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Fire, land cover, and temperature drivers of bat activity in winter

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Abstract

Background: 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 southeastern United States 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* Mill.) ecosystem is an archetypal fire-mediated ecosystem that 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 on Camp Blanding Joint Training Center (CB) in northern Florida, USA, we deployed 34 acoustic detectors across CB and recorded data from 26 February to 3 April 2019, and from 10 December 2019 to 14 January 2020.

Results: We identified eight bat species native to the region as present at CB. 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). Activity for all bat species was influenced positively by either time since fire or mean fire return interval.

Conclusion: Overall, our results suggested that 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 at CB during the dormant season and early spring.

Keywords: acoustic monitoring, bats, fire regime, Florida, longleaf pine ecosystem, mesic, *Pinus palustris*, southeastern United States

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Resumen

Antecedentes: Entender los efectos de eventos de disturbios, cobertura del suelo y tiempo meteorológico en la actividad de la fauna silvestre es fundamental para su manejo. Actualmente en Norte América, hay un alto grado de preocupación por la conservación de los murciélagos, debido al síndrome de la nariz blanca y el desarrollo de la energía de impacto, mientras que el rol del fuego como potencial estresante adicional ha recibido una menor atención. Aunque limitada, la gran mayoría de la investigación sobre murciélagos y fuegos en el sureste de los EEUU ha sido conducida durante la estación de crecimiento, creando en consecuencia faltantes en los datos de la región relacionados con su hibernación, particularmente para especies no hibernantes. Los ecosistemas de pino de hoja larga (*Pinus palustris* Mill.) son un arquetipo de ecosistemas mediados por el fuego que han sido enfocados para su restauración a nivel de paisaje en el Sudeste de EEUU. Aunque históricamente los fuegos han ocurrido en esos ecosistemas predominantemente en la estación de crecimiento, las quemas durante la estación de dormición han sido más ampliamente utilizadas por su más fácil aplicación y control como medio de manejo del hábitat en la región. Para determinar los impactos del fuego y factores ambientales en la actividad de murciélagos en el centro de entrenamiento Camp Blanding (CB) en el norte de Florida, EEUU, desplegamos 34 detectores acústicos a través del CB y registramos sus datos desde el 26 de febrero al 3 de abril de 2019, y desde el 10 de diciembre de 2019 al 14 de enero de 2020.

Resultados: Identificamos ocho especies de murciélagos nativos de la región presentes en CB. La actividad de los murciélagos estuvo relacionada con la proximidad de hábitats mésicos y también con la presencia de pinos o bosques deciduos, dependiendo de la morfología de las especies (*i.e.,* tamaño del cuerpo, envergadura de las alas, y la localización de la frecuencia del eco). La actividad para todas las especies de murciélagos estuvo influenciada positivamente tanto por el tiempo desde el último fuego o por el intervalo medio de retorno del fuego.

Conclusiones: De manera general, nuestros resultados sugieren que el uso del fuego provee un patrón de paisaje diverso en CB que mantiene un hábitat mésico y deciduo dentro de una matriz forestal de pinos, que apuntalan la diversa comunidad de murciélagos durante la estación de dormición y en la primavera temprana.

Background

Currently, in North America, bats are taxa of high conservation concern due to the deleterious impacts of white-nose syndrome on hibernating species and wind-energy development impacts on migratory species (Muthersbaugh et al. 2019; Nocera 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 tend 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 of research examining bat activity response to fire in the US Southeast has been conducted during the growing season (Ford et al. 2006; Loeb and Waldrop 2008; Perry 2012), or in upland ecosystems outside the Coastal Plain such as the Appalachians (Loeb and O'Keefe 2014; Cox et al. 2016; but see Hein et al. 2008 and Braun de Torrez et al. 2018). As such, considerable data gaps exist for both migratory and non-hibernating resident bat species in the portions of the Southeast where these species overwinter and also are often active during vegetative dormant season (Carter et al. 2002).

Pine flatwood forests found in northern Florida, USA, are typically dominated by longleaf (*Pinus palustris* Mill.) and slash pine (*Pinus elliottii* Engelm.) in the canopy, with saw palmetto (*Serenoa repens* J.K. Small) in much of the understory. Interspersed within are warm-temperate to subtropical mixed pine–hardwoods and bottomland hardwoods on side slopes and riparian zones, respectively (Florida Department of Transportation 1999; Armitage and Ober 2012). 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 or as a more than century-long legacy of species management for bobwhite quail (*Colinus virginianus* Linnaeus) and other game (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, farther from mesic vegetation types. We also predicted that bat activity would decrease as TSF and MFRI increased due to more clutter in the environment, thereby providing less 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 1997), and that temperatures and assumed prey availability would be stronger indicators of bat activity than vegetation clutter alone.

