



Research Article

Activity of an Endangered Bat Increases Immediately Following Prescribed Fire

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ABSTRACT Spatiotemporal responses of bats to fire are not well understood. Fire can indirectly influence bat activity through changes to understory vegetation, insect prey availability, and roost tree abundance. High-flying bats may be less influenced by fire-induced changes to the understory because they forage above the forest canopy. Fire-dependent forests are prevalent across the range of the endemic Florida bonneted bat (*Eumops floridanus*), a large, high-flying, and critically endangered species, yet effects of fire management on this species are completely unknown. To investigate short-term responses of these bats to fire, we conducted pre-post-treatment-control experiments in 4 prescribed burns during 2 seasons (dry, wet). For 12 nights pre-burn and 24 nights post-burn, we surveyed bat activity acoustically at 3 sites within each burn (treatment) and 3 adjacent sites (control). Using mixed-effects models to test the effect of treatment on bat activity, we found that bat activity significantly increased post-burn in treatment sites relative to control sites, with more pronounced effects during dry season burns. We also detected significantly more feeding buzzes (foraging activity) in treatment sites than control sites, and a negative trend over time in the burn effect size post-burn. We suggest that bats are attracted to increased availability of insect prey immediately following burns, particularly during the dry season when prey may be limited. Our results suggest that burns have short-term positive effects on Florida bonneted bats and that restoring fire to fire-dependent forests may improve foraging habitat for this species. © 2018 The Wildlife Society.

KEY WORDS acoustic surveys, endangered species, fire seasonality, flight activity, Florida bonneted bats (*Eumops floridanus*), foraging ecology, pine flatwoods, prescribed burning, South Florida.

Fire has shaped global biome distributions and maintained the structure and function of ecosystems for millions of years (Bond and Keeley 2005). Anthropogenic fire suppression has created ecological and economic dilemmas, reducing biodiversity in regions that naturally experience frequent fire, and prompting catastrophic wildfires from an accumulation of fuels (Gilliam and Platt 1999, Nowacki and Abrams 2008). To restore and maintain ecosystem health, prescribed burning programs have been implemented as a management strategy to mimic natural fire regimes. The goal of most burn programs has been to reduce fuel loads, lessen the risks of wildfire, and ensure maintenance of native flora and fauna dependent upon fire (Dellasala et al. 2004, Duncan et al. 2015). Frequent burning of vegetation limits tree and shrub densities, allowing growth of grasses and herbaceous plants in the understory (Peterson and Reich 2001). It also promotes forest regeneration, enhances nutrient cycling, and maintains fire-dependent plant species (Bond and Keeley 2005). In turn, these structural and compositional changes to

vegetation can influence habitat quality for vertebrate and invertebrate communities (Engstrom 2010, van Mantgem et al. 2015, Darracq et al. 2016).

Bats (Chiroptera) use fire-dependent vegetation for foraging and roosting, but an understanding of how bats respond to the effects of fire remains limited (Carter et al. 2002, Perry 2012). Fire may positively affect bats by opening up flight space under the canopy and by creating new snags and cavities in live trees for roosting (Boyles and Aubrey 2006, Hayes et al. 2009, Knapp et al. 2009, Armitage and Ober 2012). In contrast, temporary adverse effects may come from the smoke, heat, or carbon monoxide in roosts during ignition, whereas longer-term negative effects may occur with the destruction of roost trees (Morrison and Raphael 1993, Rodrigue et al. 2001, Dickinson et al. 2010). Insect communities (prey for insectivorous bats) may similarly experience benefits or harm from fire. In the short-term, fire may reduce insect abundance through direct mortality and reduction in foliar resources required for food, shelter, and oviposition sites, or increase it by attracting pyrophilous insects to freshly burned areas (Swengel 2001, New 2014). Over the longer-term, insect abundance may increase

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because of regrowth of herbaceous plants that attract recolonizing insects (Swengel 2001, Lacki et al. 2009). Many of the studies of insect response to fire focus on ground-dwelling and diurnal insects; it is still not clear how burning affects the availability of nocturnal flying insects as prey for bats (Perry 2012), if at all (Armitage and Ober 2012, Cox et al. 2016). Although there is not always a clear positive link between bat activity and insect abundance (e.g., Grindal and Brigham 1998, Armitage and Ober 2012, Wolbert et al. 2014), increasing evidence suggests that bats can shift their foraging areas in response to concentrated sources of prey (McCracken et al. 2008, 2012; Müller et al. 2012; Gonsalves et al. 2013; Charbonnier et al. 2014).

