean	46.61	23.21	21.6	13.28	1.67	2.78	1.22	1.17
SEM	7.12	1.20	2.68	0.56	0.11	0.20	0.11	0.201
Results								
F-test result	Unequal Variances		Unequal Variances		Unequal Variances		Equal Variances	
<i>t</i> -statistic	6.06		5.59		-8.5		0.44	
p- value	<0.001		<0.001		<0.001		0.66	

Table 1.2. Chi-square test results by tree species from bat roost site selection study conducted in February-March 2019 and December-January 2019-2020 at Camp Blanding, Clay County, Florida. Residuals with values greater than two denotes a major influence on the chi-square test statistic. Contributions denote the difference between expected and observed values with larger contributions signifying greater difference.

Tree Species	Residuals		Contributions		Use vs. Available
	Roost	Quadrant	Roost	Quadrant	
Loblolly bay <i>Gordonia lasianthus</i>	1.74	-0.89	5.91	1.55	Greater
Sweetbay magnolia <i>Magnolia virginiana</i>	-0.22	0.11	0.1	0.03	Less
Red bay <i>Persea borbonia</i>	0.22	-0.11	0.1	0.03	Greater
Slash pine <i>Pinus elliottii</i>	1.61	-0.82	5.04	1.32	Greater
Longleaf pine <i>Pinus palustris</i>	2.75	-1.41	14.81	3.88	Greater
Loblolly pine <i>Pinus taeda</i>	3.31	-1.69	21.36	5.6	Greater
Turkey oak <i>Quercus laevis</i>	-1.48	0.76	4.3	1.13	Less
Water oak <i>Quercus nigra</i>	-1.65	0.84	5.32	1.39	Less
Other ¹	-3.38	1.73	22.32	5.85	Less
χ^2			51.17		
<i>p</i> -value			<0.001		

¹Other = bald cypress (*Taxodium distichum*), boxelder (*Acer negundo*), red maple (*Acer rubrum*), American hornbeam (*Carpinus caroliniana*), common persimmon (*Diospyros virginiana*), Carolina holly (*Ilex ambigua*), sweetgum (*Liquidambar styraciflua*), tulip tree (*Liriodendron tulipifera*), rusty staggerbush (*Lyonia ferruginea*), Southern magnolia (*Magnolia grandiflora*), black cherry (*Prunus serotina*), swamp white oak (*Quercus bicolor*), turkey oak (*Quercus cerris*), Shumard oak (*Quercus shumardii*), post oak (*Quercus stellata*), live oak (*Quercus virginiana*), winged elm (*Ulmus alata*), and American elm (*Ulmus americana*).

Table 1.3. Akaike information criterion table with degrees of freedom for generalized linear models from the roost site selection study conducted in February-March 2019 and December-January 2019 on Camp Blanding, Clay County, Florida. MFRI= Mean Fire Return Interval in years, Mesic/Xeric = Mesic or xeric vegetative cover, Habitat = land cover reclassified based on vegetative alliances and dominate tree species into deciduous, pine, swamp, shrub/open and the presence of human structures as urban.

Model	DF	AIC _C	ΔAIC	AIC _{WT}
MFRI + Mesic/Xeric	3	157.46	0.00	0.94
Global	7	163.15	5.51	0.06
MFRI + Habitat	6	180.11	22.47	<0.001
MFRI	2	183.61	25.97	<0.001
Mesic/Xeric	2	190.10	32.46	<0.001
Mesic/Xeric + Habitat	6	192.42	34.78	<0.001
Habitat	5	230.81	73.17	<0.001
NULL	1	248.08	90.44	<0.001

Table 1.4. Top generalized linear model of mesic vs xeric habitat and mean fire return interval showing parameter estimates Seminole bat (*Lasiurus seminolus*) day-roost site selection in February-March 2019 and December-January 2019-2020 at Camp Blanding, Clay County, Florida.

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.77	0.33	-5.28	<0.001
Mesic	-1.23	0.24	-5.10	<0.001
MFRI	0.11	0.02	5.54	<0.001

Table 1.5. Bat response to roost site prescribed burns with species, burned area, evacuation response, burn start time, time to evacuation, daily temperature average, observed max flame height, tree species and height of tree from burn response study conducted in February-March 2019 and December-January 2019-2020 at Camp Blanding, Florida. Dashes denote no record.

Burn Date	Bat Species	Burn Area (ha)	Evacuated	Time to Evacuation (mins)	Air Temp (C)	Max flame height (m)	Tree Species	Height (m)
02/25/19	LASE ¹	0.44	N	-	18	4	PIPA	19.2
02/25/19	LACI	0.16	N	-	22	3	QUNI	11.8
02/26/19	LASE	0.16	N	-	18	-	PIPA	21
02/26/19	LACI	0.16	N	-	18	-	QUNI	7.6
03/01/19	LASE	0.33	N	-	26	6	PITA	22.5
03/01/19	LASE	0.62	Y	10	27	10	PIEL	13.2
12/11/19	LABO	0.09	Y	10	15	7-8	QUNI	7.32

¹Slash pine (*Pinus elliottii*) = PIEL, Longleaf pine (*Pinus palustris*) = PIPA, loblolly pine (*Pinus taeda*) = PITA, and water oak (*Quercus nigra*) = QUNI. Red bat (*Lasiurus borealis*) = LABO, hoary bat (*Lasiurus cinereus*), and Seminole bat (*Lasiurus seminolus*) = LASE.

1.9 Figures

Figure 1.1. Mist net locations (green square) relative to mesic (blue) and xeric (brown) forest stands in the area of interest relative to Camp Blanding boundaries (Red line), Clay County, Florida from the roost site and tree selection study conducted in February-March 2019 and December-January 2019-2020.

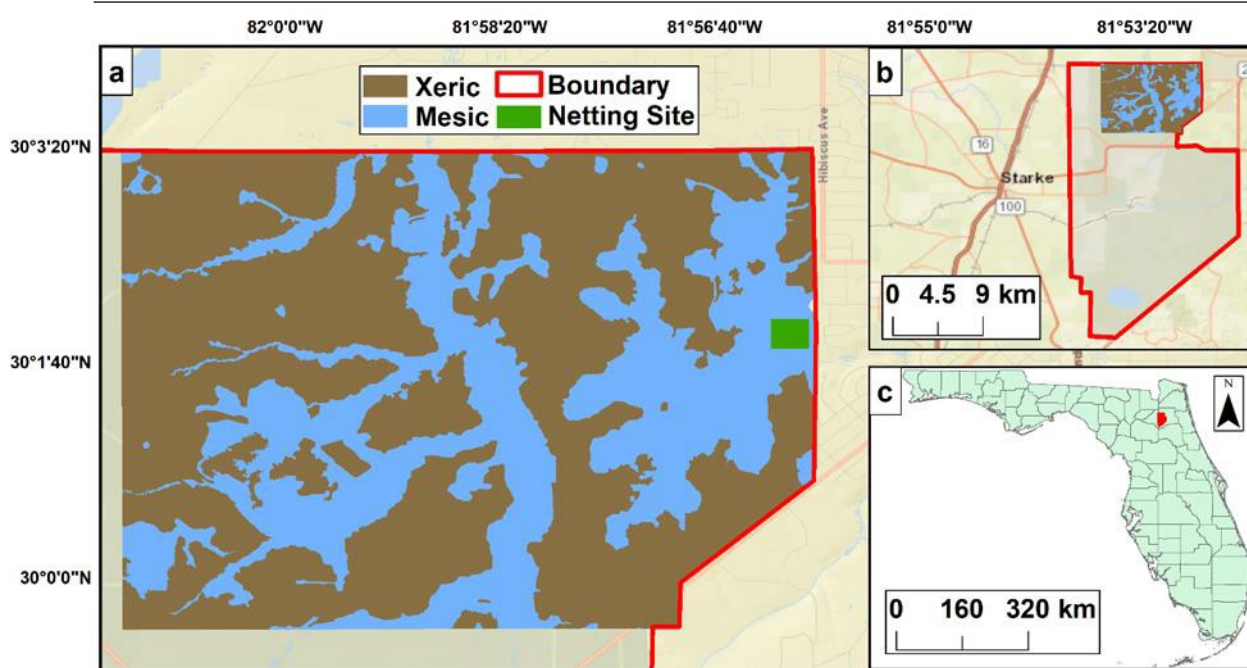
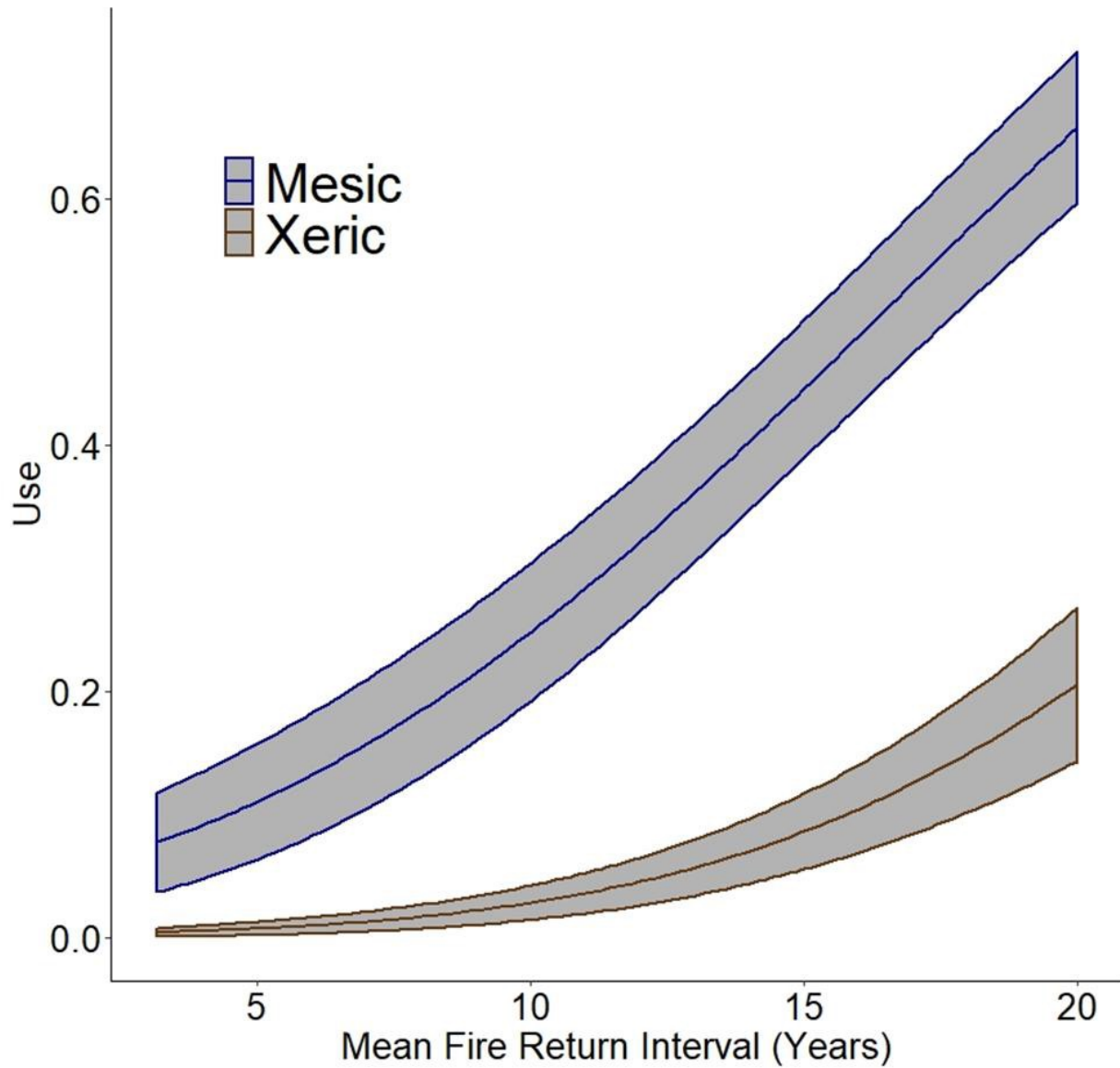


Figure 1.2. Generalized linear model of predicted probability of Seminole bat (*Lasiurus seminolus*) day-roost use at the roost area scale from study conducted in February-March 2019 and December-January 2019-2020 on Camp Blanding, Clay County, Florida. Mesic and xeric habitats were designated from forest stands and vegetative communities based on their vegetative alliances.