Methods

Study site

We conducted our study at Camp Blanding Joint Training Center and Wildlife Management Area (CB), Clay County, in northeastern Florida, USA (Fig. 1). The installation is 22 700 ha in size with an elevation range of 15 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 three- to five-year rotation, dependent on forest stand composition, and occurred throughout CB during our dormant-season survey effort. Considerable heterogeneity in site productivity exists on CB, which is at the ecotone of more fertile Sea Island Flatwoods ecoregion to the north and the productive Central Florida Ridges and Uplands ecoregion that encompasses the southern extent of the base (Omernik and Griffith 2014). Locally, major forest types include 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).

Field methods

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 ZC; Wildlife Acoustics, Inc., Maynard, Massachusetts, USA; Fig. 1) across CB. We attached microphones directly to the detectors, which were attached with bungee cords to trees at a height of 3 m above the ground. Detectors recorded one hour prior to sunset until one hour after sunrise. The detector settings were as follows: division ratio = 8, minimum duration = 1.5 ms, maximum duration = 200 ms, minimum trigger frequency = 16 kHz, trigger window = 3 s, and maximum trigger time = 15 s. We continuously deployed individual detectors using a series of pre-established 3 km^2 grids, prioritizing locations on trails, forest roads, or near water bodies to increase bat detection probabilities (Humes et al. 1999; Erickson and West 2003; Brooks and Ford 2005; Ford et al. 2005). 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 3 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 Version 5.1.9 Classifier Version 4.2.0 (Wildlife Acoustics, Inc.) using the neutral sensitivity settings for species identification, accepting only echolocation call files with >2 pulses, and using default signal parameters for the bat species known or suspected to occur in the study area (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 vegetation land cover data from the CB historical fire data since 2001 and the installation's spatially explicit GIS layers. We also collected