Most studies showing effects of fire on bats have been on small, maneuverable species that roost or forage within temperate forests (Perry 2012). Large-bodied bats, adapted to open or high-altitude flight, may be less affected by local changes to understory vegetation and insect prey because they forage above the forest canopy (Buchalski et al. 2013). Or, they may respond favorably to the reduction of structural vegetative clutter that clears flight space below the canopy (Armitage and Ober 2012). Federally endangered Florida bonneted bats (*Eumops floridanus*), endemic to south Florida, are large, subtropical bats with long, narrow wings thought to be adapted for open-space flight (Ober et al. 2017b). These bats were recently listed as federally endangered, in part because they have an extremely limited geographic distribution in a region facing increasing development pressures and extreme weather events (U.S. Fish and Wildlife Service [USFWS] 2013). Although Florida bonneted bats have been documented to roost and fly in fire-dependent vegetation communities (e.g., pine [*Pinus* spp.] flatwoods and prairies; Belwood 1981; Angell and Thompson 2015; Braun de Torrez et al. 2016, 2017; Bailey et al. 2017), we know very little about the factors influencing habitat use by these bats. With historical fire suppression leading to declines in many of Florida's rare and endemic species (Van Lear et al. 2005, Slapcinsky et al. 2010), prescribed burning is now used extensively to restore wildlife habitat on public lands across Florida (Fowler and Konopik 2007). Because Florida bonneted bats are subtropical and do not migrate or hibernate, they are susceptible to the effects of burning regimes year round. However, the effects of prescribed burning on Florida bonneted bats are completely unknown. Uncertainty regarding the response of these bats to fire precludes development of effective burn management plans to aid in their recovery, and puts them at risk of experiencing unintentional negative impacts.

Studies investigating effects of fire on other bat species have largely been correlational (e.g., association of fire frequency with some metric of habitat use by bats; Armitage and Ober 2012) or have compared burned areas and control areas after a burn, with no knowledge of habitat use by bats prior to the burn (Buchalski et al. 2013, Cox et al. 2016). Further, these studies have measured the effects of fire on bats at time scales of months or years following burns. In our study, we took an experimental approach to investigate the short-term response of Florida bonneted bats to fire in a region

frequently exposed to prescribed burns. Using acoustic surveys, we measured bat activity (frequency of detected echolocation call sequences) per night as a metric of relative habitat use (Hayes et al. 2009, Parsons and Szewczak 2009). We conducted a pre-post-treatment-control experiment to determine 1) the effect of prescribed burns on Florida bonneted bat activity relative to pre-burn levels and unburned areas, and 2) how this effect changed over the 4 weeks following prescribed burns. We hypothesized that because fire may have temporary negative effects on insect prey and disturbance to roosts 1) bat activity would decrease in freshly burned areas immediately following a fire, and 2) after the initial decrease, bat activity would increase as insects and bats recolonized the burned areas.

STUDY AREA

We conducted this study in 2015 and 2016 in 2 conservation areas within the core range of Florida bonneted bats in south Florida where the species had previously been documented (USFWS 2013, Braun de Torrez et al. 2016, Ober et al. 2017a; Fig. 1): Fred C. Babcock-Cecil M. Webb Wildlife Management Area (BWWMA) in Charlotte and Lee counties, managed by Florida Fish and Wildlife Conservation Commission (FWC) and encompassing 32,667 ha, and Florida Panther National Wildlife Refuge (FPNWR) in Collier County, managed by the USFWS and encompassing 10,688 ha. Both areas contain a mix of mesic and hydric South Florida slash pine (*Pinus elliotii* var. *densa*) flatwoods, bald and pond cypress (*Taxodium ascendens* and *T. distichum*) communities, freshwater prairies, ponds, and hardwood hammocks. Understory vegetation primarily consists of woody shrubs including cabbage palm (*Sabal palmetto*), saw palmetto (*Serenoa repens*), wax myrtle (*Morella cerifera*), and myrsine (*Myrsine floridana*), and grasses including saw grass (*Cladium jamaicense*), wiregrass (*Aristida* spp.), and muhly grass (*Muhlenbergia capillaris*). Prior to establishment as a refuge in 1989, FPNWR was used for hunting, cattle grazing, farming, and logging of pine and virgin cypress (USFWS 2000); it is now predominantly inaccessible to the public to protect the endangered Florida panther (*Puma concolor coryi*; USFWS 2000). The BWWMA, established in 1941, is managed for threatened species (e.g., endangered red-cockaded woodpeckers [*Leuconotopicus borealis*]), cattle grazing, and recreational activities such as hunting (e.g., northern bobwhite [*Colinus virginianus*]; FWC 2003). Both study areas frequently use prescribed fire and mechanical and chemical treatments, to restore habitat for wildlife. In our study, we focused on upland pine flatwoods (mesic and hydric), which are fire-maintained vegetation communities (Abrahamson and Hartnett 1990). Within the subtropical climate of south Florida, bats are active year round. There are 2 primary seasons characterized by precipitation and temperature: dry (1 Nov to mid-May) when average temperatures and precipitation are low (12–25°C, 42 ± 15 cm/yr), and wet (mid-May to 1 Nov) when average temperatures and precipitation are high (18–32°C, 89 ± 27 cm/yr; Duever et al. 1994, Slocum et al. 2010); however, onset dates and duration for these seasons can be