PART II

Fire, Land Cover, and Temperature Drivers of Bat Activity in Winter

2.1 Abstract

Understanding the effects of disturbance events, land cover, and weather on wildlife activity is fundamental to wildlife management. Currently, in North America, bats are of high conservation concern due to white-nose syndrome and wind-energy development impact, but the role of fire as a potential additional stressor has received less focus. Although limited, the vast majority of research on bats and fire in the Southeast has been conducted during the growing season thereby creating data gaps for bats in the region relative to overwintering conditions, particularly for non-hibernating species. The Longleaf pine (*Pinus palustris*) ecosystem is an archetypal (standard example) fire-mediated ecosystem which has been the focus of landscape-level restoration in the Southeast. Although historically fires predominately occurred during the growing season in these systems, dormant season fire is more widely utilized for easier application and control as a means of habitat management in the region. To assess the impacts of fire and environmental factors on bat activity, we conducted a dormant season bat activity acoustic study on Camp Blanding Joint Training Center (CB) in northern Florida. We deployed 34 zero-crossing/frequency division acoustic detectors across the installation and recorded data from 26 February to 03 April 2019, and from 10 December 2019 to 14 January 2020. We identified eight bat species native to the region as present at CB. We modeled the effects of fire and environmental factors on activity with Generalized Linear Mixed Models and used Akaike information criterion to determine top models. Bat activity was related to the proximity of mesic habitats as well as the presence of pine or deciduous forest types, depending on species morphology, i.e., body size, wing-loading and echolocation call frequency. Overall bat activity was also true for some individual species' activity and was influenced positively by either time since fire or mean fire return interval. Overall, our results suggest fire use provides a diverse landscape pattern at CB that maintains mesic, deciduous habitat within the larger pine forest matrix thereby supporting the diverse bat community during the dormant season and early spring.

2.2 Introduction

Currently, in North America, bats are a taxa of high conservation concern from the deleterious impacts of white-nose syndrome to hibernating species and wind-energy development impacts to migratory species (Nocera et al. 2019, Muthersbaugh et al. 2019). Bat

responses to fire as a habitat modifier generally are neutral to positive depending on the species, landscape and ecological context considered (Perry 2012). For tree cavity and exfoliating bark roosting species, fire can both destroy and improve day-roost availability and condition (Johnson et al. 2009, Johnson et al. 2010, Perry 2012, Ford et al. 2016). Similarly, fire application can change arthropod prey type and availability thereby modifying bat foraging ecology (Swengel 2001, Campbell et al. 2007, Lacki et al. 2009, Malison and Baxter 2010, Armitage and Ober 2012). Most research suggests that reductions in forest clutter following burning tends to increase bat foraging activity relative to unburned conditions (Ford et al. 2006, Loeb and Waldrop 2008, Cox et al. 2016, Silvis et al. 2016, Austin et al. 2018b). This is particularly true for larger-bodied, less maneuverable bats with lower echolocation call frequencies (Austin et al. 2018a) but less so for smaller-bodied, more maneuverable bats with higher echolocation call frequencies (Starbuck et al. 2020). Regardless, the vast majority research examining bat activity response to fire in the Southeast has been conducted during the growing season (Ford et al. 2006, Loeb and Waldrop 2008, Perry 2012), and/or in upland ecosystems outside the Coastal Plain such as the Appalachians (Loeb and O’Keefe 2014, Cox et al. 2016; but see Braun de Torrez et al. 2018 and Hein et al. 2008,). As such, considerable data gaps exist for both migratory or non-hibernating resident bat species in the portions of the Southeast where these species overwinter and also are often active during dormant season (Carter et al. 2000).

Pine flatwood forests found in northern Florida are typically dominated by longleaf (*Pinus palustris*) and slash pine (*Pinus elliottii*) in the canopy, with saw palmetto (*Serenoa repens*) in much of the understory. Interspersed within are warm-temperate to subtropical mixed pine-hardwood and Southern bottomland hardwoods on side slopes and riparian zones, respectively (Florida Department of Transportation 1999; Armitage and Ober 2013). Prior to European settlement, upland pine forests in much of the southeastern Coastal Plain, including northern Florida, was a short-return interval fire-dominated landscape. Fire often occurred during the growing season whether from lightning ignition or from Native American sources (Waldrop et al. 1992, Glitzenstein et al. 1995, Glitzenstein et al. 2003, Perry and McDaniel 2015). However, agricultural conversion, urban development, intensive pine plantation culture, and fire suppression have greatly altered much of this landscape (Wade et al. 1980, Brockway and Lewis 1997, Glitzenstein et al. 2003, Armitage and Ober 2012).

Recognizing the array of native, imperiled species and community types that rely on fire to maintain habitat conditions, prescribed burning programs, where applicable, have increased in scope as a means to mimic historical disturbance, promote biodiversity, maintain ecosystem function, and suppress catastrophic wildfire events (Beckage and Stout 2000, Main and Richardson 2002, Reilly et al. 2012). However, much of the burning in the region still occurs in the dormant season for easier application and control and/or as a more than century-long legacy of bobwhite quail (*Colinus virginianus*) and other game species management (Harper et al. 2016). More research is needed to fully understand the impacts that fire, and specifically dormant season fires, have on the native fauna in these communities. Bats in particular are of high conservation concern at present and understanding if fire is creating additional stressors on them is still an open question.

Accordingly, we conducted a dormant season bat activity acoustic study in a north-central Florida landscape with an average three- to five-year prescribed fire return interval, depending on individual stand forest cover type and stewardship purpose. Herein, our objective was to examine the effects of land cover, distance to mesic habitat, mean fire return interval (MFRI), time since fire (TSF), temperature, and season (i.e. early versus late dormant season) on activity for Florida bat species. We hypothesized that large-bodied bat species with higher wing-loading and lower echolocation call characteristics would have increased activity in recently burned areas, further from mesic vegetation types. We also predicted that bat activity would decrease as TSF and MFRI increases due to reduced clutter in the environment thereby providing more foraging “space” (Ford et al. 2006). Lastly, we hypothesized that bat activity would increase with increasing temperatures as lower temperatures during winter have been shown to reduce bat activity and their associated arthropod prey (Hayes et al. 1997), and that temperatures and assumed prey availability may be stronger indicators of bat activity than vegetation clutter alone.

2.3 Methods

We conducted our study at Camp Blanding Joint Training Center and Wildlife Management Area (CB), Clay County in northeastern Florida (Figure 2.1). The installation is 22,700 ha in size with an elevation range of 15 m to 74 m above sea level. Camp Blanding has a subtropical climate with a mean annual temperature of 20.5 °C and mean annual precipitation of 123.5 cm, resulting in hot humid summers and relatively mild winters. Land use at CB includes

military training, forestry and wildlife management as well as sand mining. Prescribed burning is used for habitat restoration and maintenance on a 3 to 5-year rotation dependent on forest stand composition. The considerable variation in site productivity occurs across CB which is at the nexus of the more fertile Sea Islands Flatwoods ecoregion to the north and the less productive Central Florida Ridges and Uplands ecoregion that encompasses the southern extent of the base (Omernik and Griffith, 2014). Major forest types included mesic flatwoods mixed hardwood-pine, and riparian bottomland hardwood forests, dominated by uneven-aged longleaf pine woodlands, planted pine plantations, and xeric sandhills (Jorge et al. 2020).

To assess the foraging habitat relationship of bat activity in the dormant season through early spring, we deployed 34 zero-crossing/frequency division acoustic detectors (Song Meter SM4BAT; Wildlife Acoustics, Maynard, Massachusetts, USA; Figure 2.1) across CB. We attached microphones directly to the detectors which were attached with bungee cords to trees at a height of 3 to 3.5 meters above the ground. Detectors recorded one hour prior to sunset until one hour after sunrise. We deployed individual detectors using a series of pre-established 3 km² grids, prioritizing locations on trails, forest roads, or near water bodies to increase bat detection probabilities (Brooks et al. 2005, Erickson et al. 2003, Ford et al. 2005, Humes et al. 1999, Law et al. 2001). Sample sites encompassed an array of habitats, including both deciduous and pine forest spanning the gradient of fire history and habitat conditions found across the installation. We recorded data in two sessions: late dormant season through early spring from 26 February to 03 April 2019, and then early to mid-dormant season from 10 December 2019 to 14 January 2020.

We processed the recorded acoustic data through Kaleidoscope (Wildlife Acoustics, Maynard, MA, USA; Version 5.1.9 Classifier Version 4.2.0 S/A: 0 Sensitivity Setting) for species identification, accepting only echolocation call files with > 2 pulses, and using default signal parameters for nine bat species known or suspected to occur in the study area: Rafinesque's big-eared bat (*Corynorhinus rafinesquii*), northern yellow bat (*Dasypterus intermedius*), big brown bat (*Eptesicus fuscus*), eastern red bat (*Lasiurus borealis*), hoary bat (*Lasiurus cinereus*), Seminole bat (*Lasiurus seminolus*), southeastern myotis (*Myotis austroriparius*), evening bat (*Nycticeius humeralis*), tri-colored bat (*Perimyotis subflavus*), and the Brazilian free-tailed bat (*Tadarida brasiliensis*; Trani et al. 2007).

To assess the impact of habitat and fire history on bat activity during the dormant season and early spring, we assembled fire history and landcover data from the CB historical fire data since 2001 and vegetation data. We also collected nightly Meteorological Terminal Aviation Routine Weather Report (METAR) temperature data averaged from two weather stations on CB. We created spatially explicit fire covariates that represented different fire and landcover conditions during the survey. The TSF values indicated the number of years since an area was last burned and subsequently represented the current conditions relative to fire impact and vegetation change. Conversely, MFRI values indicated the average time between burns in years and represent the historical repeated use of fire at our survey sites since 2001. The distinction between these fire covariates allowed for a nuanced examination of how fire history attributes may be influencing bat activity rather than assuming the response to fire history is uniform across its attributes. We calculated distance to land cover values using Euclidean distance for forest stand or other vegetative communities considered mesic, i.e., such as, those with laurel oak (*Quercus laurifolia*), water oak (*Quercus nigra*), and willow oak (*Quercus phellos*), other temporarily flooded forest alliances, or were considered wetland and/or seasonally or permanently flooded, using ArcMap10.3 Spatial Analyst Tools (ESRI, Redlands, CA). This Euclidean distance function created distance raster layers whereby each cell indicated the distance to the nearest representative cell of mesic habitat. We reclassified land cover data from CB based on forest community types and simply categorized as deciduous dominant or pine dominant. Lastly, we assigned surveys to either late winter/early spring 2019 sample period or early winter in 2019 to 2020 sample period to create a categorical variable to distinguish between the two bat acoustic survey periods. Because the periods occurred during two different dormant seasons, sample period can be interpreted as both as a year effect and/or a seasonal effect.

To estimate the effects of fire and site environmental conditions on bat activity during the dormant season, we modeled the effects of environmental factors on bat activity with Generalized Linear Mixed Models (GLMMs) using a negative binomial distribution with zero inflation with the *GLMMAMD* package (Skaug et al. 2006) using R programming language (R Development Core Team, 2011). We created a series of exploratory models (25) of all possible combinations of environmental and weather variables along with a null model for each species at CB. We scaled and centered all covariates for the GLMM analysis for better convergence and tested for collinearity in predictor variables using the *corrplot* function (Wei and Simko, 2017).