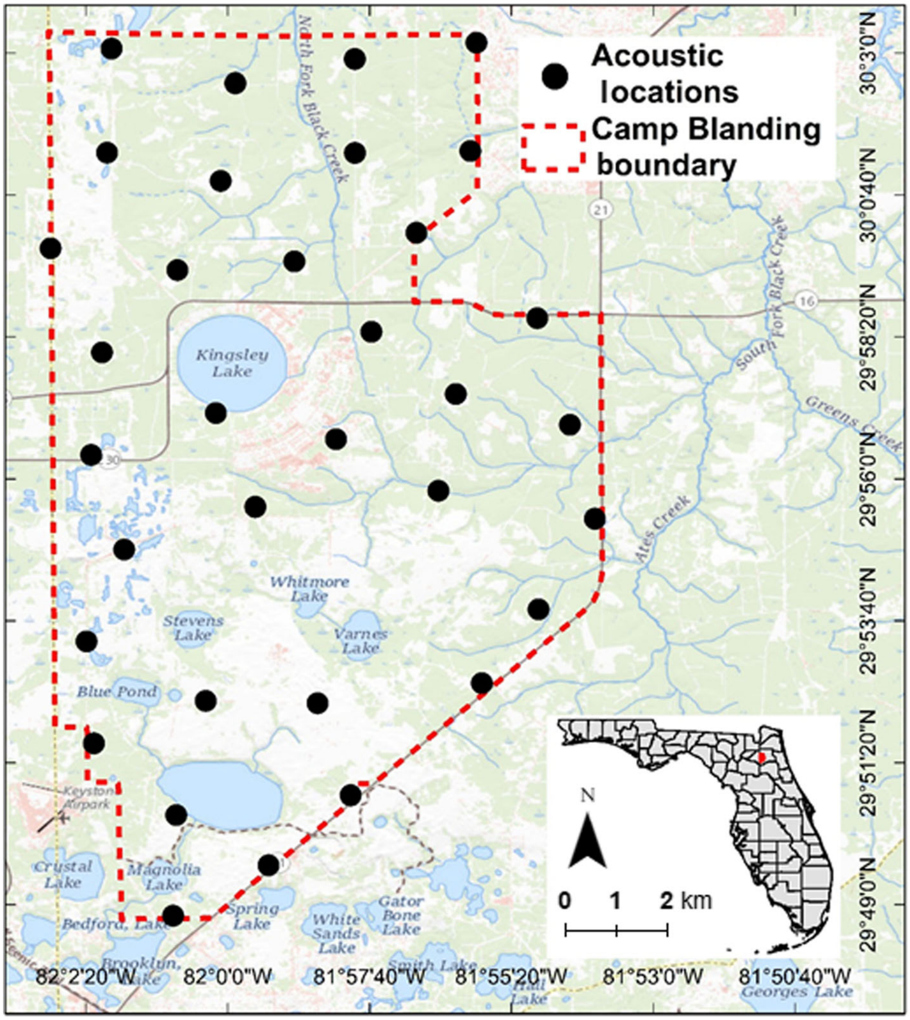

Fig. 1 Camp Blanding Joint Training Center, Clay County, Florida, USA, showing the 34 locations used in our acoustic detector bat activity survey conducted from 26 February to 03 April 2019 and 10 December 2019 to 14 January 2020

nightly Meteorological Terminal Aviation Routine Weather Report temperature data averaged from the Keystone Heights and Jacksonville weather stations (https://mesonet.agron.iastate.edu/request/download.phtml?network=FL_ASOS). We created spatially explicit fire covariates that represented different fire and land cover 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 represented the historical repeated use of fire at our survey sites since 2001. The distinction between these fire covariates allows for a nuanced examination of how fire history attributes may be influencing bat activity rather than assuming that the response to fire history is uniform across its attributes. We calculated distance to land cover values using Euclidean distance for forest stands or other vegetative communities that are considered mesic, using ArcMap10.3 Spatial Analyst Tools. These communities included those with laurel oak (*Quercus laurifolia* Michx.), water oak (*Quercus nigra* L.), and willow oak (*Quercus phellos* L.), other temporarily flooded forest alliances, or those that were considered wetland or seasonally or permanently flooded. This Euclidean distance function created distance-raster layers in which 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 to 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, as activity can vary within and among species between the beginning and end of the dormant season (Muthersbaugh et al. 2019). Because the periods occurred during two different dormant seasons, sample period can therefore be interpreted as both as a year effect or a seasonal effect.

Statistical analysis

To estimate the effects of fire and site environmental conditions on nightly bat species activity by detector site 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 `GLMMAMDB` package (Skaug et al. 2006) using R programming language. We created a series of exploratory models (64) of all possible combinations of environmental and weather variables along with a null model for each species at CB with a random effect of day (Additional file 1). 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, 2021). We then used Akaike information criterion corrected for small sample size (AIC_C; Burnham and Anderson 2002) to compare AIC_C scores and model weights to determine the top model from the GLMMs. We had sufficient data to model the activity of all bats at CB with the exception of Rafinesque's big-eared bat (*Corynorhinus rafinesquii* Lesson), a species with a low amplitude call that is not easily recorded even when known to be present (Clement and Castleberry 2011).

Results

We recorded 114 261 and 142 072 bat echolocation call files for the February to April 2019 and December 2019 to January 2020 survey periods, respectively, for a total of 256 333 calls at CB. We detected nine bat species: Rafinesque's big-eared bat, northern yellow bat (*Dasypterus intermedius* H. Allen), big brown bat (*Eptesicus fuscus* Beauvois), eastern red bat (*Lasiurus borealis* Müller), hoary bat (*Lasiurus cinereus* Beauvois), Seminole bat (*Lasiurus seminolus* Rhoads), southeastern myotis (*Myotis austroriparius* Rhoads), evening bat (*Nycticeius humeralis* Rafinesque), tri-colored bat (*Perimyotis subflavus* F. Cuvier), and the Brazilian free-tailed bat (*Tadarida brasiliensis* I. Geoffroy). The most-detected species was the tri-colored bat (n = 75 707 calls), and the least-detected species was Rafinesque's big-eared bat (n = 11).