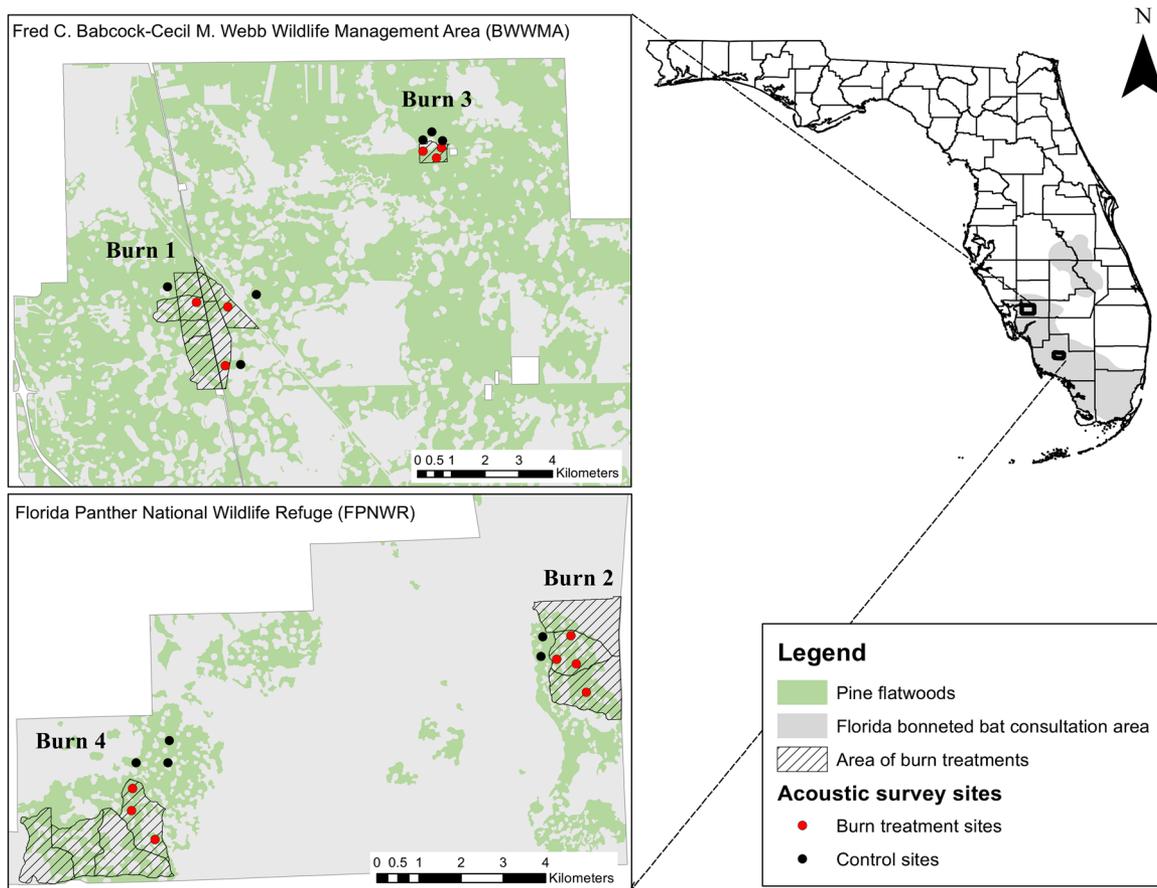


Figure 1. Two conservation areas (black boxes) where we conducted an experiment in 2015–2016 to test the effects of prescribed burns on activity of Florida bonneted bats: Fred C. Babcock-Cecil M. Webb Wildlife Management Area (BWWMA) and Florida Panther National Wildlife Refuge (FPNWR), Florida, USA. Gray shading depicts the consultation area for Florida bonneted bats as defined by the United States Fish and Wildlife Service (USFWS 2013). A burn is defined by 6 acoustic survey sites (3 burn treatment sites, 3 control sites) within an area where a prescribed burn was conducted (hashed lines).

highly variable among years (Slocum et al. 2010). During the wet season, much of the study sites are inundated with water.

METHODS

All research followed American Society of Mammalogists guidelines for research on live animals (Sikes and Animal Care and Use Committee of the American Society of Mammalogists 2016) and were in accordance with the following approved permits: University of Florida Institutional Animal Care and Use Committee (number 201308070), USFWS (number TE 23583B-1), FPNWR (number 41545-2016-IR), and FWC (number SUO-49616).