We then used Akaike information criterion (AIC; Burnham and Anderson, 2002) to compare model weights to determine the top model from the GLMMs.

2.4 Results

We recorded 114,261 and 142,072 bat echolocation call files for the February- April 2019 and December-January 2019-2020 survey periods, respectively, for a total of 256,333 calls at CB. We detected 9 bat species : Rafinesque's big-eared bat (*Corynorhinus rafinesquii*), northern yellow bat (*Dasypterus intermedius*), big brown bat (*Eptesicus fuscus*), eastern red bat (*Lasiurus borealis*), hoary bat (*Lasiurus cinereus*), Seminole bat (*Lasiurus seminolus*), southeastern myotis (*Myotis austroriparius*), evening bat (*Nycticeius humeralis*), tri-colored bat (*Perimyotis subflavus*), and the Brazilian free-tailed bat (*Tadarida brasiliensis*). The most detected species was the tri-colored bat (n= 75,707 calls) and the least was Rafinesque's big-eared bat (n=11). We had sufficient data to model the activity of all bats at CB with the exception of Rafinesque's big-eared bat, a species with a low amplitude call that is not easily recorded even when present (Clement and Castleberry 2011).

The most supported northern yellow bat model predicted increasing activity with increasing distance to mesic habitat, increasing temperature, and increasing TSF. Northern yellow bat activity was also greater in pine forest types and during the late dormant to spring (i.e. 2019) survey period than in deciduous types and during the early dormant season (i.e. 2019-2020; Table 2.1, Figures 2.2-3, 2.5-7). The most supported big brown bat model predicted increased activity with increasing distance to mesic habitat, and increasing temperature, whereby decreasing with increasing MFRI. Big brown bat activity was also greater in pine forest types and during the late dormant to spring season (February- April 2019) survey period than in deciduous types and during early dormant season survey (December-January 2019-2020; Table 1, Figures 2.2-4, 2.6-7). The most supported red bat model predicted increasing activity with increasing MFRI, and increasing temperature, whereby decreasing with increasing distance to mesic habitat. Eastern red bat activity was greater in deciduous forest types than pine types (Table 1, Figures 2.2-4,2.7). The most supported hoary bat model predicted increasing activity with increasing distance to mesic habitat, increasing temperature and increasing TSF. Hoary bat activity was also greater in pine forest types and during the late dormant to spring 2019 period than in deciduous types or during the early dormant season 2019-2020 (Table 2.1, Figures 2.2-3,

2.5-7). The most supported Seminole bat model predicted increasing activity with increasing temperature, and increasing TSF, whereby decreasing activity with increasing distance to mesic habitat. Seminole bat activity was also greater in pine forest types than in deciduous types (Table 2.1, Figures 2-3, 5, 7). The most supported southeastern myotis model predicted increased activity with increasing MFRI, increasing temperature, and increasing TSF, whereby decreasing activity with increasing distance to mesic habitat. Southeastern myotis activity was also greater in deciduous forest types and during the early dormant season period than in pine types and during the late dormant to spring season (Table 2.1, Figures 2.2-7). The most supported evening bat model predicted increased activity with increasing temperature, and TSF, whereby decreasing activity with increasing distance to mesic habitat and MFRI. Evening bat activity was also greater in deciduous forest types and during the late dormant to spring season period than in pine types and during the early dormant season (Table 2.1, Figures 2.2-7). The most supported tri-colored bat model predicted increased activity with increasing MFRI, increasing temperature, and increasing TSF, whereby decreasing with distance to mesic habitat (Table 2.1, Figures 2.2-7). The most supported Brazilian free-tailed bat model predicted increased activity with increasing distance to mesic habitat, increasing temperature, and TSF. Brazilian free-tailed activity was also greater in pine forest types and during the late dormant to spring period than in deciduous types and during the early dormant season (Table 2.1, Figures 2.2-3, 2.5-7).

2.5 Discussion

Our study examined bat activity using acoustics in a fire-dominated, southeastern Coastal Plain system during what was largely the understudied dormant season. We recorded the full suite of species that were known to or could be expected to occur at CB in the dormant season including the hoary bat, an uncommon winter migrant to the north Florida area. Interestingly, our *ad hoc* mist-netting surveys that overlapped with the initial February 2019 deployment of detectors resulted in the capture of two hoary bats, thereby providing additional confidence in our correct classification of this species from acoustics. We found that overall bat activity rates differed across land cover, fire and survey period, with land cover and fire differences likely explained by bat body size.

Dormant season bat activity response at CB varied across the suite of environmental measurements and among bat species. Consistent with findings during the growing season in the

Coastal Plain in other studies, the activity of several species was related to the proximity of mesic habitats as well as the presence of pine or deciduous forest types, depending on body size and characteristic echolocation frequency (Ford et al. 2006, Menzel et al. 2002, Menzel et al 2005a, Menzel et al 2005b). Our results showed a split in activity rates relative to distance from mesic habitat with five species (Seminole bat, Eastern red bat, southeastern myotis, evening bat, and tri-colored bat) having greater activity near mesic habitats and four species (northern yellow bat, big brown bat, hoary bat and the Brazilian free-tailed bat) with higher activity further away from mesic habitats. Arthropod prey often will aggregate near mesic habitat during dry seasons in tropical forests (Janzen 1973) and may partially explain why some bats are more active in mesic areas during the relatively dry winter season in Florida. Additionally, sources of water are a positive driver of bat activity (Ford et al. 2005, 2006), especially in more xeric environments (Szewczak et al. 1998; Adams and Simmons, 2002).

Previous research has shown varied activity rates in cluttered versus uncluttered forest environments based on bat body size, wing-loading and characteristic echolocation frequency (Brigham et al. 1997, Erickson and West 2003, Sleep and Brigham 2003, Starbuck et al. 2020). The species that avoided mesic habitats tended to be the larger bodied, higher-wing loaded bats with lower echolocation frequencies that are less adapted to forage in the cluttered mesic environment with tardily deciduous or evergreen trees and higher stand stocking rates than surrounding pine types (Norberg and Rayner 1987, Patriquin and Barclay 2003, Menzel et al. 2005a, Armitage and Ober 2012). Similarly, land cover preference paralleled this finding as our large-bodied bats, i.e., big brown, Seminole, northern yellow and Brazilian free-tailed, showed increased activity rates in pine forests versus deciduous forests irrespective of xeric or mesic condition. Much of the longleaf pine forests in the Southeast are characterized as park-like with wide tree-spacing, allowing for easier movement and foraging for large-bodied bats. In contrast, smaller bodied bats such as the southeastern myotis and evening bat had higher activity in the more cluttered deciduous forests. Seminole bats were an exception in that they had higher activity rates in pine forests and the edges of mesic habitats with pines stands, which supports previous research from the growing season in the Coastal Plain (Menzel et al. 2005a). That being said, foraging ecology is flexible for most bat species and overall activity is often higher along ecotones and edges in the Southeast within large bottomland hardwoods canopy gaps and between bottomland hardwoods and upland pines (Menzel et al. 2002). Fire-induced edges

between burned and unburned stands show the same pattern in the Appalachians (Austin et al. 2019).

The impact of prescribed fire to bats has been of considerable interest for ecologists and managers in the Southeast (Carter et al. 2000; Boyles and Aubrey, 2006). This is particularly true for non-hibernating species that occasionally day-roost in leaf litter during the dormant season and may therefore be impacted from prescribed fires (Perry 2012). Anecdotal accounts of bats, such as eastern red bats, flying from leaf litter during burns are known (Moorman et al. 1999; Mormann and Robbins 2006). Accordingly, questions have been raised about this phenomenon assuming bats, at least in the Coastal Plain, have evolved in conjunction with growing season rather than dormant season burning (Cater et al. 2002, Perry 2012). Dormant season activity of several species in our study was influenced positively by longer TSF or MFRI, yet were also linked to conditions that ultimately are maintained by fire, thereby implying fire as a habitat management tool needs to be considered from both a temporal and spatial perspective. Big brown bats and evening bats did exhibit decreased activity in forest stands with increasing MFRI. Boyles and Aubrey (2006) found relatively short-term benefits to these species following fire due to increased day-roost abundance, quality and use, i.e., increased cavities in live trees and residual snags with higher solar radiation, along with reduced vegetative clutter that enhanced foraging ability. Though speculative, warmer cavity roosts would seemingly benefit both big brown bats and evening bats at CB during the dormant season to facilitate less energetically costly torpor arousal prior to foraging. Nonetheless, using evening bats at CB as an example, positive influences from fire are nuanced in that the species benefited from longer MFRI but benefited with shorted TSF. In other words, immediately post-fire, whereas clutter is clearly reduced, the reduction in vegetation and altered substrate for insects may limit bat foraging opportunities (Kalcounis et al 1999, Menzel et al. 2002). However, burning in successive growing seasons, evening bat activity likely increases, as insect densities respond to ground and mid-story regrowth (Tibbels and Kurta 2003), while still remaining relatively uncluttered compared to unburned stands. Nonetheless, in the long-growing seasons experienced at CB, this optimal condition for bats is transitory as TSF is correlated with increased clutter, thereby necessitating repeated entry over time to re-burn.

Though the area is subtropical with mild winters, colder weather with sub- to freezing temperatures does occur in northern Florida. Not surprisingly, over both our survey periods,

overall bat activity and that for each individual species detected was positively correlated to higher nighttime temperatures. Increased insect availability typically occurs with increasing temperatures (Zinn and Humphrey 1981, Richards 1989, Hayes 1997), a relationship documented in the Southeast in both warm-temperate/subtropical (Grider et al. 2016) and cool-temperate environments (Muthersbaugh et al. 2019). Additionally, warmer temperatures allow bats to better maintain homeothermic stasis during foraging (Hayes 1997). Furthermore, with the exception of the southeastern myotis, most species had higher activity rates in the late dormant to early spring versus during early dormant period. Given our study design, the survey period could be interpreted as an early/late dormant season or yearly effect as our survey spanned across both. However, we suggest the response to be more due to seasonal changes because of changes in temperature and differences in migration, i.e., movement to or from our study site. Higher overall bat activity for most species during the late dormant to spring sampling period would coincide with steady increase in overall nightly temperatures at CB. Also, this could be the period when an area such as CB in this part of the Coastal Plain is hosting both resident and some remaining overwintering migrants as well as migrants passing through from the south or west (Cryan 2003). Greater activity of the southeastern myotis in the early winter period may be a function of the numerous culverts and anthropogenic structures on the installation that structurally mimic large, hollow bald cypress (*Taxodium distichum*) or swamp tupelo (*Nyssa aquatica*) where this species day-roost year-round (Clement and Castleberry 2013) or caves used by the southeastern myotis to just west of CB for longer winter torpor bouts whereby formerly they would have left CB to find suitable winter day-roosts or hibernacula (Rice 1957).

2.6 Conclusion

Our findings add to the body of literature on bat activity response to fire in the Southeastern United States (Perry 2012, Austin et al. 2019) by examining fire regimes during the relatively unstudied dormant season. For this part of the Coastal Plain in the Southeast, it would appear that maintaining mesic, deciduous habitat within the larger pine forest matrix to meet the full foraging (and presumably day-roosting) habitat needs for these bat species is an important bat conservation consideration. Although fire is a crucial aspect of longleaf pine ecology at CB and throughout the Southeast, very short fire-return intervals over larger landscapes may be less optimal for bats. Similar to previous work in the Coastal Plain during the growing season (Ford

et al. 2006), a diverse, shifting mosaic approach to burning to maximize diversity of post-fire conditions, while still meeting other fire management objectives to support the military mission or other stewardship needs, particularly where mesic, deciduous forest types are less abundant, better suit the general habitat needs of bats. Therefore, maintaining diverse land cover (i.e. mesic versus xeric, deciduous versus pine) and post-fire conditions, through mosaic burning, would benefit the bat community by providing for the varying needs of large and small-bodied bats. Maintaining these diverse conditions not only benefit the bat community but have also been shown to benefit other species within longleaf pine ecosystems (Lashley et al. 2015) including CB (Jorge et al. 2020). We see this study as the first step in more clearly examining dormant season bat ecology in the Southeast generally and within fire-dominated landscapes specifically.