Northern yellow bat activity increased with distance to mesic habitat, higher temperatures, and increasing TSF. Northern yellow bat activity was also greater in pine forest types and during the late dormant to spring survey period than in deciduous types, and during the early dormant season (Table 1, Figs. 2, 3, 4, 5, 6 and 7). Big brown bat activity increased with increased distance to mesic habitat and higher temperatures but decreased with increasing MFRI. Big brown bat activity was also greater in pine forest types and during the late dormant to spring season survey period than in deciduous types and during early dormant season survey (Table 1, Figs. 2, 3, 4, 5, 6 and 7). Eastern red bat activity was higher with increasing MFRI and higher temperatures, but decreased with increasing distance to mesic habitat. Eastern red bat activity was greater in deciduous forest types than in pine types (Table 1, Figs. 2, 3, 4, 5, 6 and 7). Hoary bat activity increased with increasing distance to mesic habitat, higher temperatures, and increasing TSF. Hoary bat activity was also greater in pine forest types and during the late dormant to spring period than in deciduous types or during the early dormant season (Table 1, Figs. 2, 3, 4, 5, 6 and 7). Seminole bat activity increased with higher temperatures and increasing TSF, but decreased with increasing distance to mesic habitat. Seminole bat activity was also greater in pine forest types than in deciduous types (Table 1, Figs. 2, 3, 4, 5, 6 and 7). Southeastern myotis activity increased with increasing MFRI, higher temperatures, and increasing TSF, but decreased 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 1, Figs. 2, 3, 4, 5, 6 and 7). Evening bat activity increased with higher temperatures and greater TSF, but decreased 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 1, Figs. 2, 3, 4, 5, 6 and 7). Tri-colored bats activity increased with increasing MFRI, higher temperatures, and increasing TSF, but decreased with distance to mesic habitat (Table 1, Figs. 2, 3, 4, 5, 6 and 7). Brazilian free-tailed bat activity increased with increasing distance to mesic habitat, higher temperatures, and increasing 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 1, Figs. 2, 3, 4, 5, 6 and 7).

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 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

Table 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 3 April 2019 and 10 December 2019 to 14 January 2020 at 34 acoustic-survey points on Camp Blanding Joint training Center, Clay County, Florida, USA. A plus sign (+) denotes an increase in activity with increases in the associated factors, whereas a negative sign (−) denotes a significant decrease. The name of the land cover or survey period denotes a significant increase compared to the alternative name (Pine versus Deciduous or late dormant and spring season [Feb−April] versus early dormant season [Dec−Jan]). Mesic habitat effect directions are opposite to parameter estimate because it is distance metric *NA*= not applicable when the variable was not included in parameter estimates of the top model for that species, *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
	NYHU	+	−0.19	0.04	<0.001
	PESU	+	−0.81	0.04	<0.001
	TABR	−	0.35	0.04	<0.001
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
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

Table 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 3 April 2019 and 10 December 2019 to 14 January 2020 at 34 acoustic-survey points on Camp Blanding Joint training Center, Clay County, Florida, USA. A plus sign (+) denotes an increase in activity with increases in the associated factors, whereas a negative sign (–) denotes a significant decrease. The name of the land cover or survey period denotes a significant increase compared to the alternative name (Pine versus Deciduous or late dormant and spring season [Feb–April] versus early dormant season [Dec–Jan]). Mesic habitat effect directions are opposite to parameter estimate because it is distance metric *NA*= not applicable when the variable was not included in parameter estimates of the top model for that species, *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*) *(Continued)*

Variable	Species	Effect direction	Parameter estimate	Standard error	*P*-value
	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
Land cover					
	DAIN	Pine	0.46	0.12	<0.001
	EPFU	Pine	0.19	0.09	0.044
	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	0.10	<0.001
Survey period					
	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

our correct classification of this species from acoustics (Jorge et al. 2021). Dormant-season bat activity response at CB varied across the suite of environmental measurements and among bat species.

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. Consistent with findings during the growing season in the Coastal Plain in other studies, the activity of several species was related to the distance to mesic habitats as well as forest type, (*i.e.*, pine or deciduous depending on body size and characteristic echolocation frequency; Menzel et al. 2002; Menzel et al. 2005a; Menzel et al. 2005b; Ford et al. 2006). 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 farther away from mesic habitats. The arthropod prey for bats will aggregate near mesic habitat during dry seasons in tropical forests (Janzen 1973), and this 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