Experimental Design

To investigate the short-term response of Florida bonneted bats to fire, we used acoustic surveys to document changes in relative Florida bonneted bat activity in burned versus unburned areas. Acoustic surveys are routinely used to monitor bat activity patterns and changes in habitat use (Hayes et al. 2009, Parsons and Szewczak 2009). They are particularly effective for high-flying species not easily captured in mist nets, such as Florida bonneted bats (Braun de Torrez et al. 2017), which have distinct, identifiable echolocation calls (Belwood 1992, Bailey et al. 2017).

Further, Florida bonneted bats have low frequency, high intensity calls that are much less sensitive to attenuation (from distance and vegetation) than higher frequency calls of other species (Parsons and Szewczak 2009), thus reducing site-specific biases associated with vegetation structure. We recognize that bat activity does not equate with bat abundance (Hayes et al. 2009) and acknowledge the limitations associated with acoustic data (Hayes 2000, Gannon et al. 2003). We assumed that sites with greater levels of bat activity received greater use by bats, and that temporal changes in activity corresponded to temporal changes in use of those habitats (Frick 2013). We also recognize that detectability can change with the height at which bats fly above the microphone or the extent to which they echolocate; thus, we were unable to distinguish between spatial and altitudinal patterns of habitat use and were only able to make inferences based on echolocating individuals that flew within the range of our detectors (~20 m).

We conducted a pre-post-treatment-control experiment on 4 prescribed burns in 2015 and 2016, 1 in the dry season (spring) and 1 in the wet season (summer) for each study area: FPNWR (dry: 21 Feb 2016, wet: 15 Jul 2016) and BWWMA (dry: 22 Mar 2016 and wet: 26 Jun 2015; Fig. 1). The burns were backing head fires with moderate to high

control of understory and midstory vegetation that had previously experienced fire 1.5–4 years before the study; total burned areas ranged from 46 ha to 549 ha (Table S1 and Fig. S1, available online in Supporting Information). We surveyed bat activity at 3 sites within each burn area (treatment) and 3 sites adjacent to each burn area (control). Using ArcMap version 10.2.2 (Environmental Systems Research Institute, Redlands, CA, USA) and regional land cover maps (Florida Cooperative Land Cover Map version 3.1), we randomly selected sites ≥ 100 m from the edge of each fire management unit or vegetation community (pine flatwoods), and ≥ 300 m from all other sites. Pre-burn, we surveyed potential burn areas for 14 consecutive nights until a burn occurred. Post-burn, we surveyed continuously from night 4 to night 28. One of our control sites was unintentionally burned; thus, we changed its classification to a burn site (burn 2: 4 burn sites and 2 control sites).

Acoustic Surveys, Analysis, and Species Identification

We conducted all acoustic surveys using full spectrum Song Meter SM3BAT detectors and SM3-U1 ultrasonic microphones (Wildlife Acoustics, Maynard, MA, USA). To maximize bat detections and the quality of recordings (Britzke et al. 2013, Loeb et al. 2015), we located each detector in open areas away from vegetative clutter and flat surfaces prone to acoustic echoes. We connected 1 omnidirectional, external microphone to each detector by a 3-m cable and extended it to 3 m above ground level, as recommended by national survey protocols (Loeb et al. 2015); at this height, microphones were unobstructed by understory vegetation that may reduce detectability. Prior to deployment of equipment, we used an ultrasonic calibrator (Wildlife Acoustics) to verify the sensitivity of the microphones and overall system performance. We programmed the detectors to record from 30 minutes before sunset to 30 minutes after sunrise (Table S2, available online in Supporting Information). We defined each recorded file as a sequence of calls separated by ≥ 3 seconds and ≤ 15 seconds.

We used Kaleidoscope Pro 3.14B (Wildlife Acoustics) for automated noise (non-bat ultrasound) filtering, initial species classification, and to manually review the spectrograms of acoustic files. We processed all acoustic files with the Bats of Florida Classifier (beta version) to identify calls from Florida bonneted bats. We required that each bat file contain ≥ 2 bat calls and used the number of bat files/night as an index of bat activity (Britzke et al. 1999, Tibbels and Kurta 2003, Davidai et al. 2015). To reduce species identification error (Lemen et al. 2015) and erroneous classification of lower quality bat calls (false positives and false negatives), we manually reviewed 100% of the files classified by Kaleidoscope Pro as Florida bonneted bats, NoID (unable to identify), or noise. We also reviewed all ambiguous files for which the software provided multiple species identifications that included Florida bonneted bats (i.e., Florida bonneted bat was listed as an alternate species). We classified files that contained calls with a characteristic frequency (f_c) of 10–18 kHz and maximum frequency (f_{max}) of 16–22 kHz as Florida bonneted bats (Bailey et al. 2017).

