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Cover Photograph: An example of one of our study sites following shelterwood harvest at Fort Indiantown Gap, Pennsylvania. Photograph © Chris L. Hauer.

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Effects of Shelterwood Harvest and Prescribed Fire on Site Occupancy of Bats in Oak Forest, at Fort Indiantown Gap, Pennsylvania

Christopher L. Hauer[1,2,*], Lisa E. Powers[1,3], Jarrid P. Doyle[2,4], Jon-Dimitri Lambrinos[2], Joseph C. Hovis[2], Shannon W. Henry[2], and Brent J. Sewall[1]

Abstract - Overstory thinning and prescribed fire are increasingly being used to restore *Quercus* spp. (oak) forests. Here, we investigated the effects of shelterwood harvest and prescribed fire on habitat use by bats in 3 forest stands at Fort Indiantown Gap, Pennsylvania. We monitored for bats using acoustic detectors at 77 sites from May to August 2017–2018. We fit multi-season occupancy models for resident species to examine the effects of management treatment, vegetation structure, distance to water, and survey year on occupancy. Occupancy of *Eptesicus fuscus* (Big Brown Bat), *Lasiurus cinereus* (Hoary Bat), and *Lasionycteris noctivagans* (Silver-haired Bat) was highest in shelterwood sites, where mid-story stem density and overstory basal area was lowest. Contrary to our prediction, occupancy of *Myotis leibii* (Eastern Small-footed Myotis) was higher in shelterwood and burned sites than in unmanaged (control) sites. *M. septentrionalis* (Northern Long-eared Myotis) also appeared less likely to use unmanaged sites.

Introduction

Oak (*Quercus*) forests account for over half of forested areas in the eastern United States (Smith et al. 2009) and provide food resources for wildlife, as well as valuable timber (Brose et al. 2013). Because oaks are of such high ecological and economic value, forest management practices designed to promote oak regeneration, such as overstory thinning and prescribed fire, have been increasingly used by forest managers throughout the region (Signell et al. 2005), yet uncertainty remains as to how these practices affect forest-dependent wildlife, including bats (Harper et al. 2016). Forests provide critical roosting, foraging, and drinking resources for bats (Law et al. 2016). Use of forests by bats is closely associated with the complexity of vegetation structure or "clutter" (Ford et al. 2005), and the extent to which bats use cluttered forests varies by species, due to differences in body size, wing morphology, foraging strategy, and echolocation call characteristics (Lacki et al. 2007). In general, medium-to-large species with long, narrow wings produce low frequency, narrowband echolocation calls and are better adapted to foraging in open areas with low structural complexity (e.g., above forest canopy, canopy gaps), whereas small-bodied species with short, broad wings produce high frequency, broadband echolocation calls and are better able to forage in cluttered, structurally complex sites (Aldridge and Rautenbach 1987).

Forest management practices that reduce clutter in the understory and mid-story of forests (Guldin et al. 2007) may improve foraging habitat for at least some bats (Perry 2012). Previous studies have generally found that activity or occupancy of medium-to-large

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[1] Department of Biology, Temple University, 1900 North 12th Street, Philadelphia, PA 19122. [2] Current address - Pennsylvania Department of Military and Veterans Affairs, Fort Indiantown Gap National Guard Training Center, Building 26-151, Tomstown Road, Annville, PA 17003. [3] Current address - U.S. Geological Survey, National Wildlife Health Center, 6006 Schroeder Road, Madison, WI 53711. [4] Current address - Pennsylvania Game Commission, 253 Snyder Road, Reading, PA 19605. [*] Corresponding author - chauer@pa.gov.

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species increases following overstory thinning (Dodd et al. 2012, Titchenell et al. 2011), prescribed fire (Burns et al. 2019), or a combination of both thinning and fire (Cox et al. 2016), largely as the result of reductions in vegetation density and volume. However, the response of small-bodied species to vegetation structure is less clear. Several studies have documented greater activity of *Myotis* species in cluttered, closed-canopy forests (Ford et al. 2005), yet others have found negligible or positive effects of thinning or fire on *Myotis* species and *Perimyotis subflavus* (F. Cuvier) (Tricolored Bat) (Caldwell et al. 2019). Given these conflicting results, it is unclear how some bats, particularly small-bodied species, respond to forest management.

Passive acoustic monitoring has become an increasingly common technique for studying habitat use by bats (Britzke et al. 2013). However, the ability to record echolocating bats using acoustic detectors is influenced by various factors (Ratcliffe and Jakobsen 2018) such that acoustic detection of bat species is imperfect (Duchamp et al. 2006). One method to account for this limitation is occupancy modeling, which uses detection/non-detection data to evaluate factors that influence occupancy while simultaneously accounting for imperfect species detection (MacKenzie 2006). Occupancy modeling has recently been applied to acoustic surveys to evaluate habitat use in response to forest management (Bender et al. 2015). However, research examining habitat use by bats in managed oak forests of the northeastern United States is limited (Gallagher et al. 2021).

Given the increased use of overstory thinning and prescribed fire to manage and restore oak forests in the eastern United States, forest managers should understand how these management practices influence use of forests by bats. In this study, we used occupancy modeling to examine the relationship between occupancy of bats and vegetation structure in a recently managed oak forest in southeastern Pennsylvania. Our objective was to examine the influence of forest management practices on habitat use by bats in 3 forest stands: a stand that was thinned using the shelterwood harvest method, a stand that was managed using prescribed fire, and an unmanaged (control) stand. We hypothesized that the influence of management techniques would vary among species due to differences in body size, which is associated with wing morphology and echolocation characteristics. We predicted that medium-to-large species such as *Lasiurus cinereus* (Palisot de Beauvois) (Hoary Bat), *Lasionycteris noctivagans* (Le Conte) (Silver-haired Bat), *Eptesicus fuscus* (Palisot de Beauvois) (Big Brown Bat), and *L. borealis* (Müller) (Eastern Red Bat) would use the recently managed stands with reduced structural complexity (low overstory basal area and mid-story stem density), whereas small-bodied species, such as *Myotis* species and Tricolored Bats, would use the unmanaged stand with greater structural complexity (high overstory basal area and mid-story stem density).