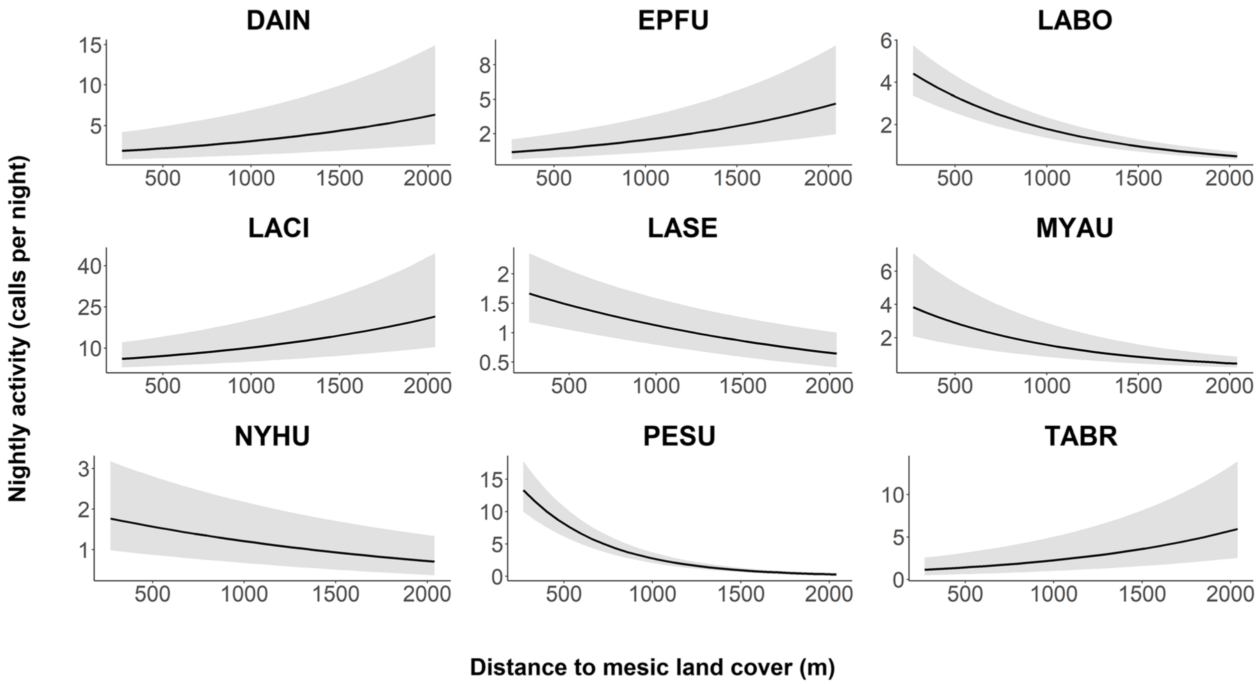

Fig. 2 Predicted relative mean nightly activity, based on calls per site, given distance to mesic land cover for nine bat species from acoustic surveys conducted 26 February to 3 April 2019, and from 10 December 2019 to 14 January 2020 at 34 plots on Camp Blanding Joint Military Center, Clay County, Florida, USA. Gray 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*)

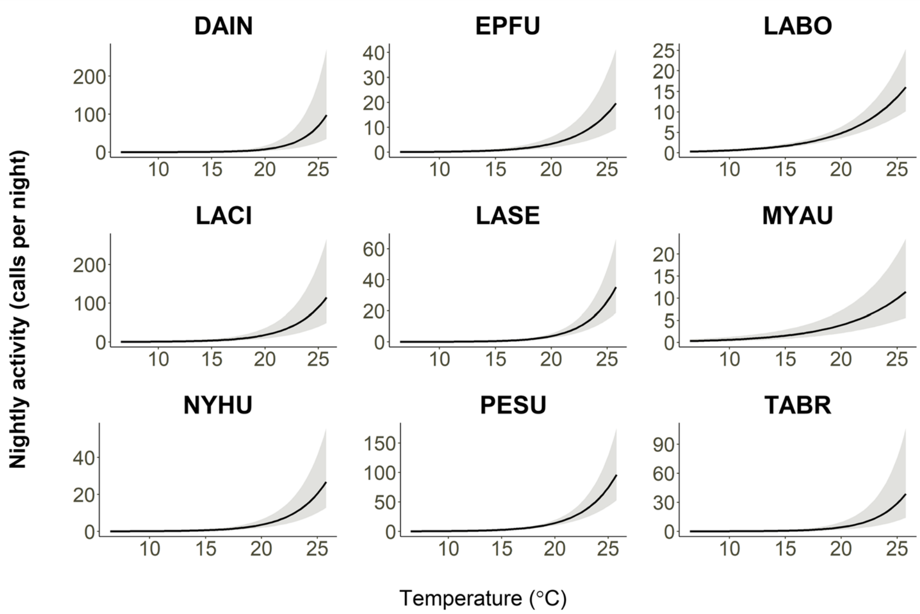

Fig. 3 Predicted relative mean nightly activity, based on calls per site, across temperature range for nine bat species from acoustic surveys conducted 26 February to 3 April 2019, and from 10 December 2019 to 14 January 2020 at 34 plots on Camp Blanding Joint Military Center, Clay County, Florida, USA. Gray 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*)