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2.8 Tables

Table 2.1. Variable names, direction effects, parameter estimates, standard errors and p-values for each bat species detected in acoustic surveys conducted from 26 February to 03 April 2019, 10 December 2019 to 14 January 2020, at 34 acoustic-survey points on Camp Blanding Joint training Center, Clay County, Florida. The + sign denotes an increase in activity with increases in the associated factors, while the name of the land cover or survey period denotes a significant increase compared to alternative name (i.e., Pine vs. Deciduous, and late dormant and spring season (Feb-April) versus early dormant season (Dec-Jan)). DAIN = northern yellow bat (*Dasypterus intermedius*), EPFU = big brown bat (*Eptesicus fuscus*), LABO = eastern red bat (*Lasiurus borealis*), LACI= hoary bat (*Lasiurus cinereus*), LASE= Seminole bat (*Lasiurus seminolus*), MYAU= southeastern myotis (*Myotis austroriparius*), NYHU= evening bat (*Nycticeius humeralis*), PESU= tri-colored bat (*Perimyotis subflavus*), and TABR= Brazilian free-tailed bat (*Tadarida brasiliensis*).

Variable	Species	Effect Direction	Parameter Estimate	Standard Error	P-Value
Temperature					
	DAIN	+	1.97	0.18	<0.001
	EPFU	+	1.35	0.13	<0.001
	LASE	+	1.73	0.14	<0.001
	LABO	+	0.93	0.10	<0.001
	LACI	+	1.42	0.14	<0.001
	MYAU	+	0.82	0.12	<0.001
	NYHU	+	1.55	0.13	<0.001
	PESU	+	1.47	0.14	<0.001
	TABR	+	1.69	0.17	<0.001
Mesic Habitat					
	DAIN	-	0.26	0.04	<0.001
	EPFU	-	0.30	0.03	<0.001
	LASE	+	-0.20	0.04	<0.001
	LABO	+	-0.46	0.03	<0.001
	LACI	-	0.27	0.03	<0.001
	MYAU	+	-0.46	0.04	<0.001

Table 2.1 cont.

	NYHU	+	-0.19	0.04	<0.001
	PESU	+	-0.81	0.04	<0.001
	TABR	-	0.35	0.04	<0.001
<hr/>					
Mean Fire Return Interval					
	DAIN	NA	NA	NA	NA
	EPFU	-	-0.25	0.04	<0.001
	LASE	NA	NA	NA	NA
	LABO	-	0.48	0.03	<0.001
	LACI	NA	NA	NA	NA
	MYAU	+	0.24	0.05	<0.001
	NYHU	-	-0.22	0.05	<0.001
	PESU	+	0.81	0.06	<0.001
	TABR	NA	NA	NA	NA
<hr/>					
Time Since Fire					
	DAIN	+	0.29	0.05	<0.001
	EPFU	NA	NA	NA	NA
	LASE	+	0.14	0.04	<0.001
	LABO	NA	NA	NA	NA
	LACI	+	0.10	0.03	0.004
	MYAU	+	0.17	0.05	0.001
	NYHU	+	0.32	0.05	<0.001
	PESU	+	0.20	0.06	0.001
	TABR	+	0.19	0.04	<0.001
<hr/>					
Land Cover					
	DAIN	Pine	0.46	0.12	<0.001
	EPFU	Pine	0.19	0.09	0.044

Table 2.1. cont.

LASE	Pine	0.19	0.09	0.038
LABO	Deciduous	-0.72	0.07	<0.001
LACI	Pine	0.54	0.08	<0.001
MYAU	Deciduous	-1.33	0.09	<0.001
NYHU	Deciduous	-0.52	0.08	<0.001
PESU	NA	NA	NA	NA
TABR	Pine	0.63	0.1	<0.001
<hr/>				
Survey Period				
<hr/>				
DAIN	Feb- April	1.93	0.31	<0.001
EPFU	Feb- April	1.2	0.23	<0.001
LASE	NA	NA	NA	NA
LABO	NA	NA	NA	NA
LACI	Feb- April	0.58	0.27	0.034
MYAU	Dec- April	-1.58	0.23	<0.001
NYHU	Feb- April	0.67	0.23	0.004
PESU	NA	NA	NA	NA
TABR	Feb- April	0.64	0.3	0.035
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Figure 2.1. Camp Blanding Joint Training Center, Clay County, Florida showing the 34 acoustic detector bat activity acoustic survey locations from the 26 February to 03 April 2019 and 10 December 2019 to 14 January 2020.

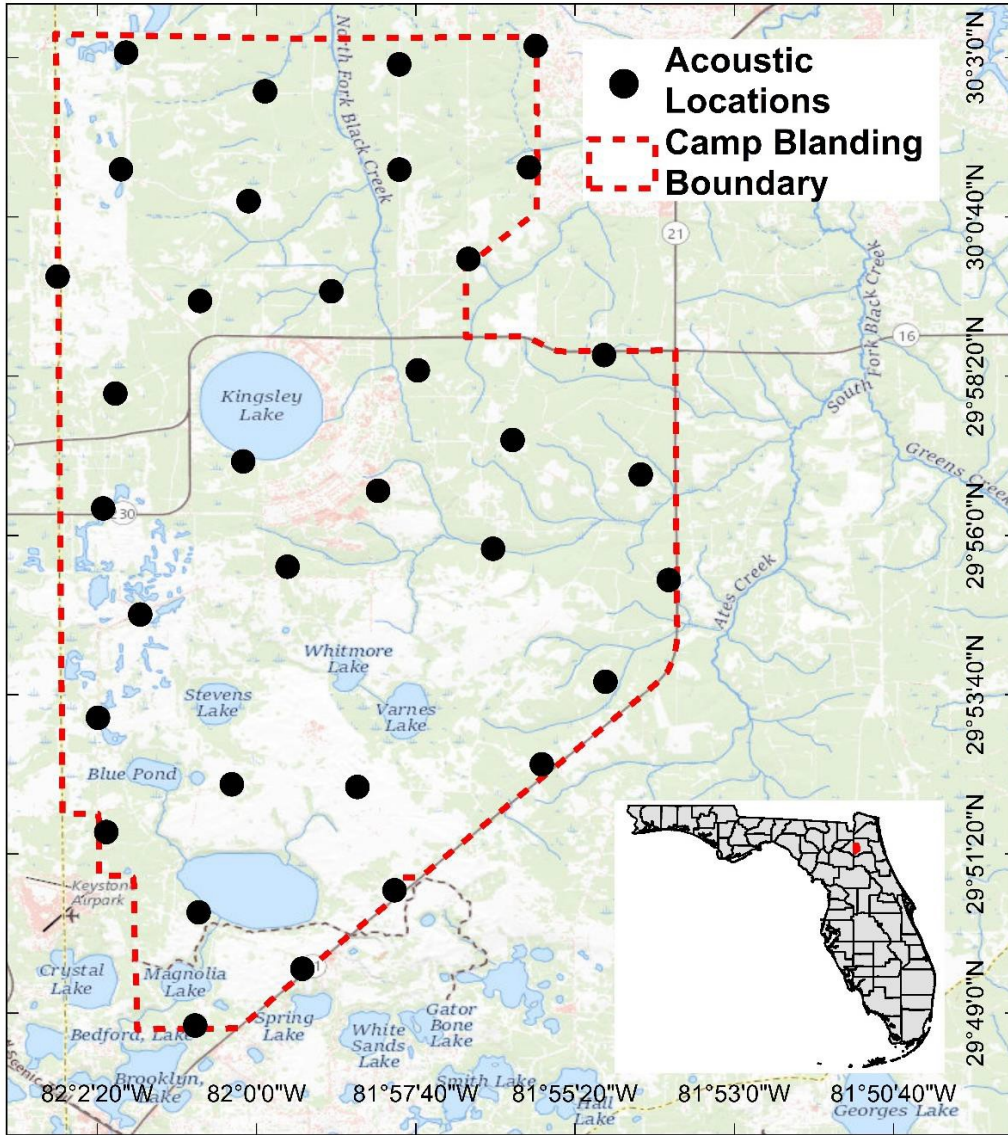


Figure 2.2. Predicted relative mean nightly activity, based on calls per site, given distance to mesic land cover for nine bat species from acoustic surveys conducted 26 February - 03 April 2019, and from 10 December 2019 - 14 January 2020 at 34 plots on Camp Blanding Joint Military Center, Clay County, Florida. Grey shading denotes 95% confidence intervals. DAIN = northern yellow bat (*Dasypterus intermedius*), EPFU = big brown bat (*Eptesicus fuscus*), LABO = eastern red bat (*Lasiurus borealis*), LACI= hoary bat (*Lasiurus cinereus*), LASE= Seminole bat (*Lasiurus seminolus*), MYAU= southeastern myotis (*Myotis austroriparius*), NYHU= evening bat (*Nycticeius humeralis*), PESU= tri-colored bat (*Perimyotis subflavus*), and TABR= Brazilian free-tailed bat (*Tadarida brasiliensis*).

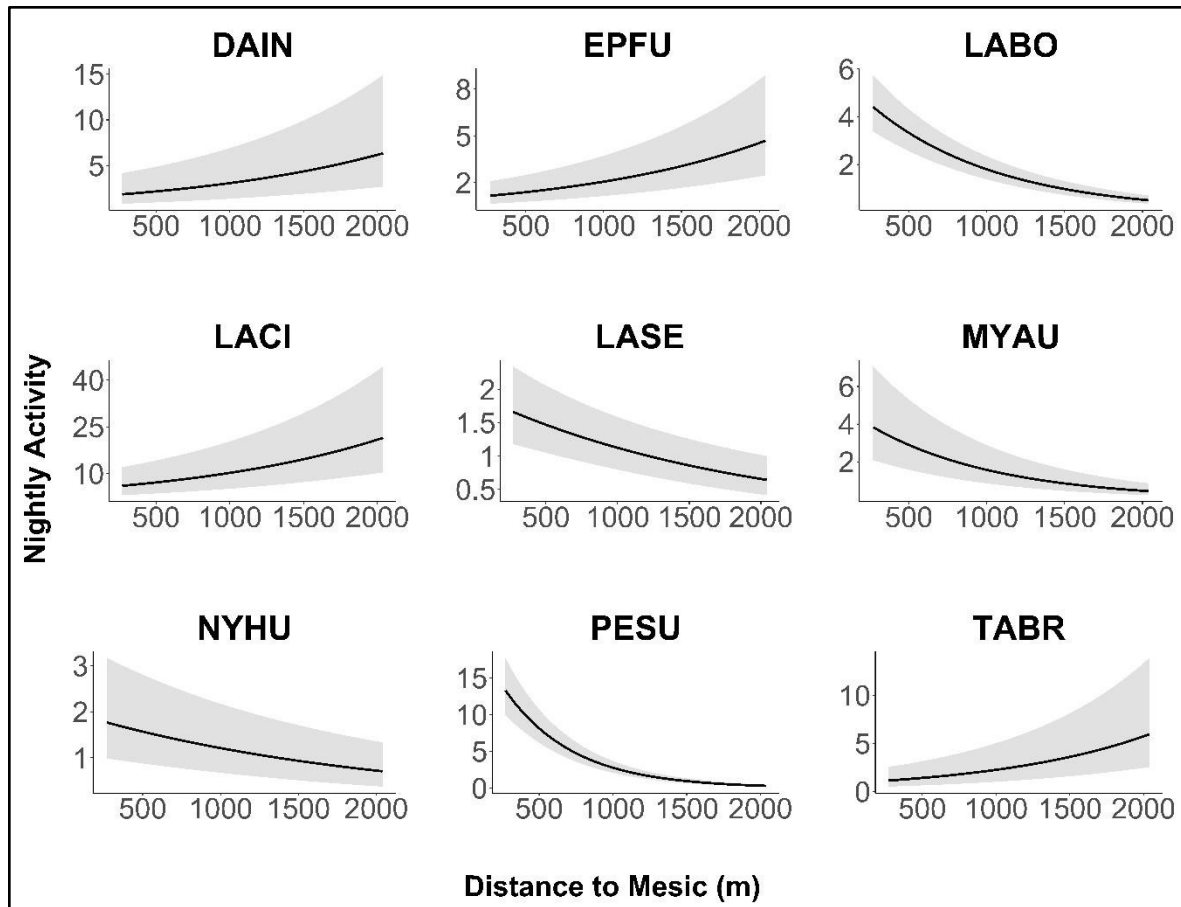


Figure 2.3. Predicted relative mean nightly activity, based on calls per site, across temperature range for nine bat species from acoustic surveys conducted 26 February - 03 April 2019, and from 10 December 2019 - 14 January 2020 at 34 plots on Camp Blanding Joint Military Center, Clay County, Florida. Grey shading denotes 95% confidence intervals. DAIN = northern yellow bat (*Dasypterus intermedius*), EPFU = big brown bat (*Eptesicus fuscus*), LABO = eastern red bat (*Lasiurus borealis*), LACI= hoary bat (*Lasiurus cinereus*), LASE= Seminole bat (*Lasiurus seminolus*), MYAU= southeastern myotis (*Myotis austroriparius*), NYHU= evening bat (*Nycticeius humeralis*), PESU= tri-colored bat (*Perimyotis subflavus*), and TABR= Brazilian free-tailed bat (*Tadarida brasiliensis*).