Field-site Description

We conducted our research at Fort Indiantown Gap National Guard Training Center (FIG-NGTC), a 6,920-ha live-fire, military training installation in Lebanon and Dauphin counties, Pennsylvania, within the Ridge and Valley physiographic province (Fig. 1; PADCNR 2018). Most of FIG-NGTC is forested, with xeric upland areas dominated by an oak and hickory (*Carya*) overstory, and mesic bottomlands dominated by mixed deciduous forest. Within our study area, the overstory is primarily composed of *Quercus montana* (Willd.) (Chestnut Oak), *Q. rubra* (L.) (Northern Red Oak), and hickory. The mid-story layer is dominated by *Nyssa sylvatica* (Marshall) (Black Gum), *Acer rubrum* (L.) (Red Maple), *Betula lenta* (L.) Sweet Birch, and *Sassafras albidum* (Nutt.) (Sassafras). Understory vegetation consists of *Vaccinium* spp. (blueberry), *Kalmia latifolia* (L.) (Mountain Laurel), and a mixture of grasses, forbs, and woody regeneration. Elevations within the study area range from 122 m to 439 m above sea level. The climate is humid continental, with an average annual temperature of 11.3 °C and average precipitation of 117.9 cm (NOAA 2023).

Prescribed fire has been implemented on the installation since 2004, with an average of 625 ha burned per year since 2015. Forested units are typically burned on a 3–5-year rotation, while military training ranges (i.e., grasslands) are burned annually. Roughly one-third of forested areas (1,578 of 4,390 ha) on the installation have received some form of timber harvest over the past 20 years. This includes clearcuts to construct military training ranges, even-aged shelterwood harvests and timber stand improvements to promote oak regeneration, and salvage cuts to remove trees impacted by *Lymantria dispar* (L.) (Spongy Moth) and *Agrilus planipennis* (Fairmaire) (Emerald Ash Borer).

Materials and Methods

Study design

We conducted this study within a forested area totaling ~85 ha, in the southwestern corner of the installation (Fig. 1). Prior to this study, in April 2017, a stand within the study area (16.2 ha) received the first (preparatory) cut of a 3-stage shelterwood harvest (hereafter, "shelterwood") to promote mixed-oak regeneration (Fig. 1). To achieve the initial shelterwood cut, contractors removed mid-story and understory stems of undesirable, shade-tolerant tree species and poor-form oaks and snags, resulting in a residual basal area of 18.4–20.7 m^2/ha. An adjacent stand (27.9 ha), which was not harvested during this study, was burned in April 2014 (hereafter "burned") as a part of the installation's prescribed burn program (Fig. 1). Fire behavior was of low intensity, with flame lengths <2 m (PADMVA 2014). We selected an adjacent, intact stand (40.5 ha) with no recent history (within the last 75–100 years) of overstory thinning or prescribed fire, to serve as the control (Fig. 1). All 3

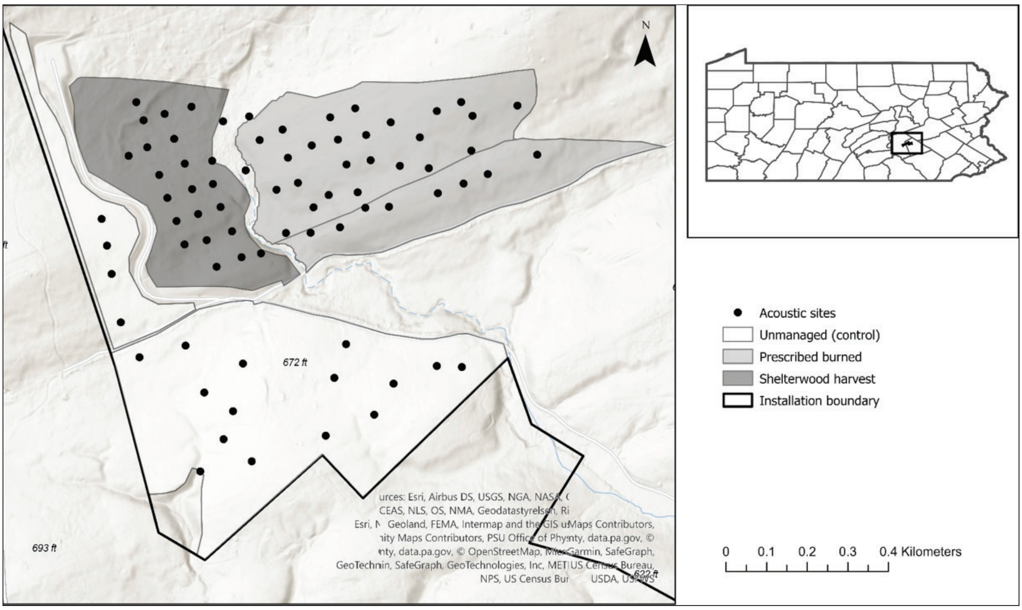


Figure 1. Study area and location (shown in Pennsylvania in inset) of acoustic sites (n = 77) within unmanaged (control), prescribed burned, and shelterwood harvest treatments, at Fort Indiantown Gap National Guard Training Center, Pennsylvania.

focal stands (hereafter, "treatments") were immediately adjacent to each other at a similar elevation (range = 204.8 to 257.9 m), had similar forest composition and structure, and no wildfire or other management treatments since 2011. The shelterwood and burned stands mentioned above were also burned in March 2011; however, that burn was a low-intensity entry burn used to reduce fuels in the understory layer and had little-to-no discernable impact on forest structure and composition (i.e., no mid-story or overstory mortality). Therefore, we will focus on the more recent and extensive management treatments (prescribed burn in 2014 and shelterwood harvest in 2017).