We were conservative in our classifications, only including files that we confidently identified based on visual and audio examination of the entire bat sequence. We excluded all calls that overlapped with the range of f_c for Brazilian free-tailed bats (*Tadarida brasiliensis*; 18–33 kHz; Szewczak 2011), or that may have been low frequency social calls from non-target bat species, acoustic echoes, insects, birds, or electronic noise. To aid in manual validation, we compiled a reference library of echolocation calls from hand-released bats captured in mist nets and around known roost locations in south Florida (Braun de Torrez et al. 2016, 2017). We further examined all files identified as Florida bonneted bats to classify those containing feeding buzzes, reflective of foraging activity (Fenton 1970, Coleman and Barclay 2013). Feeding buzzes are characterized by increasing call repetition rates culminating in a rapid burst of calls as the bat attacks its prey (Griffin et al. 1960, Kalko 1995). To reduce subjectivity, 2 researchers experienced in bat call identification independently confirmed all manually validated files. We used our validation protocols consistently across detector sites; thus, despite any possible identification error, we were able to compare relative bat activity at each site.

Statistical Analysis

We conducted all graphical and statistical analyses in the statistical software language R (version 3.1.2; R Foundation for Statistical Computing, Vienna, Austria) in conjunction with RStudio (version 0.98.1102). All reported errors are standard error of the mean (\pm SE) unless otherwise noted. To evaluate the response of Florida bonneted bats to fire, we compared levels of bat activity and foraging activity before and after prescribed burns in treatment sites relative to control sites, and temporal patterns in bat activity post-burn in treatment sites relative to control sites.

To test if bat activity changed after a prescribed burn in treatment sites relative to control sites, we used generalized linear mixed-effects models (GLMMs; function `glmmadmb`, R package `glmmADMB`; Skaug et al. 2012). We first standardized the number of post-burn survey nights to the number of pre-burn survey nights by selecting the closest 12 complete survey nights before and after each burn. We pooled the 4 burns together and used site (detector location) nested within burn (individual burn) as a random effect; this accounted for spatial and seasonal variation associated with each burn and multiple survey nights at each detector. We fitted a null model and alternative models to a negative binomial distribution (zero inflated data) with the following categorical predictors: prepost (pre-burn or post-burn), treatment (burn or control), prepost \times treatment, prepost + treatment, and a null model. We used Akaike's Information Criterion (AIC) and Akaike weights (ω_i), to determine the best model (Burnham and Anderson 2002). If models were considered to be equivalent ($\leq 2 \Delta$ AIC), we selected the model with the fewest parameters and calculated evidence ratios (ratios of Akaike weights, which indicate the likelihood of one model vs. another Burnham and Anderson 2002). We tested the effect of predictors by comparing 2 nested models using a likelihood ratio test

(function `anova`, R Stats package; significance threshold $\alpha = 0.05$). We conducted *post hoc* Tukey pair-wise comparisons between levels of factors using the function `glht` (R package `Multcomp`), which adjusts significance values for multiple comparisons. For interaction terms, we created a new interaction variable, which we used in the *post hoc* tests. To visualize the change in Florida bonneted bat activity after prescribed burns in treatment sites relative to control sites, we calculated and plotted the burn effect size, or the difference between mean bat activity in treatment sites and control sites on each survey night pre- and post-burn. Because of very few detections of feeding buzzes, we were unable to model foraging activity in a mixed-model framework; instead we used Fisher's exact test for small sample sizes to compare the number of feeding buzzes detected between treatment and control sites post-burn.

To investigate how Florida bonneted bat activity changed temporally post-burn in treatment sites relative to control sites, we used data collected from survey nights 4–28 post-burn. We tested the association between the burn effect size (treatment—control) and the number of nights post-burn by constructing a linear mixed-effects model (Gaussian distribution; function `lmer`, R package `lme4`; Bates et al. 2015), with burn as the random effect. We tested the significance of the predictor (nights post-burn) using a likelihood ratio test.

RESULTS

We recorded acoustic data from 24 detector locations across the 4 prescribed burns in 2015 and 2016 (864 detector nights). We eliminated all files associated with nights when data were not recorded throughout the entire night (89 detector nights). We removed 1 site entirely because of failed post-burn recording (burn 4 control site). Our final dataset included 129,561 acoustic files. Using `Kaleidoscope Pro` and manual validation to remove files containing non-bat ultrasonic or acoustic noise (e.g., wind, insects, birds), we identified 79,305 files that contained bat sequences. Of these, we identified 3,305 files as containing Florida bonneted bat calls (4.17% of bat files). We detected Florida bonneted bats at every detector site and on 72.38% of detector nights. Mean

activity for this species was 4.26 ± 0.27 files/night and foraging activity was 0.036 ± 0.007 feeding buzz files/night.