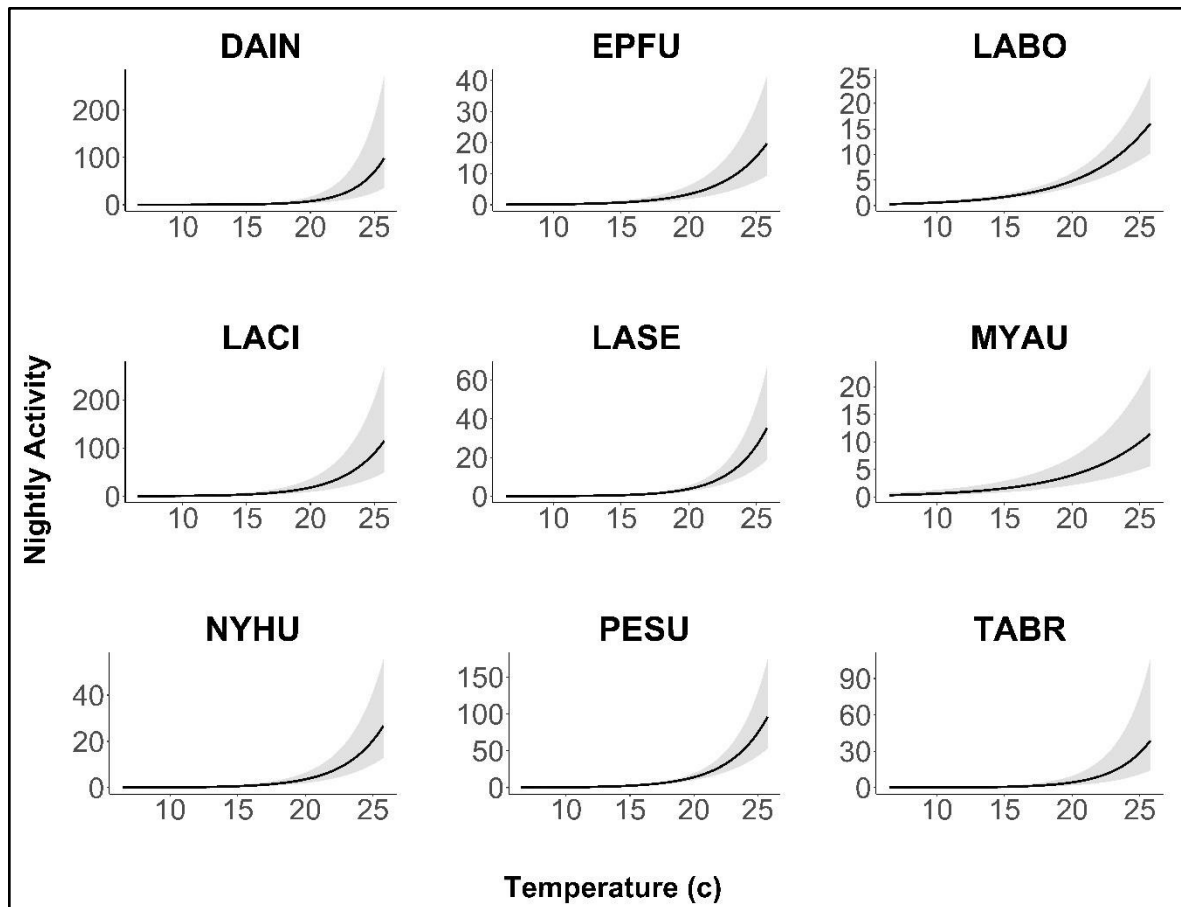


Figure 2.4. Predicted relative mean nightly activity, based on calls per site, given mean fire return interval for five bat species from acoustic surveys conducted 26 February - 03 April 2019, and from 10 December 2019 - 14 January 2020 at 34 plots on Camp Blanding Joint Military Center, Clay County, Florida. Grey shading denotes 95% confidence intervals. EPFU = big brown bat (*Eptesicus fuscus*), LABO = eastern red bat (*Lasiurus borealis*), MYAU= southeastern myotis (*Myotis austroriparius*), NYHU= evening bat (*Nycticeius humeralis*), and PESU= tri-colored bat (*Perimyotis subflavus*).

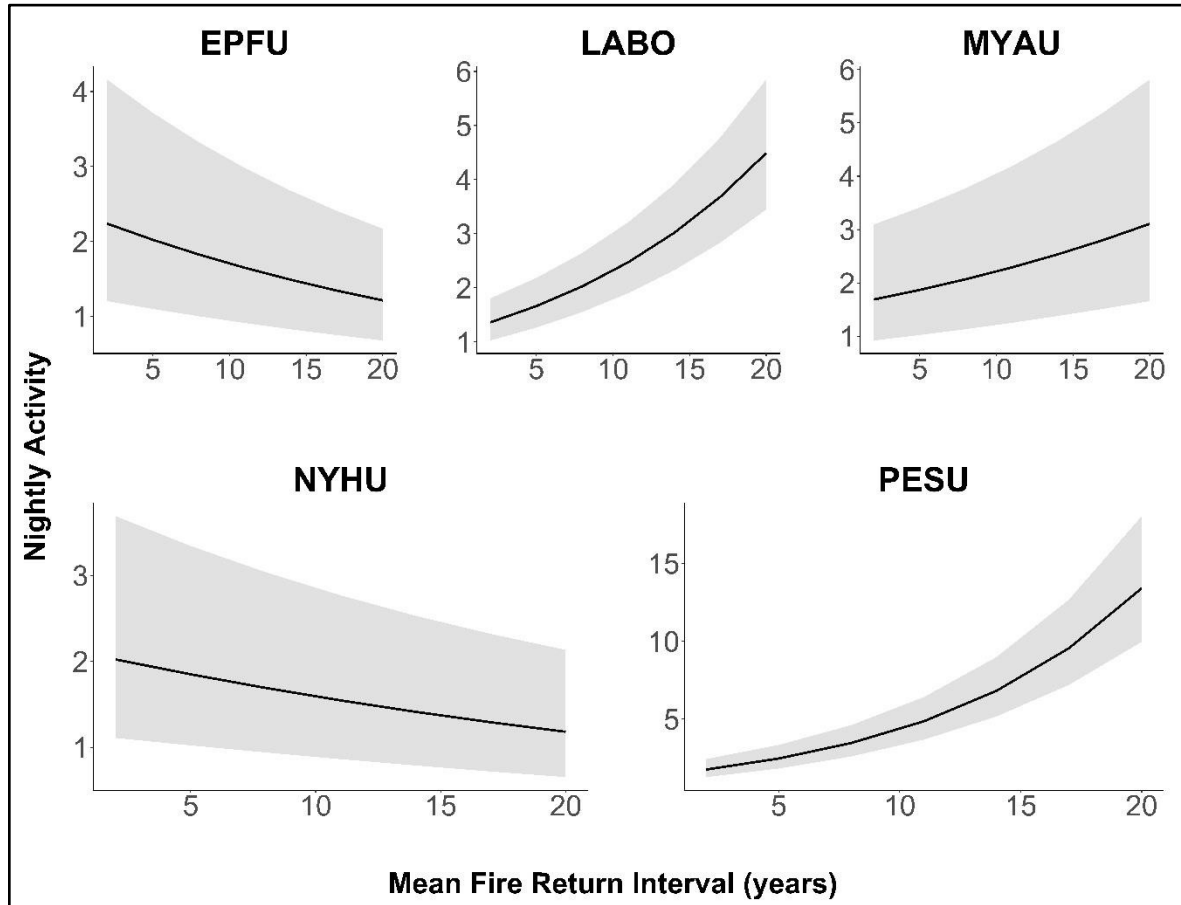


Figure 2.5. Predicted relative mean nightly activity, based on calls per site, given time since fire for seven bat species from acoustic surveys conducted 26 February - 03 April 2019, and from 10 December 2019 - 14 January 2020 at 34 plots on Camp Blanding Joint Military Center, Clay County, Florida. Grey shading denotes 95% confidence intervals. DAIN = northern yellow bat (*Dasypterus intermedius*), LACI= hoary bat (*Lasiurus cinereus*), LASE= Seminole bat (*Lasiurus seminolus*), MYAU= southeastern myotis (*Myotis austroriparius*), NYHU= evening bat (*Nycticeius humeralis*), PESU= tri-colored bat (*Perimyotis subflavus*), and TABR= Brazilian free-tailed bat (*Tadarida brasiliensis*).