We constructed a rectangular grid of sampling points (sites) within each treatment using the Fishnet tool in ArcMap 10.7 (ESRI, Redlands, CA). We established sites at 60-m intervals on linear transects located 60 m from each other (Titchenell et al. 2011). To minimize potential edge effects, we removed any sampling sites from the grid that were located within 50 m of a forest or anthropogenic edge (e.g., road, fire break; Froidevaux et al. 2014). From the set of potential sites, we selected 77 sites (control *n* = 19; burned *n* = 35; shelterwood *n* = 23) to conduct acoustic and vegetation sampling during summer 2017 and 2018.

Acoustic sampling

We passively recorded bat echolocation calls (hereafter, "bat passes") using full-spectrum ultrasound detectors (D500x, Pettersson Electronik AB, Uppsala, Sweden). We powered detectors using 6-v, deep-cycle batteries (PS-6200, Power-Sonic Corp., San Diego, CA) and stored them within weatherproof plastic containers. We mounted external, directional microphones to collapsible camping poles at a 45° angle above horizontal, elevated approximately 1.5 m above the ground. We deployed microphones away from surrounding vegetation and in the direction with the least clutter to increase the number and quality of bat passes (Weller and Zabel 2002). We programmed detectors to record continuously from sunset to sunrise each night. We used the following settings for all detectors: sampling frequency = 500 kHz; pre-trigger = off; recording length = 5 sec; high pass filter = on; auto recorder = on; trigger sensitivity = high; trigger level = 80; and input gain = 80 (Reichert et al. 2017). We geo-referenced each detector using a global positioning system receiver (Oregon 450, Garmin International, Inc., Olathe, KS).

We deployed a single detector at each of 2–4 sampling sites per night. We randomly selected detectors for each sampling site to avoid potential bias resulting from differences in microphone sensitivities (Larson and Hayes 2000). We sampled sites in each of the 3 treatments simultaneously, except in a few cases for which logistical constraints and restrictions from military training prevented access. We did not select the sampling sequence for sites randomly, but instead chose sites to maximize the distance between detectors (>200 m) on the same night, thereby reducing the risk of multiple detectors recording data from the same bat simultaneously (Coleman et al. 2014). We deployed detectors for a minimum of 3 consecutive nights at a site to account for temporal variation in bat activity (Hayes 1997). Following each sampling period of ≥3 nights, we relocated detectors to 2–4 new sampling sites. We repeated this process throughout the sampling period of May–August 2017 and 2018. We sampled each site once per year, and we sampled the same sites in both years with few exceptions (in 2018, we were unable to resample 3 sites in the control treatment due to military training, and no data were collected from 1 site in the shelterwood treatment due to equipment failure).

Vegetation sampling

At each site, we characterized vegetation structure by creating a 0.04-ha (fixed radius = 11.3 m) circular plot centered on the detector. Within each plot, we measured overstory basal area and mid-story stem density, as these variables have previously been found to be effective measures of clutter for foraging bats (O'Keefe et al. 2014). We estimated basal area (m^2/ha) by measuring diameter at breast height (DBH) of all overstory trees (live trees and snags) with a DBH ≥10 cm. To determine mid-story stem density (stems/ha), we counted all tree saplings and shrubs with a DBH ≤10 cm and >1.4-m tall within the same circular plot. We sampled vegetation at all sites in May–August 2017, which was during the first growing season following the shelterwood harvest, and 3 growing seasons following the prescribed burn.

Echolocation call analysis

We stored recorded full-spectrum (.wav) bat passes to compact flash (CF) cards within detectors and downloaded them to a computer 1–2 times per week. We uploaded bat passes to a file attributer (D500x File Attributer 2.7, SonoBat, Inc., Arcata, CA) and scrubbed them using a high-grade filter to remove noise and poor-quality files. When possible, we then identified the remaining bat passes to species using SonoBat call analysis software (version 4.0.7, New York-Pennsylvania-West Virginia classifier, SonoBat, Inc.). We used the default sequence decision threshold of 0.90 and acceptable call quality of 0.80, as well as a 20-kHz filter (Goodwin and Gillam 2021). To minimize errors in species identification, we only included search-phase sequences with ≥3 pulses if SonoBat assigned them an accepted species classification (SppAccp). Bat passes that met these criteria were then manually vetted to verify species identifications using qualitative characteristics (e.g., minimum frequency, maximum frequency, characteristic frequency, duration, slope; Szewczak 2018). We considered 8 bat species as potential residents on the installation based on previous capture surveys (Chenger 2004, Hauer et al. 2019). These species included Big Brown Bat, Eastern Red Bat, Hoary Bat, Silver-haired Bat, Tricolored Bat, *Myotis septentrionalis* (Trouessart) (Northern Long-eared Myotis), *M. leibii* (Audubon and Bachman) (Eastern Small-footed Myotis), and *M. lucifugus* (Le Conte) (Little Brown Myotis). *Myotis sodalis* Miller and Allen (Indiana Myotis) has yet to be confirmed in our study area (Chenger 2004, Hauer et al. 2019), but they occur in surrounding areas (G. Turner, Pennsylvania Game Commission, Harrisburg, PA, USA, 2021 pers. comm.). Thus, we deemed the presence of Indiana Myotis to be possible, and we conservatively grouped bat passes identified as Little Brown Myotis or Indiana Myotis into a single phonic group due to similarities in their echolocation calls (Gorman et al. 2021).

Statistical analysis

We compared vegetation structure among treatments (control, burned, and shelterwood) using Kruskal-Wallis tests and evaluated pairwise differences between means using post-hoc Dunn's tests in JMP Pro 13.0 (SAS Inc., Cary, NC). We report least square means ± 1 *SE*.