Florida bonneted bat activity levels varied by individual burn and treatment (Table S1). The best model explaining variation in bat activity was the prepost \times treatment model ($\Delta\text{AIC} = 0.00$, $\omega_i = 0.796$; evidence ratio = 6.80; Table 1), which included an interaction term that significantly improved the model (likelihood ratio test: $\chi^2 = 5.84$, $P = 0.016$). Using *post hoc* pair-wise comparisons, we found that in the 12 days post-burn, mean bat activity increased relative to pre-burn levels in burn treatment sites (pre-burn vs. post-burn: $\beta = 0.668 \pm 0.248$, $Z = 2.692$, $P = 0.028$) but did not change in control sites (pre-control vs. post-control: $\beta = 0.105 \pm 0.177$, $Z = 0.912$, $P = 0.912$). Similarly, bat activity levels in burn treatment sites and control sites were not different before burns (pre-control vs. pre-burn: $\beta = 0.142 \pm 0.393$, $Z = 0.361$, $P = 0.978$) but were higher in burn treatment sites than control sites after burns (post-control vs. post-burn: $\beta = 0.705 \pm 0.270$, $Z = 2.609$, $P = 0.036$). This pattern of an increase of bat activity in treatment sites relative to control sites post-burn was evident across all 4 burns (Fig. 2); although activity in the treatment site remained lower than the control after burn 4, the difference in activity between treatment and control was reduced post-burn. We did not statistically compare burn effect sizes between seasons because of a small sample size but note that the burn effect size was greater in burns 2 and 3, conducted during the dry season, than in burns 1 and 4, conducted during the wet season. Using Fisher's exact test, we found a significantly higher total number of feeding buzzes in treatment sites than control sites post-burn (post-burn: 11, post-control: 1, pre-burn: 1, pre-control: 0, $P = 0.034$; Table S1).

Florida bonneted bat activity exhibited nightly variation in the 4 to 28 nights following prescribed burns in treatment sites relative to control sites (Fig. 3). The burn effect size peaked on night 9 following the fire and decreased over time until nights 25–27, exhibiting a weak negative association between the burn effect and the number of nights post-burn treatment ($\beta = -0.195 \pm 0.102$, $t = -1.902$; $\chi^2 = 3.587$, $P = 0.058$).

Table 1. Set of alternative models (generalized linear mixed-effects models; negative binomial distribution) and predictor variables explaining Florida bonneted bat activity (files/night) across 4 experimental prescribed burn treatments, Florida, USA, 2015–2016. Categorical variables are prepost (distinguishing between pre-burn and post-burn acoustic surveys) and treatment (distinguishing between acoustic surveys conducted in burn treatment sites and control sites). We present the number of parameters (K), difference between Akaike's Information Criterion (AIC) score of each alternative model and model with the lowest AIC score (ΔAIC), and Akaike weights (ω_i). Reference values for the model output are pre-burn surveys and control sites.

Models	K	ΔAIC	ω_i	β	SE	Z	P
Prepost \times treatment	7	0.00	0.796				
Intercept				0.666	0.317	2.10	0.036
Prepost				0.105	0.177	0.59	0.553
Treatment				0.142	0.273	0.52	0.603
Prepost \times treatment				0.564	0.232	2.43	0.015
Prepost + treatment	6	3.84	0.117				
Prepost	5	4.42	0.087				
Treatment	5	15.36	<0.001				
Null	4	16.36	<0.001				

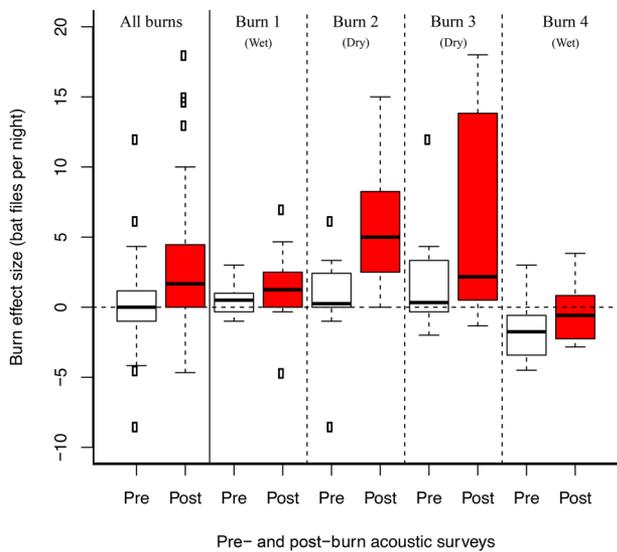


Figure 2. Change in relative activity (acoustic files recorded/night) of Florida bonneted bats, pre-burn (white boxes), and post-burn (red boxes) in treatment sites relative to control sites, for all burns combined, and for each burn independently, Florida, USA, 2015–2016. The y-axis represents the burn effect size: the difference between mean Florida bonneted bat activity recorded at treatment sites and control sites on each survey night pre- and post-burn. Each boxplot represents the first quartile, median, and third quartile, with bars (whiskers) extending to the most extreme data point that is no more than 1.5 times the interquartile range from the box. Positive values indicate higher bat activity in treatment sites than in control sites.