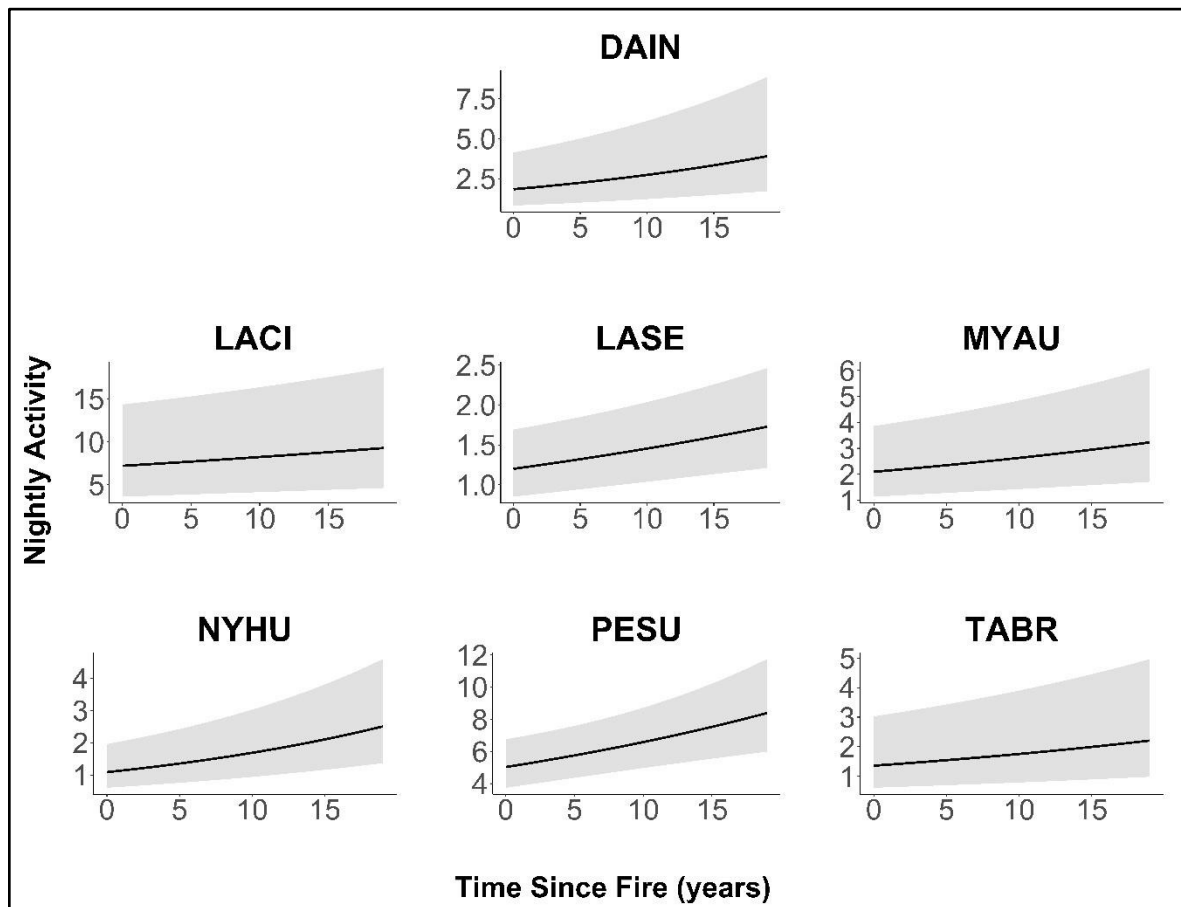


Figure 2.6. Predicted relative mean nightly activity, based on calls per site, given survey period, late dormant and spring season (Feb-April) versus early dormant season (Dec-Jan), for six bat species from acoustic surveys conducted 26 February - 03 April 2019, and from 10 December 2019 - 14 January 2020 at 34 plots on Camp Blanding Joint Military Center, Clay County, Florida. Error bar denotes 95% confidence intervals. DAIN = northern yellow bat (*Dasypterus intermedius*), EPFU = big brown bat (*Eptesicus fuscus*), LACI= hoary bat (*Lasiurus cinereus*), MYAU= southeastern myotis (*Myotis austroriparius*), NYHU= evening bat (*Nycticeius humeralis*), and TABR= Brazilian free-tailed bat (*Tadarida brasiliensis*).

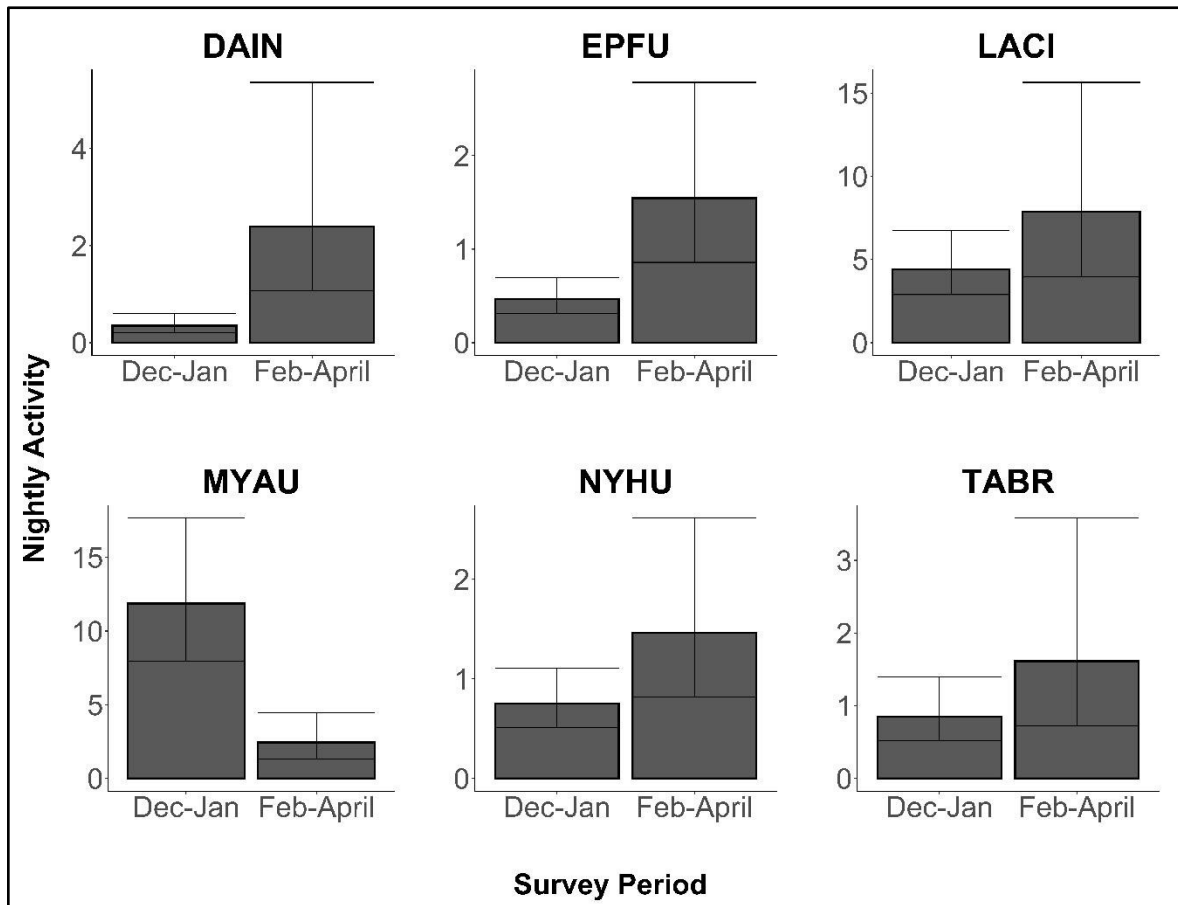
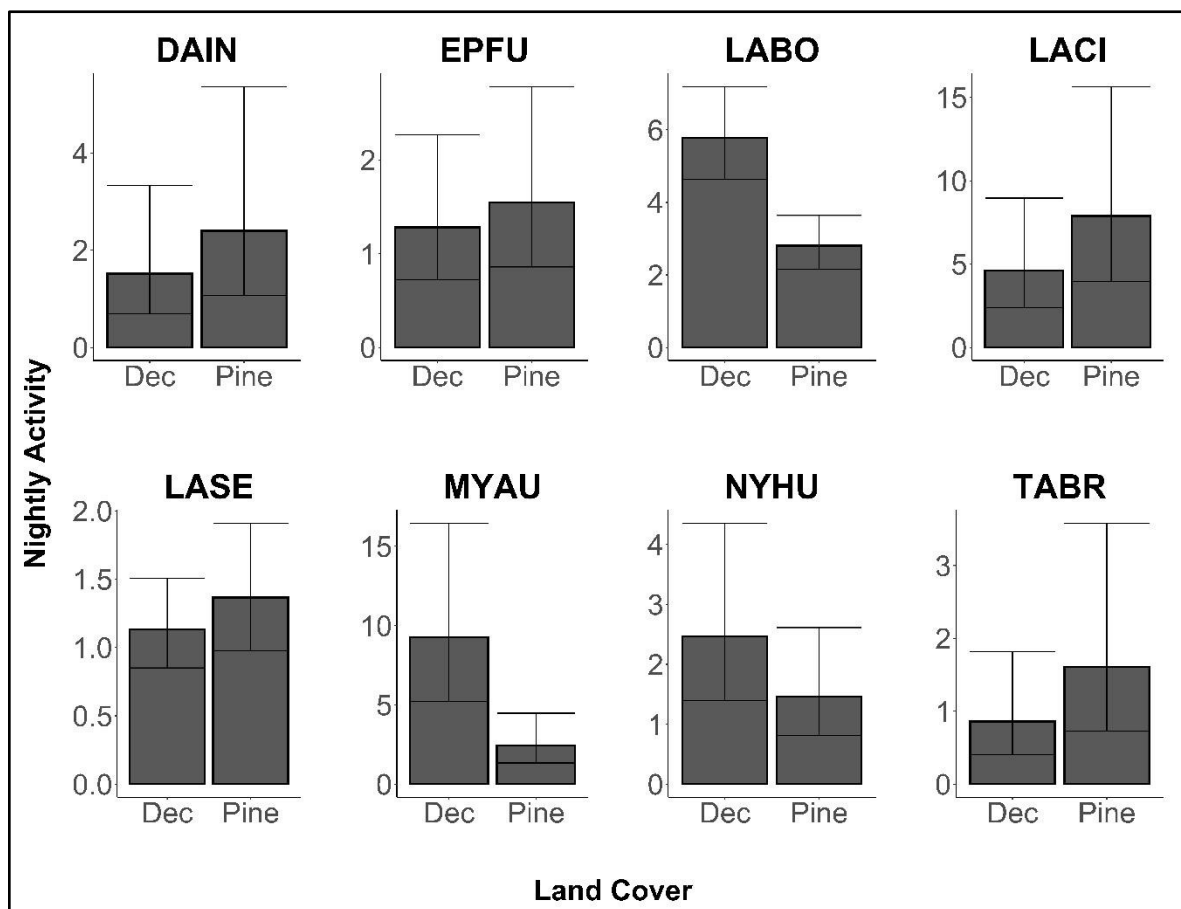


Figure 2.7. Predicted relative nightly activity, based on calls per site, given land cover for eight bat species from acoustic surveys conducted 26 February - 03 April 2019, and from 10 December 2019 - 14 January 2020 at 34 plots on Camp Blanding Joint Military Center, Clay County, Florida. Error bar denotes 95% confidence intervals. DAIN = northern yellow bat (*Dasypterus intermedius*), EPFU = big brown bat (*Eptesicus fuscus*), LASE= Seminole bat (*Lasiurus seminolus*), LABO = eastern red bat (*Lasiurus borealis*), LACI= hoary bat (*Lasiurus cinereus*), MYAU= southeastern myotis (*Myotis austroriparius*), NYHU= evening bat (*Nycticeius humeralis*), TABR= Brazilian free-tailed bat (*Tadarida brasiliensis*), Dec= Deciduous forest, Pine = pine forests.



2.10. Appendices

Appendix 1. Akaike Information Criterion (AIC) table from Generalized linear models for nine bat species from acoustic surveys conducted 26 February - 03 April 2019, and from 10 December 2019 - 14 January 2020 at 34 plots on Camp Blanding Joint Military Center, Clay County, Florida. DAIN = northern yellow bat (*Dasypterus intermedius*), EPFU = big brown bat (*Eptesicus fuscus*), LABO = eastern red bat (*Lasiurus borealis*), LACI= hoary bat (*Lasiurus cinereus*), LASE= Seminole bat (*Lasiurus seminolus*), MYAU= southeastern myotis (*Myotis austroriparius*), NYHU= evening bat (*Nycticeius humeralis*), PESU= tri-colored bat (*Perimyotis subflavus*), and TABR= Brazilian free-tailed bat (*Tadarida brasiliensis*), Mesic= distance to mesic land, Land= pine or deciduous land cover, Survey= survey period, Temp= temperature, TSF= time since fire, MFRI= mean fire return interval.