We used bat passes from the first 3 nights of sampling at each site during which there were suitable weather conditions for bat activity (e.g., temperatures >10 °C for the first 5 hours after sunset, little to no precipitation, sustained wind speeds <4 m/s; USFWS 2024) and no equipment malfunctions (e.g., full CF card, power loss). We then created nightly histories of detections (1) and non-detections (0) for each species or phonic group (hereafter, "species") using acoustic data from the first 3 nights with suitable conditions at each site (MacKenzie 2006). We considered a site to be occupied if at least 1 bat pass was identified on a given night of sampling (Yates and Muzika 2006).

We fit multi-season occupancy models in Program PRESENCE version 2.12.36 (USGS

2019) to evaluate occupancy ψ (i.e., the probability of a site being occupied) of bats across 2 seasons (i.e., years; MacKenzie et al. 2003). We used an alternate parameterization of the multi-season model, which is designated in PRESENCE as "seasonal occupancy ($\varepsilon = 1 - \gamma$) and detection", to estimate seasonal occupancy ψ_i (USGS 2019). In contrast to the default parameterization, occupancy at a site is random and does not depend upon the occupancy state of the site in the previous season (MacKenzie et al. 2018). We selected this parameterization because it requires estimating fewer parameters, and it was adequate for our goal of estimating occupancy in each year. We fit models for species with naïve occupancies (i.e., the proportion of occupied sites without correcting for detection) >0.1, since detection histories were too sparse to fit models for rare species (Furnas and Callas 2015). Although our analyses were in an occupancy modelling framework, our results should be interpreted as site use, as bats are highly mobile and do not constantly occupy a site (MacKenzie 2006).

For each species, we used a 2-stage process to select detection covariates and then occupancy covariates. First, prior to occupancy analysis, we determined the most plausible probability-of-detection (*p*) portion of the model, by fitting different combinations of site- and survey-specific covariates based on published literature. We considered overstory basal area, mid-story stem density, minimum nightly temperature, Julian date, and survey year as covariates that could affect detection probability *p* (i.e., the probability that a species is detected during sampling occasion *t,* given that the species is present at a site; Table 1). We averaged hourly temperatures obtained from a Remote Automated Weather Station (RAWS) located on the installation. The average (± *SE*) minimum nightly temperature was 14.4 ± 0.23 °C (range = 0.0 to 21.7 °C). We included a linear term (date) and a quadratic term (date^2) for Julian date to account for potential changes in detection due to seasonal movements and the addition of volant juveniles in the later part of the sampling period (Hoff et al. 2024). We standardized all continuous site- and survey-specific covariates using a *z*-score transformation prior to model fitting (Burns et al. 2019). To avoid multicollinearity, we calculated correlation coefficients of continuous covariates and did not include highly correlated covariates (Pearson's $|r| \geq 0.70$) in the same model (Bender et al. 2015). Preliminary correlation analyses found no strong correlation between overstory basal area and mid-story stem density ($|r| = 0.40$) or Julian date and nightly minimum temperature ($|r| = 0.47$), so we included these covariates in the same candidate models. We found a relationship between treatment and both stem density and basal area; thus, we did not include these covariates in the same candidate model. We evaluated 14 candidate detection models, which included single covariate models and additive combinations of covariates, as well as a null model that represented constant detection (see Supplemental Table 1, available online at https://eaglehill.us/NABRonline/suppl-files/nabr-013-Hauer-s1.pdf). We evaluated all detection models using an occupancy portion of the model that contained the covariates treatment, survey year, and distance to water. We identified the best-supported probability-of-detection model for each species and included this same set of detection covariate(s) from the best detection model in all subsequent occupancy models for that species.

We then developed and compared a candidate set of 8 occupancy models to test *a priori* hypotheses about the influence of management treatment (control, burned, shelterwood), vegetation structure, distance to water, and survey year on seasonal occupancy. We included distance to water, calculated as the Euclidean distance (m) from each sampling site to the nearest permanent water source, as an occupancy covariate because proximity of water sources to roosting and foraging locations is important for bats in managed forests (Gallagher et al. 2021). We estimated seasonal occupancy (ψ_i) as a function of the singular effects of treatment, survey year, mid-story stem density, overstory basal area, and distance to water, as well as the additive effects of treatment and year, and stem density and basal area (see Supplemental Table 2, available online at https://eaglehill.us/NABRonline/suppl-files/nabr-013-Hauer-s2.pdf).

We used an information theoretic approach using Akaike's Information Criterion corrected for small sample sizes (AIC_c) to select the most parsimonious detection and occupancy model from the candidate sets for each species (Burnham and Anderson 2002). We used the difference between the model with the lowest AIC_c and all other models (ΔAIC_c) to evaluate the relative strength of our candidate models (Burnham and Anderson 2002).

Table 1. Variable names, descriptions, and hypotheses (including predicted positive [+] or negative [-] effect) for covariates used in probability-of-detection (p) and seasonal occupancy (ψ_i) models for bats in a managed oak forest, at Fort Indiantown Gap National Guard Training Center, Pennsylvania, May–August 2017 and 2018.

Variable	Description	Hypothesis
p variables		
Temp	Minimum nightly temperature (°C)	Bat activity more easily detected with increasing temperature (+)
Date	Linear term for Julian date	Bat activity increases throughout the summer (+)
$Date^2$	Quadratic term for Julian date	Bat activity increases through July, but subsequently decreases by the end of August (+/-)
Basal area	Basal area (m^2/ha) of overstory trees DBH ≥10 cm	Vegetative clutter reduces ability to record bat echolocation calls (-)
Stem density	Density (stems/ha) of woody stems DBH ≤10 cm and >1.4 m tall	Vegetative clutter reduces ability to record bat echolocation calls (-)
Year	Survey year (2017 or 2018)	Seasonal changes in abundance resulting in higher or lower detection of bat activity (+/-)
ψ_i variables		
Treatment	3 categories: unmanaged (control), prescribed burned (burned), or shelterwood harvest (shelterwood)	Reduction in vegetative clutter increases foraging efficiency resulting in higher site use, but may increase predation risk and reduce prey availability resulting in lower site use (+/-)
Basal area	Basal area (m^2/ha) of overstory trees DBH ≥10 cm	Reduces foraging efficiency resulting in lower site use (-)
Stem density	Density (stems/ha) of woody stems DBH ≤10 cm and >1.4 m tall	Reduces foraging efficiency resulting in lower site use (-)
Water	Distance (m) to nearest permanent water source	Bats use areas near water bodies as foraging/drinking habitat resulting in higher site use (+)
Year	Survey year (2017 or 2018)	Annual changes in abundance or weather conditions resulting in higher or lower site use (+/-)