DISCUSSION

We found no indication that prescribed burns negatively affected flight activity of endangered Florida bonneted bats. Rather, our results suggest that these bats were attracted to freshly burned areas in pine flatwoods immediately following prescribed burns. Contrary to the suggestion that large-bodied bats would not respond to fires in forests because of their tendency to fly in open areas (Buchalski et al. 2013), we found a clear effect of fire on this large, high-flying bat species. The patterns we observed could be due to changes in the spatial use of habitat or vertical shifts in flight altitude (i.e., detectability increases as bats fly closer to the microphone). Our findings support studies from bat assemblages in other regions showing that bat activity either increased or did not change in response to forest burns (Loeb and Waldrop 2008, Armitage and Ober 2012, Perry 2012, Buchalski et al. 2013, Cox et al. 2016), contributing to mounting evidence that bats are resilient to or benefit from fire. However, these studies were all based on correlations or post-fire site comparisons over longer time periods following a burn. We are not aware of any pre-post-treatment-control experiments, such as ours, that documented changes in bat activity directly before and after a fire, or examined temporal patterns in the bats' immediate response.

The mechanism behind a positive response to fire by Florida bonneted bats is not clear. Bat activity may increase following prescribed burns because of improvements in roosting habitat (Boyles and Aubrey 2006; Johnson et al. 2009, 2010), a reduction of understory vegetative clutter

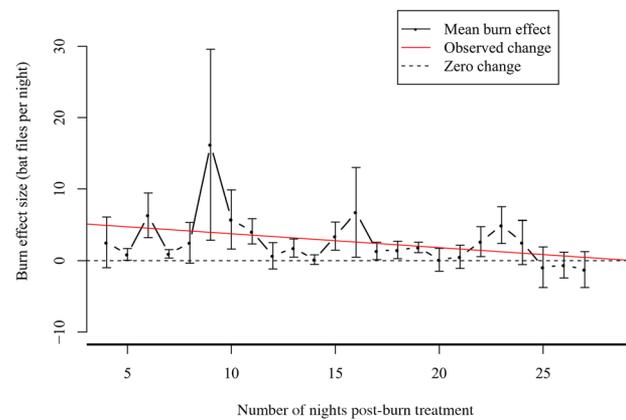


Figure 3. Temporal patterns of the burn effect size, or the difference in mean activity (acoustic files/night) of Florida bonneted bats recorded in treatment sites relative to control sites after a prescribed burn, for all 4 burn experiments combined, Florida, USA, 2015–2016. Positive values indicate higher bat activity in treatment sites than in control sites on a given night. Red solid line represents the negative relationship between the effect size and nights post-burn treatment, fitted with a linear mixed-effects model (Gaussian distribution; burn as random effect).

(Armitage and Ober 2012, Buchalski et al. 2013), an increase in availability of insect prey (Lacki et al. 2009), or some combination of these factors. Although changes to forest structure (e.g., roost creation or clutter reduction) cannot be ruled out, we argue that it is less relevant in our study. Creation of new cavity trees and colonization by bats likely occur over a longer time scale following a burn than the 4 weeks we surveyed (Haslem et al. 2012, Stojanovic et al. 2016). Armitage and Ober (2012) suggested that large, less-maneuverable bat species benefit from reduction in mid-story vegetative clutter in infrequently burned sites. Although the change in vegetation was not explicitly quantified in our study, we noted reduced herbaceous ground cover and foliage on low understory shrubs (<3 m) as a result of burn treatments, but there was not considerable addition of flight space relative to the canopy layer (~15 m; Table S1 and Fig. S1). Similarly, because of this minimal reduction in vegetation and because microphones were located above the understory vegetation in all sites, we would not expect a substantial increase in bat detectability (i.e., reduced sound attenuation) post-burn.