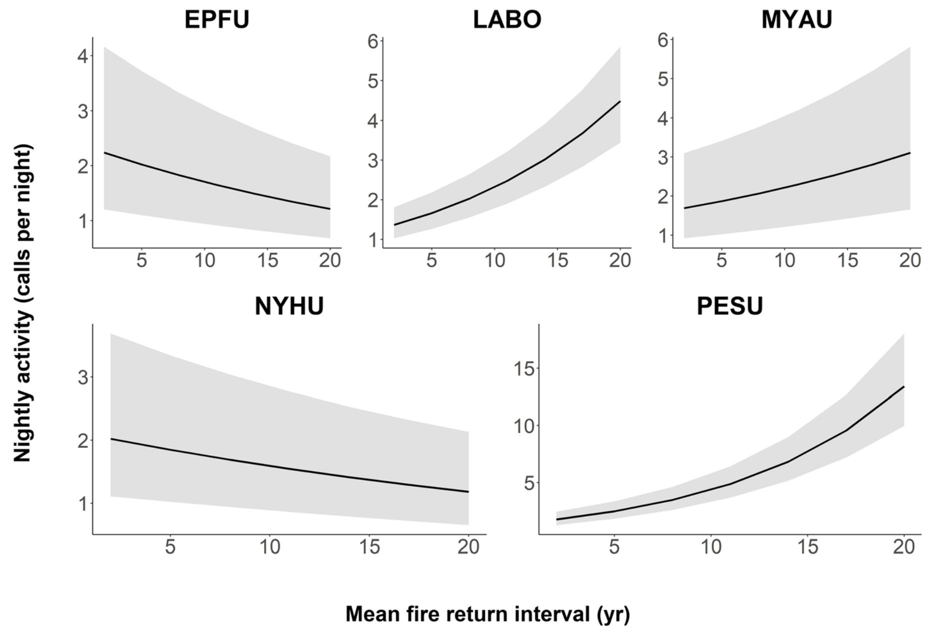

Fig. 4 Predicted relative mean nightly activity, based on calls per site, given mean fire return interval for five bat species from acoustic surveys conducted 26 February to 3 April 2019, and from 10 December 2019 to 14 January 2020 at 34 plots on Camp Blanding Joint Military Center, Clay County, Florida, USA. Gray 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*)

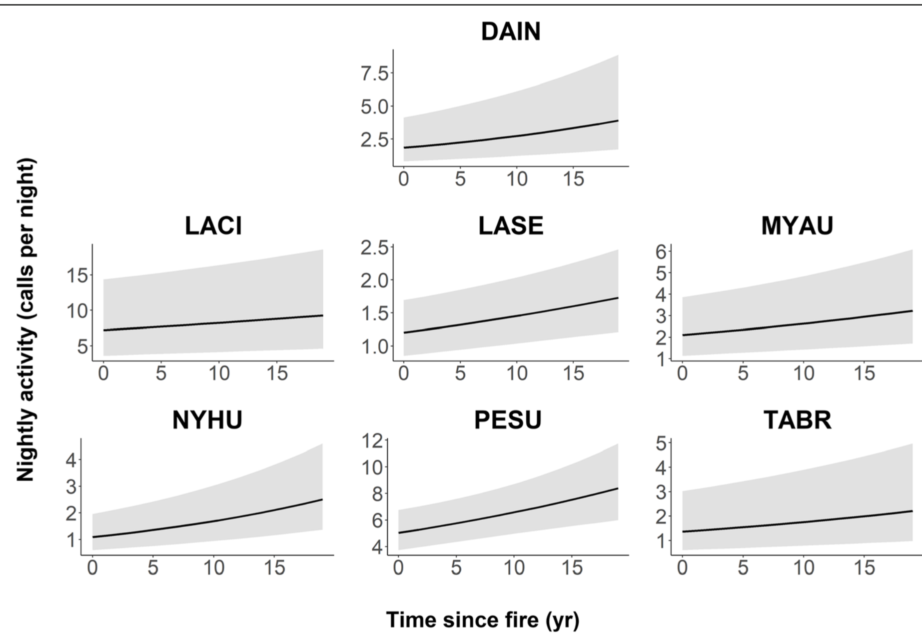

Fig. 5 Predicted relative mean nightly activity, based on calls per site, given time since fire for seven bat species from acoustic surveys conducted 26 February to 3 April 2019, and from 10 December 2019 to 14 January 2020 at 34 plots on Camp Blanding Joint Military Center, Clay County, Florida, USA. Gray 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*)