For occupancy models, we considered models ≤2 $\mathrm{AIC_c}$ units from the best-supported model to have substantial support, and these models were included in the confidence model set (Burnham and Anderson 2002). To account for model selection uncertainty, we used $\mathrm{AIC_c}$ model weights (w_i) (i.e., relative likelihood of a model) to calculate model-averaged parameter estimates, unconditional standard errors, and their associated 85% confidence intervals for only those covariates appearing in the confidence set (Burnham and Anderson 2002). We considered covariates to be significant if their 85% confidence intervals did not include zero (Arnold 2010).

Results

Mid-story stem density was approximately 10.5 times lower at the shelterwood sites (50.0 ± 14.5 stems/ha) than at the burned sites (528.8 ± 46.2 stems/ha) and 18 times lower than at the control sites (911.8 ± 156.3 stems/ha) (Kruskal-Wallis $\chi^2_2 = 43.36$, $P < 0.001$; Fig. 2). Overstory basal area was approximately 2 times lower at the shelterwood sites (13.6 ± 1.6 m^2/ha) than at the burned (24.2 ± 1.6 m^2/ha) and control sites (25.8 ± 1.3 m^2/ha) (Kruskal-Wallis $\chi^2_2 = 23.83$, $P < 0.001$; Fig. 2).

In summer 2017 and 2018, we detected bats at 73 of 77 sites (94.8%). We recorded 33,727 bat passes in 450 detector-nights across both years. After removing bat passes that did not meet our selection criteria, we identified 15,824 (46.9%) bat passes to 8 species. Of the identified passes, 67.2% (n = 10,630 passes) were Big Brown Bats, 26.4% (n = 4,178) were Eastern Red Bats, 2.0% (n = 322) were Eastern Small-footed Myotis, 1.9% (n = 302) were Hoary Bats, 1.2% (n = 187) were Silver-haired Bats, and 0.8% (n = 126) were Northern Long-eared Myotis. We detected Little Brown Myotis–Indiana Myotis and Tricolored Bats at <10.0% of sites (naïve $\psi < 0.1$), and thus, we did not include these species in occupancy modeling.

We detected Big Brown Bats at 68 sites (88.3%). Probability of detection decreased with increasing stem density and increased with date (Table 2). There were 2 models in the confidence set for occupancy; occupancy covariates in these models included treatment and year (Table 3). Model-averaged parameter estimates indicated that treatment was the only informative occupancy covariate (Table 2), with occupancy being 2.3 times higher in burned sites and 7.3 times higher in shelterwood sites, compared to control sites (Fig. 3a).

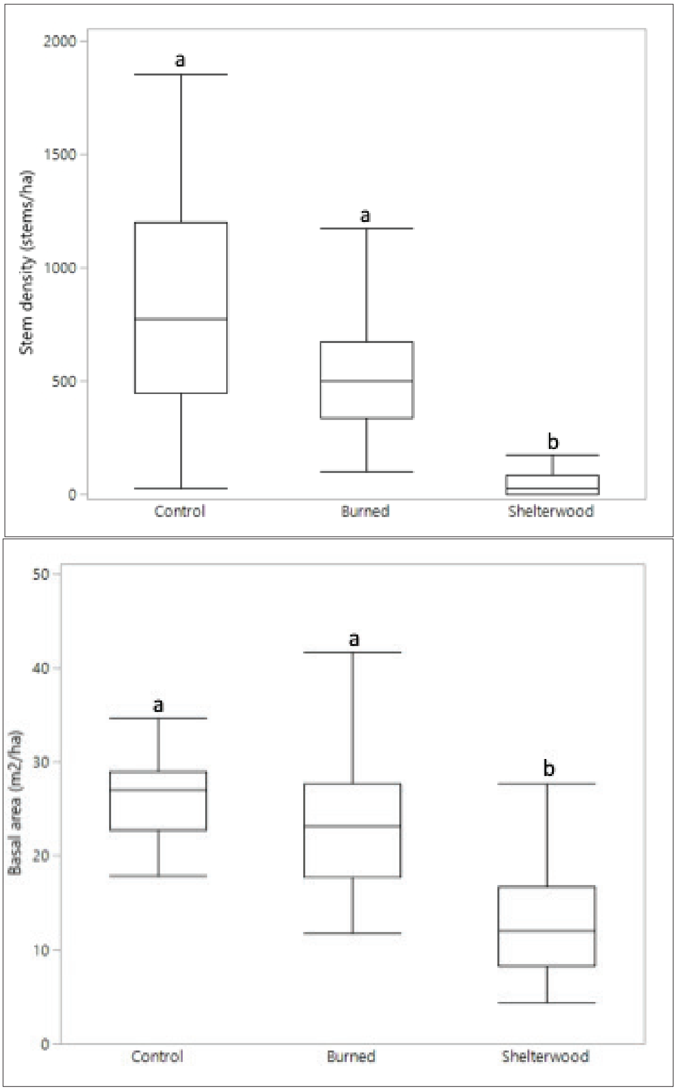
We detected Eastern Red Bats at 52 sites (67.5%). Probability of detection decreased with increasing stem density and increased with date (Table 2). There were 4 models in the confidence set for occupancy; occupancy covariates in these models included treatment, year, basal area, and stem density (Table 3). On average, occupancy of Eastern Red Bats was higher in the shelterwood and burned sites compared to control sites (Fig. 3b), but 85% confidence intervals for parameter estimates included zero (Table 2).