Species	Model	df	AIC _c	ΔAIC	AIC _{wT}
DAIN					
	Act ~ Mesic + Land + Survey + Temp + TSF + (1 sample)	9	8938.83	0.00	0.60
	Act ~ Mesic + Land + MFRI + Survey + Temp + TSF + (1 sample)	10	8939.64	0.82	0.40
	Act ~ Mesic + MFRI + Survey + Temp + TSF + (1 sample)	9	8949.65	10.82	0.00
	Act ~ Mesic + Land + MFRI + Survey + Temp + (1 sample)	9	8953.41	14.58	0.00
	Act ~ Mesic + Survey + Temp + TSF + (1 sample)	8	8953.92	15.09	0.00
	Act ~ Mesic + MFRI + Survey + Temp + (1 sample)	8	8962.04	23.21	0.00
	Act ~ Mesic + Land + Survey + Temp + (1 sample)	8	8968.92	30.09	0.00
	Act ~ Mesic + Land + MFRI + Temp + TSF + (1 sample)	9	8970.17	31.34	0.00
	Act ~ Mesic + Land + Temp + TSF + (1 sample)	8	8971.78	32.95	0.00
	Act ~ Land + MFRI + Survey + Temp + TSF + (1 sample)	9	8978.61	39.78	0.00
	Act ~ Mesic + MFRI + Temp + TSF + (1 sample)	8	8980.06	41.23	0.00
	Act ~ Land + Survey + Temp + TSF + (1 sample)	8	8980.86	42.03	0.00
	Act ~ MFRI + Survey + Temp + TSF + (1 sample)	8	8981.16	42.33	0.00
	Act ~ Mesic + Land + MFRI + Temp + (1 sample)	8	8981.84	43.01	0.00
	Act ~ Mesic + Temp + TSF + (1 sample)	7	8983.46	44.63	0.00
	Act ~ Survey + Temp + TSF + (1 sample)	7	8990.34	51.51	0.00
	Act ~ Mesic + MFRI + Temp + (1 sample)	7	8990.56	51.73	0.00

Act ~ Land + MFRI + Survey + Temp + (1 sample)	8	8990.64	51.81	0.00
Act ~ MFRI + Survey + Temp + (1 sample)	7	8993.72	54.89	0.00
Act ~ Mesic + Land + Temp + (1 sample)	7	8997.24	58.41	0.00
Act ~ Mesic + Survey + Temp + (1 sample)	7	9005.84	67.01	0.00
Act ~ Land + MFRI + Temp + TSF + (1 sample)	8	9010.30	71.47	0.00
Act ~ MFRI + Temp + TSF + (1 sample)	7	9015.64	76.81	0.00
Act ~ Land + MFRI + Temp + (1 sample)	7	9018.82	79.99	0.00
Act ~ Mesic + Land + Survey + TSF + (1 sample)	8	9019.58	80.75	0.00

EPFU

Act ~ Mesic + Land + MFRI + Survey + Temp + (1 sample)	9	7904.67	0.00	0.52
Act ~ Mesic + Land + MFRI + Survey + Temp + TSF + (1 sample)	10	7906.34	1.68	0.22
Act ~ Mesic + MFRI + Survey + Temp + (1 sample)	8	7906.72	2.05	0.19
Act ~ Mesic + MFRI + Survey + Temp + TSF + (1 sample)	9	7908.47	3.80	0.08
Act ~ Mesic + Survey + Temp + TSF + (1 sample)	8	7919.98	15.31	0.00
Act ~ Mesic + Land + Survey + Temp + TSF + (1 sample)	9	7920.13	15.46	0.00
Act ~ Mesic + Land + MFRI + Temp + (1 sample)	8	7926.98	22.31	0.00
Act ~ Mesic + Land + MFRI + Temp + TSF + (1 sample)	9	7928.25	23.58	0.00
Act ~ Mesic + MFRI + Temp + (1 sample)	7	7928.72	24.05	0.00
Act ~ Mesic + MFRI + Temp + TSF + (1 sample)	8	7930.42	25.75	0.00
Act ~ Mesic + Survey + Temp + (1 sample)	7	7932.62	27.95	0.00
Act ~ Mesic + Land + Survey + Temp + (1 sample)	8	7934.64	29.97	0.00
Act ~ Mesic + Temp + TSF + (1 sample)	7	7943.58	38.91	0.00
Act ~ Mesic + Land + Temp + TSF + (1 sample)	8	7945.14	40.47	0.00
Act ~ Mesic + Temp + (1 sample)	6	7956.89	52.22	0.00
Act ~ Mesic + Land + Temp + (1 sample)	7	7958.90	54.23	0.00
Act ~ Mesic + Land + MFRI + Survey + (1 sample)	8	7980.92	76.25	0.00
Act ~ Mesic + Land + MFRI + Survey + TSF + (1 sample)	9	7982.55	77.88	0.00
Act ~ Mesic + MFRI + Survey + (1 sample)	7	7983.10	78.43	0.00

Act ~ MFRI + Survey + Temp + (1 sample)	7	7984.10	79.43	0.00
Act ~ Mesic + MFRI + Survey + TSF + (1 sample)	8	7984.84	80.17	0.00
Act ~ Land + MFRI + Survey + Temp + (1 sample)	8	7985.30	80.63	0.00
Act ~ MFRI + Survey + Temp + TSF + (1 sample)	8	7986.04	81.37	0.00
Act ~ Land + MFRI + Survey + Temp + TSF + (1 sample)	9	7987.23	82.56	0.00
Act ~ Survey + Temp + TSF + (1 sample)	7	7988.54	83.87	0.00

LABO

Act ~ Mesic + Land + MFRI + Temp + (1 sample)	8	12710.20	0.00	0.40
Act ~ Mesic + Land + MFRI + Temp + TSF + (1 sample)	9	12710.63	0.43	0.33
Act ~ Mesic + Land + MFRI + Survey + Temp + (1 sample)	9	12712.17	1.97	0.15
Act ~ Mesic + Land + MFRI + Survey + Temp + TSF + (1 sample)	10	12712.62	2.43	0.12
Act ~ Mesic + Land + MFRI + (1 sample)	7	12762.42	52.23	0.00
Act ~ Mesic + Land + MFRI + TSF + (1 sample)	8	12762.78	52.58	0.00
Act ~ Mesic + Land + MFRI + Survey + (1 sample)	8	12764.28	54.08	0.00
Act ~ Mesic + Land + MFRI + Survey + TSF + (1 sample)	9	12764.61	54.41	0.00
Act ~ Mesic + MFRI + Temp + TSF + (1 sample)	8	12804.78	94.58	0.00
Act ~ Mesic + MFRI + Survey + Temp + TSF + (1 sample)	9	12806.77	96.57	0.00
Act ~ Mesic + MFRI + Temp + (1 sample)	7	12814.38	104.19	0.00
Act ~ Mesic + MFRI + Survey + Temp + (1 sample)	8	12816.40	106.20	0.00
Act ~ Mesic + Land + Temp + TSF + (1 sample)	8	12855.34	145.14	0.00
Act ~ Mesic + MFRI + TSF + (1 sample)	7	12857.22	147.03	0.00
Act ~ Mesic + Land + Survey + Temp + TSF + (1 sample)	9	12857.29	147.09	0.00
Act ~ Mesic + MFRI + Survey + TSF + (1 sample)	8	12858.86	148.66	0.00
Act ~ Mesic + MFRI + (1 sample)	6	12866.97	156.78	0.00
Act ~ Mesic + MFRI + Survey + (1 sample)	7	12868.68	158.49	0.00
Act ~ Mesic + Land + TSF + (1 sample)	7	12900.92	190.73	0.00
Act ~ Mesic + Land + Survey + TSF + (1 sample)	8	12902.86	192.66	0.00
Act ~ Land + MFRI + Temp + TSF + (1 sample)	8	12909.38	199.18	0.00

Act ~ Land + MFRI + Survey + Temp + TSF + (1 sample)	9	12911.25	201.05	0.00
Act ~ Mesic + Land + Survey + Temp + (1 sample)	8	12913.00	202.80	0.00
Act ~ Mesic + Land + Temp + (1 sample)	7	12914.02	203.83	0.00
Act ~ Land + MFRI + Temp + (1 sample)	7	12921.02	210.83	0.00

LACI

Act ~ Mesic + Land + Survey + Temp + TSF + (1 sample)	9	15055.75	0.00	0.42
Act ~ Mesic + Land + MFRI + Survey + Temp + TSF + (1 sample)	10	15056.72	0.98	0.26
Act ~ Mesic + Land + Temp + TSF + (1 sample)	8	15058.12	2.37	0.13
Act ~ Mesic + Land + MFRI + Survey + Temp + (1 sample)	9	15058.21	2.46	0.12
Act ~ Mesic + Land + MFRI + Temp + (1 sample)	8	15061.02	5.27	0.03
Act ~ Mesic + Land + MFRI + Temp + TSF + (1 sample)	9	15061.75	6.00	0.02
Act ~ Mesic + Land + Survey + Temp + (1 sample)	8	15062.12	6.37	0.02
Act ~ Mesic + Land + Temp + (1 sample)	7	15064.22	8.47	0.01
Act ~ Mesic + MFRI + Survey + Temp + TSF + (1 sample)	9	15090.49	34.74	0.00
Act ~ Mesic + MFRI + Temp + TSF + (1 sample)	8	15092.42	36.67	0.00
Act ~ Mesic + MFRI + Survey + Temp + (1 sample)	8	15092.64	36.89	0.00
Act ~ Mesic + MFRI + Temp + (1 sample)	7	15095.00	39.25	0.00
Act ~ Mesic + Survey + Temp + TSF + (1 sample)	8	15096.92	41.17	0.00
Act ~ Mesic + Temp + TSF + (1 sample)	7	15099.52	43.77	0.00
Act ~ Mesic + Survey + Temp + (1 sample)	7	15113.72	57.97	0.00
Act ~ Mesic + Temp + (1 sample)	6	15117.13	61.38	0.00
Act ~ Land + MFRI + Survey + Temp + TSF + (1 sample)	9	15117.85	62.10	0.00
Act ~ Land + Survey + Temp + TSF + (1 sample)	8	15118.98	63.23	0.00
Act ~ Land + MFRI + Survey + Temp + (1 sample)	8	15119.74	63.99	0.00
Act ~ Land + MFRI + Temp + TSF + (1 sample)	8	15120.94	65.19	0.00
Act ~ Mesic + Land + MFRI + Survey + (1 sample)	8	15121.40	65.65	0.00
Act ~ Land + Temp + TSF + (1 sample)	7	15124.06	68.31	0.00
Act ~ Mesic + Land + Survey + TSF + (1 sample)	8	15125.66	69.91	0.00

Act ~ Mesic + Land + MFRI + Survey + TSF + (1 sample)	9	15126.87	71.12	0.00
Act ~ Mesic + Land + TSF + (1 sample)	7	15127.16	71.41	0.00

LASE

Act ~ Mesic + Land + Temp + TSF + (1 sample)	8	9731.18	0.00	0.34
Act ~ Mesic + Land + MFRI + Temp + TSF + (1 sample)	9	9732.59	1.41	0.17
Act ~ Mesic + Land + Survey + Temp + TSF + (1 sample)	9	9733.15	1.97	0.13
Act ~ Mesic + MFRI + Temp + TSF + (1 sample)	8	9734.00	2.82	0.08
Act ~ Mesic + Temp + TSF + (1 sample)	7	9734.00	2.83	0.08
Act ~ Mesic + Land + MFRI + Survey + Temp + TSF + (1 sample)	10	9734.58	3.41	0.06
Act ~ Mesic + Survey + Temp + TSF + (1 sample)	8	9735.36	4.18	0.04
Act ~ Mesic + MFRI + Survey + Temp + TSF + (1 sample)	9	9735.95	4.77	0.03
Act ~ Mesic + Land + MFRI + Temp + (1 sample)	8	9736.36	5.18	0.03
Act ~ Mesic + MFRI + Temp + (1 sample)	7	9737.50	6.33	0.02
Act ~ Mesic + Land + MFRI + Survey + Temp + (1 sample)	9	9738.37	7.19	0.01
Act ~ Mesic + MFRI + Survey + Temp + (1 sample)	8	9739.50	8.32	0.01
Act ~ Mesic + Land + Temp + (1 sample)	7	9745.58	14.41	0.00
Act ~ Mesic + Land + Survey + Temp + (1 sample)	8	9746.08	14.90	0.00
Act ~ Mesic + Temp + (1 sample)	6	9750.19	19.02	0.00
Act ~ Mesic + Survey + Temp + (1 sample)	7	9751.28	20.11	0.00
Act ~ Land + Temp + TSF + (1 sample)	7	9754.58	23.41	0.00
Act ~ Land + MFRI + Temp + TSF + (1 sample)	8	9756.54	25.36	0.00
Act ~ Land + Survey + Temp + TSF + (1 sample)	8	9756.58	25.40	0.00
Act ~ Land + MFRI + Survey + Temp + TSF + (1 sample)	9	9758.51	27.33	0.00
Act ~ Land + MFRI + Temp + (1 sample)	7	9763.34	32.17	0.00
Act ~ Land + Temp + (1 sample)	6	9763.43	32.26	0.00
Act ~ Temp + TSF + (1 sample)	6	9764.71	33.54	0.00
Act ~ Land + MFRI + Survey + Temp + (1 sample)	8	9765.36	34.18	0.00
Act ~ Land + Survey + Temp + (1 sample)	7	9765.38	34.21	0.00