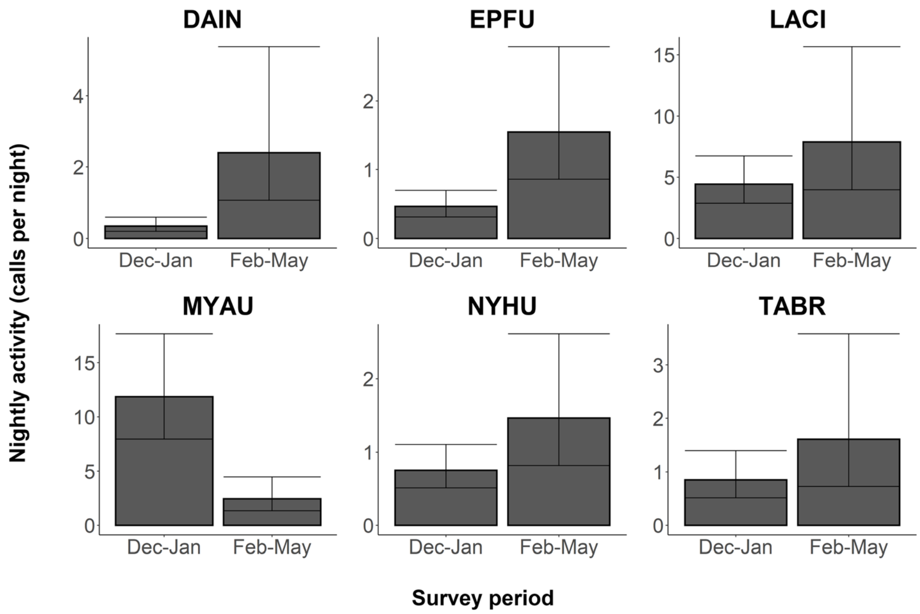

Fig. 6 Predicted relative mean nightly activity, based on calls per site from acoustic surveys, given survey period, late dormant and spring season (Feb-April; 26 February to 3 April 2019) versus early dormant season (Dec-Jan; 10 December 2019 to 14 January 2020), for six bat species at 34 plots on Camp Blanding Joint Military Center, Clay County, Florida, USA. Box plot height represents mean nightly activity; whisker represents the 95% credible interval above and below the mean value. 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*)

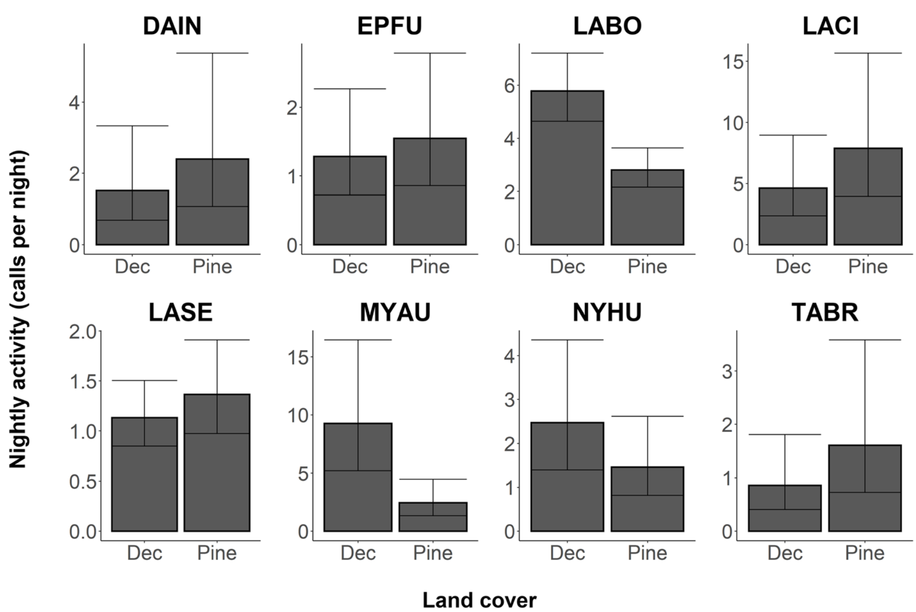

Fig. 7 Predicted relative mean nightly activity, based on calls per site from acoustic surveys, given land cover, late dormant and spring season (26 February to 3 April 2019) and early dormant season (10 December 2019 to 14 January 2020), for eight bat species at 34 plots on Camp Blanding Joint Military Center, Clay County, Florida, USA. Box plot height represents mean nightly activity; whisker represents the 95% credible interval above and below the mean value. 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

positive driver of bat activity (Ford et al. 2005; Ford et al. 2006), especially in more xeric environments (Szewczak et al. 1998; Adams and Simmons 2002).