We detected Hoary Bats at 32 sites (41.6%). Probability of detection decreased with increasing stem density (Table 2). There were 2 models in the confidence set for occupancy; occupancy covariates in these models included treatment and year (Table 3). Model-averaged parameter estimates indicated that treatment was informative (Table 2), with occupancy being 9.6 times higher in shelterwood sites, compared to control sites (Fig. 3c). Model-averaged parameter estimates also indicated that year was informative, but the model containing treatment and year was only 0.12 $\mathrm{AIC_c}$ units lower than the model that contained treatment alone, suggesting that occupancy was not substantially different between years (Table 2).

We detected Silver-haired Bats at 41 sites (53.2%). Probability of detection decreased with date, but 85% confidence intervals for the parameter estimate included zero (Table 2). There was a single model in the confidence set for occupancy that included the covariates treatment and year (Table 3). Model-averaged parameter estimates indicated that treatment was informative (Table 2), with occupancy being 2.3 times higher in burned sites and 22.6 times higher in shelterwood sites, compared to control sites (Fig. 3d). The model containing treatment and year was 2.5 AIC_c units lower than the model that contained treatment alone, suggesting that survey year was also an important variable in explaining occupancy. Silver-haired Bat occupancy was 1.4 times higher in 2018 ($\psi_{i+1} = 0.524$, 85% CI: 0.409–0.640) than in 2017 ($\psi_i = 0.365$, 85% CI: 0.253–0.477; Fig. 4).

We detected Eastern Small-footed Myotis at 31 sites (40.3%). Probability of detection decreased with increasing temperature (Table 2). There were 3 models in the confidence set for occupancy; occupancy covariates in these models included treatment, year, and distance to water (Table 3). Model-averaged parameter estimates indicated that treatment was informative (Table 2), with occupancy being 6.5 times higher in burned sites and 10.6 times higher in shelterwood sites, compared to control sites (Fig. 3e).

We detected Northern Long-eared Myotis at 14 sites (18.2%), but we did not detect this



.Figure 2. Vegetation characteristics sampled at acoustic sites, at Fort Indiantown Gap National Guard Training Center, Pennsylvania. Letters represent pairwise differences (*P* < 0.05) among treatments.

species in any control sites. Probability of detection increased with increasing stem density and basal area, but 85% confidence intervals for the stem density parameter estimate included zero (Table 2). There were 2 models in the confidence set for occupancy; occupancy covariates in these models included stem density and basal area (Table 3). Model-averaged parameter estimates indicated that basal area was informative (Table 2). An increase in basal area had a negative effect on occupancy as every 1 m^2/ha increase in basal area resulted in a 0.7% decrease in occupancy (Fig. 5).

Discussion

In this study, we evaluated habitat use of 6 bat species within 3 forest stands that received recent management treatments at Fort Indiantown Gap. Overall, we found that most species were more likely to use recently harvested or burned sites, where vegetation structure had been reduced, compared to unmanaged controls. Due to the lack of spatial replication,

Table 2. Model-averaged parameter estimates, unconditional standard errors (*SE*), and 85% confidence intervals (CI) for covariates included in the confidence set of models ($\Delta AIC_c \leq 2.0$) used to estimate seasonal occupancy (ψ_i) and probability-of-detection (p) of 6 bat species in a managed oak forest, at Fort Indiantown Gap National Guard Training Center, Pennsylvania, May–August 2017 and 2018. Variables following p, γ, and ψ_i intercepts are detection, colonization, and occupancy parameters, respectively. Important covariates (85% confidence intervals that do not include zero) are denoted with an asterisk (*).

			85% confidence interval	
Covariate (by species)	Estimate	SE	Lower	Upper
Big Brown Bat				
p intercept	0.417	0.148	0.205	0.630
stem density*	-0.905	0.259	-1.278	-0.531
date*	0.346	0.141	0.143	0.548
γ intercept	0.794	0.703	-0.129	1.807
ψ_i intercept	0.087	0.283	-0.320	0.494
treatment (burned)*	0.832	0.564	0.020	1.643
treatment (shelterwood)*	1.983	0.845	0.767	3.199
year	0.086	0.276	-0.312	0.484
Eastern Red Bat				
p intercept	0.414	0.209	0.112	0.715
stem density*	-0.938	0.314	-1.390	-0.486
date*	0.609	0.190	0.334	0.883
γ intercept	0.072	0.392	-0.492	0.636
ψ_i intercept	-0.176	0.213	-0.483	0.131
treatment (burned)	0.067	0.465	-0.603	0.737
treatment (shelterwood)	1.048	0.751	-0.033	2.129
year	-0.173	0.205	-0.469	0.122
stem density	-0.376	0.282	-0.783	0.030
basal area	-0.095	0.093	-0.230	0.039

Table 2. Continued.

Covariate (by species)	Estimate	SE	85% confidence interval Lower	Upper
Hoary Bat				
p intercept	-0.439	0.308	-0.883	0.005
stem density*	-0.539	0.358	-1.055	-0.024
γ intercept	-1.215	0.626	-2.115	-0.314
ψ_i intercept	-0.889	0.578	-1.721	-0.057
treatment (burned)	0.192	0.613	-0.690	1.075
treatment (shelterwood)*	2.264	0.742	1.196	3.332
year*	-0.888	0.578	-1.721	-0.056
Silver-haired Bat				
p intercept	-0.107	0.143	-0.314	0.099
Date	-0.197	0.140	-0.399	0.004
γ intercept	-1.052	0.511	-1.788	-0.317
ψ_i intercept	-1.746	0.68	-2.725	-0.767
treatment (burned)*	0.834	0.518	0.088	1.580
treatment (shelterwood)*	3.118	1.075	1.570	4.666
year*	-1.854	0.664	-2.809	-0.898
Eastern Small-footed Myotis				
p intercept	-0.186	0.239	-0.530	0.158
temp*	-0.335	0.179	-0.593	-0.078
γ intercept	-2.495	1.464	-4.603	-0.388
ψ_i intercept	-1.129	0.81	-2.295	0.038
treatment (burned)*	1.876	0.938	0.524	3.227
treatment (shelterwood)*	2.361	1.067	0.825	3.897
water	-0.338	0.243	-0.688	0.012
year	-0.605	0.529	-1.366	0.156
Northern Long-eared Myotis				
p intercept	0.211	0.719	-0.824	1.246
stem density	0.255	0.631	-0.654	1.164
basal area*	0.772	0.406	0.187	1.356
γ intercept	-0.871	0.380	-1.418	-0.324
ψ_i intercept	-0.587	0.389	-1.147	-0.028
stem density	-0.257	0.266	-0.640	0.127
basal area*	-0.737	0.450	-1.386	-0.089