MYAU

Act ~ Mesic + Land + MFRI + Survey + Temp + TSF + (1 sample)	10	15244.20	0.00	0.98
Act ~ Mesic + Land + MFRI + Survey + Temp + (1 sample)	9	15252.29	8.08	0.02
Act ~ Mesic + Land + Survey + Temp + TSF + (1 sample)	9	15265.77	21.56	0.00
Act ~ Mesic + Land + MFRI + Temp + TSF + (1 sample)	9	15277.99	33.78	0.00
Act ~ Mesic + Land + MFRI + Survey + TSF + (1 sample)	9	15280.25	36.04	0.00
Act ~ Mesic + Land + MFRI + Temp + (1 sample)	8	15284.36	40.15	0.00
Act ~ Mesic + Land + MFRI + Survey + (1 sample)	8	15287.38	43.17	0.00
Act ~ Mesic + Land + MFRI + TSF + (1 sample)	8	15298.08	53.87	0.00
Act ~ Mesic + Land + Temp + TSF + (1 sample)	8	15298.80	54.59	0.00
Act ~ Mesic + Land + Survey + TSF + (1 sample)	8	15301.40	57.19	0.00
Act ~ Mesic + Land + MFRI + (1 sample)	7	15304.34	60.14	0.00
Act ~ Mesic + Land + TSF + (1 sample)	7	15318.80	74.60	0.00
Act ~ Mesic + Land + Survey + Temp + (1 sample)	8	15329.32	85.11	0.00
Act ~ Mesic + Land + Temp + (1 sample)	7	15357.20	113.00	0.00
Act ~ Mesic + Land + Survey + (1 sample)	7	15361.36	117.16	0.00
Act ~ Land + MFRI + Survey + Temp + TSF + (1 sample)	9	15367.47	123.26	0.00
Act ~ Mesic + Land + (1 sample)	6	15376.25	132.05	0.00
Act ~ Land + MFRI + Survey + Temp + (1 sample)	8	15376.62	132.41	0.00
Act ~ Land + Survey + Temp + TSF + (1 sample)	8	15381.36	137.15	0.00
Act ~ Land + MFRI + Survey + TSF + (1 sample)	8	15401.42	157.21	0.00
Act ~ Land + MFRI + Temp + TSF + (1 sample)	8	15402.90	158.69	0.00
Act ~ Land + MFRI + Temp + (1 sample)	7	15409.98	165.78	0.00
Act ~ Land + MFRI + Survey + (1 sample)	7	15410.98	166.78	0.00
Act ~ Land + Survey + TSF + (1 sample)	7	15414.88	170.68	0.00
Act ~ Land + Temp + TSF + (1 sample)	7	15416.56	172.36	0.00

NY IU

Act ~ Mesic + Land + MFRI + Survey + Temp + TSF + (1 sample)	10	9342.44	0.00	0.95
Act ~ Mesic + Land + MFRI + Temp + TSF + (1 sample)	9	9348.51	6.06	0.05
Act ~ Mesic + Land + Survey + Temp + TSF + (1 sample)	9	9357.35	14.90	0.00
Act ~ Mesic + Land + Temp + TSF + (1 sample)	8	9364.00	21.55	0.00
Act ~ Land + MFRI + Survey + Temp + TSF + (1 sample)	9	9370.19	27.74	0.00
Act ~ Land + MFRI + Temp + TSF + (1 sample)	8	9375.82	33.37	0.00
Act ~ Mesic + Land + Survey + Temp + (1 sample)	8	9378.56	36.11	0.00
Act ~ Mesic + MFRI + Survey + Temp + TSF + (1 sample)	9	9379.67	37.22	0.00
Act ~ Mesic + Land + MFRI + Survey + Temp + (1 sample)	9	9380.29	37.84	0.00
Act ~ Mesic + Land + Temp + (1 sample)	7	9386.32	43.88	0.00
Act ~ Mesic + MFRI + Temp + TSF + (1 sample)	8	9387.58	45.13	0.00
Act ~ Mesic + Land + MFRI + Temp + (1 sample)	8	9388.02	45.57	0.00
Act ~ Land + Survey + Temp + TSF + (1 sample)	8	9394.14	51.69	0.00
Act ~ MFRI + Survey + Temp + TSF + (1 sample)	8	9395.80	53.35	0.00
Act ~ Land + Temp + TSF + (1 sample)	7	9400.42	57.98	0.00
Act ~ MFRI + Temp + TSF + (1 sample)	7	9403.20	60.76	0.00
Act ~ Mesic + Survey + Temp + TSF + (1 sample)	8	9404.06	61.61	0.00
Act ~ Land + Survey + Temp + (1 sample)	7	9409.42	66.98	0.00
Act ~ Land + MFRI + Survey + Temp + (1 sample)	8	9411.06	68.61	0.00
Act ~ Mesic + Survey + Temp + (1 sample)	7	9411.96	69.52	0.00
Act ~ Mesic + MFRI + Survey + Temp + (1 sample)	8	9412.20	69.75	0.00
Act ~ Mesic + Temp + TSF + (1 sample)	7	9412.92	70.48	0.00
Act ~ Land + Temp + (1 sample)	6	9416.73	74.29	0.00
Act ~ Land + MFRI + Temp + (1 sample)	7	9418.38	75.94	0.00
Act ~ Mesic + Temp + (1 sample)	6	9421.63	79.19	0.00

PE U

Act ~ Mesic + MFRI + Temp + TSF + (1 sample)	8	14490.72	0.00	0.79
Act ~ Mesic + Land + MFRI + Temp + TSF + (1 sample)	9	14494.31	3.59	0.13
Act ~ Mesic + Land + MFRI + Survey + Temp + TSF + (1 sample)	10	14496.16	5.45	0.05
Act ~ Mesic + MFRI + Survey + Temp + TSF + (1 sample)	9	14499.13	8.41	0.01
Act ~ Mesic + MFRI + Temp + (1 sample)	7	14499.76	9.05	0.01
Act ~ Mesic + MFRI + Survey + Temp + (1 sample)	8	14500.90	10.18	0.01
Act ~ Mesic + Land + MFRI + Temp + (1 sample)	8	14504.86	14.14	0.00
Act ~ Mesic + Land + MFRI + Survey + Temp + (1 sample)	9	14506.29	15.57	0.00
Act ~ Mesic + Land + MFRI + TSF + (1 sample)	8	14552.80	62.08	0.00
Act ~ Mesic + Land + MFRI + Survey + TSF + (1 sample)	9	14553.85	63.13	0.00
Act ~ Mesic + MFRI + TSF + (1 sample)	7	14554.44	63.73	0.00
Act ~ Mesic + MFRI + Survey + TSF + (1 sample)	8	14555.44	64.72	0.00
Act ~ Mesic + MFRI + (1 sample)	6	14562.05	71.34	0.00
Act ~ Mesic + MFRI + Survey + (1 sample)	7	14562.66	71.95	0.00
Act ~ Mesic + Land + MFRI + (1 sample)	7	14563.36	72.65	0.00
Act ~ Mesic + Land + MFRI + Survey + (1 sample)	8	14564.00	73.28	0.00
Act ~ Mesic + Land + Temp + TSF + (1 sample)	8	14680.68	189.96	0.00
Act ~ Mesic + Land + Survey + Temp + TSF + (1 sample)	9	14682.67	191.95	0.00
Act ~ Mesic + Survey + Temp + TSF + (1 sample)	8	14689.24	198.52	0.00
Act ~ Mesic + Temp + TSF + (1 sample)	7	14704.50	213.79	0.00
Act ~ Land + MFRI + Temp + TSF + (1 sample)	8	14744.38	253.66	0.00
Act ~ Land + MFRI + Survey + Temp + TSF + (1 sample)	9	14746.39	255.67	0.00
Act ~ Mesic + Land + Survey + TSF + (1 sample)	8	14754.24	263.52	0.00
Act ~ MFRI + Temp + TSF + (1 sample)	7	14754.62	263.91	0.00
Act ~ Mesic + TSF + (1 sample)	6	14754.91	264.20	0.00
TABLE				
Act ~ Mesic + Land + Survey + Temp + TSF + (1 sample)	9	8947.55	0.00	0.32
Act ~ Mesic + Land + MFRI + Temp + TSF + (1 sample)	9	8947.85	0.30	0.28

Act ~ Mesic + Land + MFRI + Survey + Temp + TSF + (1 sample)	10	8948.92	1.38	0.16
Act ~ Mesic + Land + MFRI + Survey + Temp + (1 sample)	9	8948.97	1.42	0.16
Act ~ Mesic + Land + MFRI + Temp + (1 sample)	8	8951.44	3.89	0.05
Act ~ Mesic + Land + Temp + TSF + (1 sample)	8	8952.28	4.73	0.03
Act ~ Mesic + Land + Survey + Temp + (1 sample)	8	8959.28	11.73	0.00
Act ~ Mesic + Land + Temp + (1 sample)	7	8963.46	15.91	0.00
Act ~ Mesic + MFRI + Temp + TSF + (1 sample)	8	8976.64	29.09	0.00
Act ~ Mesic + MFRI + Survey + Temp + (1 sample)	8	8977.90	30.35	0.00
Act ~ Mesic + MFRI + Temp + (1 sample)	7	8979.98	32.43	0.00
Act ~ Mesic + MFRI + Survey + Temp + TSF + (1 sample)	9	8980.99	33.44	0.00
Act ~ Mesic + Survey + Temp + TSF + (1 sample)	8	8982.50	34.95	0.00
Act ~ Mesic + Temp + TSF + (1 sample)	7	8984.46	36.91	0.00
Act ~ Mesic + Survey + Temp + (1 sample)	7	9004.22	56.67	0.00
Act ~ Mesic + Temp + (1 sample)	6	9012.65	65.10	0.00
Act ~ Land + MFRI + Survey + Temp + TSF + (1 sample)	9	9015.75	68.20	0.00
Act ~ Mesic + Land + MFRI + Survey + TSF + (1 sample)	9	9016.77	69.22	0.00
Act ~ Mesic + Land + TSF + (1 sample)	7	9017.48	69.93	0.00
Act ~ Mesic + Land + MFRI + TSF + (1 sample)	8	9018.20	70.65	0.00
Act ~ Land + MFRI + Temp + TSF + (1 sample)	8	9018.86	71.31	0.00
Act ~ Mesic + Land + Survey + TSF + (1 sample)	8	9019.28	71.73	0.00
Act ~ Land + Survey + Temp + TSF + (1 sample)	8	9019.36	71.81	0.00
Act ~ Land + MFRI + Survey + Temp + (1 sample)	8	9021.16	73.61	0.00
Act ~ MFRI + Survey + Temp + TSF + (1 sample)	8	9021.26	73.71	0.00