Although we do not present data on insect abundance, we suggest that Florida bonneted bats were attracted to possible increases in available insect prey immediately following burns, tracking insects as they moved into or became more accessible in freshly burned areas. Despite a poor understanding of the foraging behavior of Florida bonneted bats (USFWS 2013) and of the associations between bat activity and insect abundance for bats in general, many bats appear to quickly respond to changes in prey availability across the landscape (McCracken et al. 2012, Müller et al. 2012, Gonsalves et al. 2013, Charbonnier et al. 2014), or altitudinally (McCracken et al. 2008). At least 40 species of flying insects, capable of rapid dispersal, are attracted to fires and subsequent burned areas to exploit fire-killed wood and reproduce (e.g., fire beetles [*Melanophila* spp.],

long-horned beetles [Cerambycidae], cigarette beetles [*Lasioderma serricorne*], smoke flies [*Microsania* spp.]; Hart 1998, Perry 2012, New 2014). Fire beetles, which mate and lay eggs on recently burned woody debris, detect fires from up to 100 km away using specialized infrared receptors (Schmitz et al. 1997) and smoke sensing antennae (Schütz et al. 1999, Bousack et al. 2015). Smoke, and the odor from burns can continue to attract insects from surrounding unburned areas for several days after a fire. Alternatively, flying insects already present in an area may be flushed from the freshly burned understory into or above the canopy to avoid flames and smoldering vegetation (Komarek 1969), rendering these insects more accessible to foraging bats. Because insect abundance is often greater in the understory than near the canopy (Adams et al. 2009), insects displaced from the understory by a burn may enhance foraging conditions for bats, as has been noted for other aerial insectivores (Komarek 1969). Our finding that feeding buzzes were detected almost exclusively in post-burn treatment sites provides some evidence that Florida bonneted bats were foraging in burned areas. Because feeding buzzes attenuate quickly with distance and in vegetation (Parsons and Szewczak 2009), our ability to detect them was likely greatly reduced if bats were foraging above the canopy.

Our observation that the 2 burns conducted in the dry season elicited a stronger response by bats than did the 2 burns conducted in the wet season suggests that bats may react to fire differently depending on the seasonality of burns. During the cooler dry season when prey are likely more limited, bats may be particularly attracted to the concentrated insect sources associated with freshly burned sites. This is also when many female Florida bonneted bats are likely in the early stages of pregnancy (Ober et al. 2017a), an energetically demanding reproductive stage. During the wet season, when temperatures and insect prey availability are higher overall within this region (Amalin et al. 2009), bats may not be as prey limited and selection of prime foraging sites may be less critical. Alternatively, there may be a seasonal difference in how insects respond to fires (Swengel 2001), and hence how bats respond. The dry season, which is characterized by low rainfall, temperatures, soil moisture, and relative humidity, typically has higher availability of dry fine fuels than the wet season, leading to higher fuel connectivity and more complete burns (Slocum et al. 2007, Platt et al. 2015). These higher intensity burns may in turn result in a greater effect on the insect community (Swengel 2001). In this region, there may also be a third season, the fire season, at the transition of the dry to wet season when conditions for fire spread may be most favorable (Platt et al. 2015); however, none of the burns in our study were conducted during this period. With a sample size of 4 prescribed burns, we were limited in our ability to conclude that the observed differences across burns were due to season rather than to some other uncontrolled factor associated with each burn.

In contrast to what we predicted, we did not observe an initial decrease in Florida bonneted bat activity following prescribed burns. Our finding of an increase in bat activity

immediately after the burns and subsequent decrease over time suggests that the initial positive effect of prescribed burns on Florida bonneted bats may be temporary. This could be due to the initial attraction by insects to fires as they burn and smolder, before subsiding over time. With no published studies that examine temporal patterns of bat activity immediately after a fire, it is difficult to put our results in context. Examining roost use and foraging behavior of northern long-eared bats (*Myotis septentrionalis*) with radio-telemetry, Dickinson et al. (2009) observed that bats abandoned their roosts for 1 day following a prescribed burn, and that flying insect activity initially decreased before increasing again 6–7 nights after the burn. This roughly coincides with a spike in Florida bonneted bat activity that we observed in treatment sites on nights 6 and 9. Access was restricted to our sites during the first 4 days after each burn; thus, we may have missed any initial reduction in bat (and insect) activity that occurred during the first 3 nights as a result of fire. Because the prescribed burns in our study were relatively small (<550 ha; <3.5 km at widest point), burn units may have experienced a brief reduction in insects due to mortality, followed by quick recolonization of mobile insects from surrounding unburned areas (Swengel 2001, Perry 2012).

MANAGEMENT IMPLICATIONS

Restoring fire to fire-dependent forests may contribute to improvement of foraging habitat for the critically endangered Florida bonneted bat in the short-term. Our study provides land managers with the first evidence that Florida bonneted bats may benefit from fire, particularly burns conducted in the dry (spring) season. Although our study demonstrates the immediate response of Florida bonneted bats in flight to prescribed burns, we still do not know how this translates into their use of roost trees or the use of burned areas for foraging over the longer term. Burns conducted close to roost trees may still have negative impacts on bats if there are not sufficient alternate roosts available for bats to use during the fires to avoid smoke or to replace roost trees destroyed in fires. We encourage more research on the long-term effects of prescribed burning on foraging activity and roosting behavior of Florida bonneted bats and the local bat assemblage as a whole to develop appropriate land management recommendations for this taxonomic group of high conservation concern.

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