we caution that our findings are limited to our study area on the installation. Despite this limitation, our study provides important information for the conservation and management of imperiled species and, when compared to findings of other studies, can contribute more broadly to our understanding of the effects of forest management on habitat use by bats.

Occupancy of Big Brown Bats, Hoary Bats, and Silver-haired Bats was highest in shelterwood sites, which had the lowest basal area and stem densities, suggesting that methods of overstory removal (at least at the tree-retention level in our study) may have a greater or more immediate potential than burning to increase habitat suitability for these species. Occupancy of Eastern Red Bats and Hoary Bats was also higher, on average, in burned sites relative to control sites. This is consistent with our analyses of vegetation structure, in which burned sites had basal area and stem densities intermediate to control and shelterwood sites. Occupancy of Big Brown Bats and Silver-haired Bats was significantly higher in burned and shelterwood sites compared to control sites.

Our findings support the prediction that medium-to-large species would be positively associated with forest management due to reductions in vegetation structure (Loeb and Waldrop 2008). Bat species adapted to forage in open areas and along forest edges may avoid densely vegetated areas because clutter makes flight and prey detection more difficult (Schnitzler and Kalko 2001). The negative association between forest clutter and habitat use has been documented in other studies in the eastern U.S. (Ford et al. 2006). For example, Silvis et al. (2016) found that activity of Big Brown Bats was negatively related to forest

Table 3. Model with covariates, number of model parameters (*K*), Akaike's Information Criterion adjusted for small sample size (AIC$_c$), difference in AIC$_c$ between a model and the model with the lowest AIC$_c$ value (ΔAIC$_c$), and model weights (w_i) for the confidence set of models (ΔAIC$_c \leq 2.0$) used to estimate seasonal occupancy (ψ_i) and probability-of-detection (*p*) of 6 bat species in a managed oak forest, at Fort Indiantown Gap National Guard Training Center, Pennsylvania, May–August 2017 and 2018. Covariates are defined in Table 1.

Model (by species)	*K*	AIC$_c$	ΔAIC$_c$	w_i
Big Brown Bat				
ψ_i(treatment + year), γ(.), ε = 1-γ, *p*(stem density + date)	7	489.94	0.00	0.499
ψ_i(treatment), γ(.), ε = 1-γ, *p*(stem density + date)	6	491.12	1.18	0.277
Eastern Red Bat				
ψ_i(treatment + year), γ(.), ε = 1-γ, *p*(stem density + date)	7	411.32	0.00	0.330
ψ_i(treatment), γ(.), ε = 1-γ, *p*(stem density + date)	6	412.15	0.83	0.218
ψ_i(stem density + basal area), γ(.), ε = 1-γ, *p*(stem density + date)	6	412.17	0.85	0.216
ψ_i(stem density), γ(.), ε = 1-γ, *p*(stem density + date)	5	413.08	1.76	0.137
Hoary Bat				
ψ_i(treatment + year), γ(.), ε = 1-γ, *p*(stem density)	6	320.30	0.00	0.463
ψ_i(treatment), γ(.), ε = 1-γ, *p*(stem density)	5	320.42	0.12	0.436
Silver-haired Bat				
ψ_i(treatment + year), γ(.), ε = 1-γ, *p*(date)	6	381.34	0.00	0.758
Eastern Small-footed Myotis				
ψ_i(treatment), γ(.), ε = 1-γ, *p*(temp)	5	332.06	0.00	0.483
ψ_i(water), γ(.), ε = 1-γ, *p*(temp)	4	332.81	0.75	0.332
ψ_i(treatment + year), γ(.), ε = 1-γ, *p*(temp)	6	333.98	1.92	0.185
Northern Long-eared Myotis				
ψ_i(stem density + basal area), γ(.), ε = 1-γ, *p*(stem density + basal area)	6	176.20	0.00	0.371
ψ_i(basal area), γ(.), ε = 1-γ, *p*(stem density + basal area)	5	176.35	0.15	0.344