Previous research documented 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 less correlated with proximity to mesic habitats in our study tended to be the larger-bodied, higher wing-loaded bats with lower echolocation frequencies that are less adapted to foraging in cluttered mesic environments with tardily deciduous (Oefinger and Halls 1974) or evergreen trees or with greater forest stand stem densities as compared to many of the surrounding pine savannas (Norberg and Rayner 1987; Patriquin and Barclay 2003; Menzel et al. 2005a; Armitage and Ober 2012). Similarly, land cover preference mirrored 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 bats, 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 at the edges of mesic habitats with pines stands, as similarly noted from previous research during the growing season in the Coastal Plain (Menzel et al. 2005a). That said, foraging ecology is flexible for most bat species and overall activity is often higher along ecotones and edges in the Southeast within the mesic bottomland hardwood canopy gaps and between bottomland hardwoods and xeric upland pines (Menzel et al. 2002). Fire-induced edges between burned and unburned stands show the same pattern in the central Appalachian Mountains, USA (Austin et al. 2019).

The impact of prescribed fire on bats has been of considerable interest for ecologists and managers in the Southeast (Carter et al. 2002; 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 affected by prescribed fire (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 that bats have evolved in conjunction with growing-season rather than dormant-season burning in the Coastal Plain (Carter et al. 2002; Perry 2012). Dormant-season activity of several species in our study was influenced positively by longer TSF or MFRI, yet was also linked to conditions that ultimately are maintained by fire, thereby implying that fire as a habitat management tool needs to be considered from both a temporal and spatial perspective. This would be the case particularly for big brown bats and evening bats that decreased their activity in forest stands with increasing MFRI. Boyles and Aubrey (2006) found immediate 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). Although speculative, warmer cavity roosts would seemingly benefit both big brown bats and evening bats at CB during the dormant season, facilitating arousal from torpor prior to foraging, which requires less energy. Nonetheless, using evening bats at CB as an example, fire effects are nuanced in that the species benefited from longer MFRI but shorter TSF. Immediately post fire, when 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, by 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 the area still remains relatively uncluttered compared to unburned stands. Nonetheless, in the long growing seasons at CB, this optimal condition for bats is transitory as TSF is correlated with increased clutter, thereby necessitating repeated burning.

Although the area is subtropical with mild winters, colder weather with sub-freezing to freezing temperatures does occur on average 10 to 20 days per year in northern Florida. Accordingly, for both of 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 to subtropical (Grider et al. 2016) and cool-temperate environments (Muthersbaugh et al. 2019). 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 period versus during the early-dormant period. Given our study design, the survey period could be interpreted as an early to late dormant season or yearly effect as our survey spanned across both sub-seasons. However, we suggest that the response was 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 in passage 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 hollow bald cypress (*Taxiodium distichum* Rich.) or swamp tupelo (*Nyssa aquatica* Walter), in which this species day-roosts year-round (Clement and Castleberry 2013), or in caves to the west of Camp Blanding used for their longer winter torpor bouts (Rice 1957).

Conclusions

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 a diverse bat community is an important conservation consideration. Although fire is crucial aspect of longleaf pine ecology at CB and throughout the Southeast, very short fire return intervals that create a homogenous pattern over larger landscapes may be less beneficial for the area's whole bat community. 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, better suit the habitat needs of bats. This is particularly true where mesic, deciduous forest types are less abundant within the context of large pine-dominated landscapes with frequent fire. Therefore, maintaining diverse land cover through mosaic burning in time and space would benefit the bat community by providing for the needs of both large- and small-bodied bats as well as other taxa within the longleaf pine ecosystem (Lashley et al. 2015; 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 specifically within fire-dominated landscapes.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-021-00105-4.

Additional file 1. Akaike Information Criterion (AIC) table for the top 25 models based on AIC_C values from generalized linear models for nine bat species from acoustic surveys conducted 26 February to 3 April 2019, and from 10 December 2019 to 14 January 2020, at 34 plots on Camp Blanding Joint Military Center, Clay County, Florida, USA. 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, date = random effect of each survey day, df = model degrees of freedom, LogLik = negative log likelihood of model, AICc = Akaike Information Criteria corrected for small sample, Delta AIC = difference in Akaike Information Criteria value from best supported model, and Weight = the probability that a given model is the best approximating model.

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Authors' contributions

WMF and MJC devised the study and obtained funding. MHJ, SES, MCT, SRF, EPG, HT, KMG, and WMF performed fieldwork and data collection. MHJ, WMF, and SRF analyzed data. MHJ led manuscript preparation and WMF, MJC, MCT, HT, KMG, and EPG provided editorial assistance. All authors read and approved the final manuscript.

Availability of data and materials

Available from the corresponding author upon request.

Declarations

Ethics approval and consent to participate

Not applicable as no live vertebrates were handled for this research.

Consent for publication

Not applicable.

Competing interests

We declare no competing interests.

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