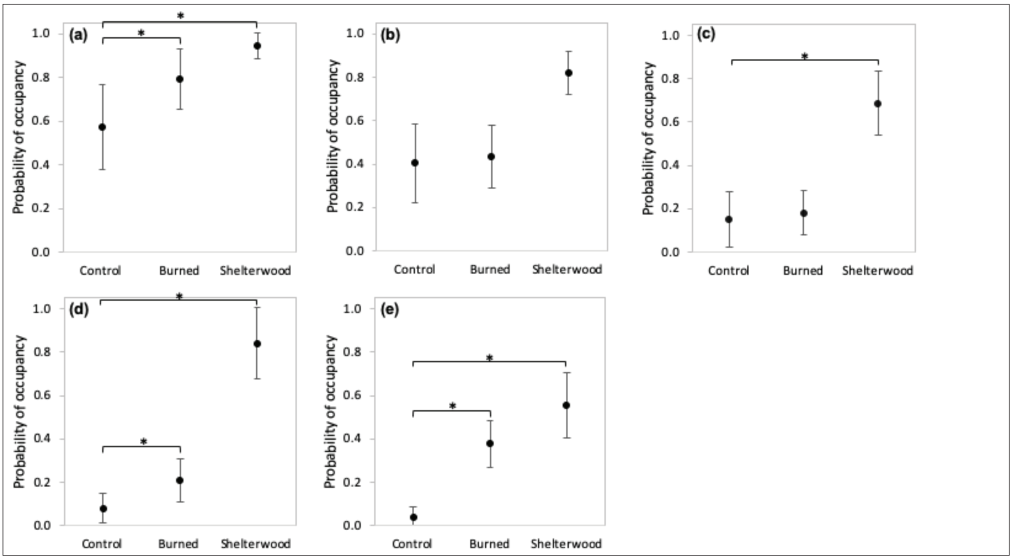


Figure 3. Model-averaged estimates of bat occupancy (ψ_i) as a function of treatment (control, burned, shelterwood), at Fort Indiantown Gap National Guard Training Center, Pennsylvania, May–August 2017 and 2018. Species include: (a) Big Brown Bat; (b) Eastern Red Bat; (c) Hoary Bat; (d) Silver-haired Bat; and (e) Eastern Small-footed Myotis. Error bars represent 85% confidence intervals. Differences in bat occupancy between treatments are denoted with an asterisk (*). Other covariates were assigned to their mean values.

clutter in recently managed forests in Ohio. In Tennessee, activity of Big Brown Bats, Eastern Red Bats, Hoary Bats, and Silver-haired Bats was higher in burned and thinned stands where overstory basal area was lower (Cox et al. 2016). While it is possible that changes in insect prey availability, which we did not directly assess in this study, contributed to higher occupancy in shelterwood and burned sites, previous studies have found little effect of overstory thinning (Dodd et al. 2012) or prescribed fire (Cox et al. 2016) on insect abundance, suggesting that the occupancy patterns we observed were likely in response to structural changes to the forest.

We predicted that small-bodied species would prefer areas with high basal area and stem densities, as their small body size and high-frequency, low-amplitude echolocation calls enable them to exploit cluttered, forested areas (Ratcliffe and Dawson 2003). Contrary to our prediction, occupancy of Eastern Small-footed Myotis was significantly higher in shelterwood and burned sites than control sites. Because we did not record Northern Long-eared Myotis in any control sites, the data were not sufficient to estimate the effect of management treatment on occupancy, but Northern Long-eared Myotis also appeared less likely to use unmanaged sites. A longer sampling duration may have been necessary to document presence of this species, particularly in control sites (USFWS 2024). Because we did not collect pre-treatment data, we were unable to determine whether Eastern Small-footed Myotis and Northern Long-eared Myotis were already present in the shelterwood and burned stands before our recent management treatments were implemented (O'Keefe et al. 2013).

Our findings are consistent with several previous studies that also documented use of recently thinned or burned forests by *Myotis* species. For example, *Myotis* species were more likely to use areas with low stem densities in the mid- and understory layers resulting from recent shelterwood cuts in New York (Gallagher et al. 2021). Similarly, Northern Long-eared Myotis selected harvested forest stands more often than intact stands in West Virginia

Figure 4. Model averaged estimates of Silver-haired Bat occupancy (ψ_i) as a function of survey year, at Fort Indiantown Gap National Guard Training Center, Pennsylvania, May–August 2017 and 2018. Error bars represent 85% confidence intervals.

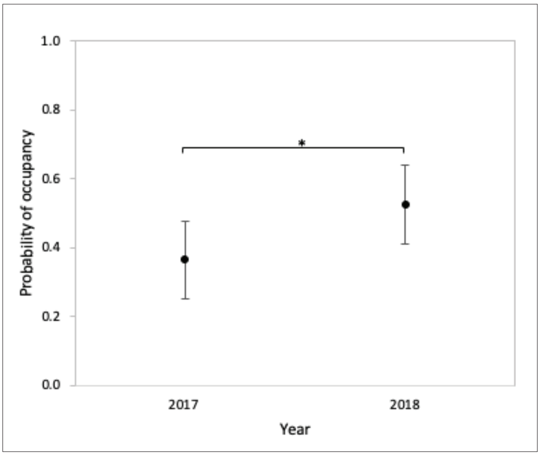
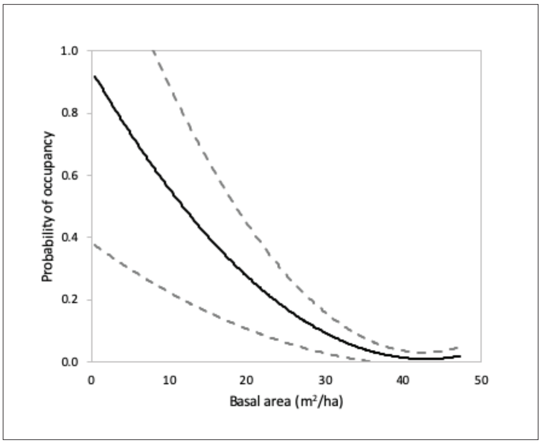


Figure 5. Model averaged estimates of Northern Long-eared Myotis occupancy (ψ_i) as a function of overstory basal area, at Fort Indiantown Gap National Guard Training Center, Pennsylvania, May–August 2017 and 2018. Dashed lines represent 85% confidence intervals.



(Owen et al. 2003). Burns et al. (2019) also found that occupancy of *Myotis* species was positively associated with burning in mixed pine-oak forests in Tennessee and Kentucky. Overall, it appears that, although small-bodied species can tolerate a greater degree of forest clutter, they may also often benefit from more open conditions created by overstory thinning and prescribed fire.

An increase in stem density had a negative effect on the probability of detecting Big Brown Bats, Eastern Red Bats, and Hoary Bats. This was expected as dense vegetation attenuates echolocation calls, thereby reducing the distance from a detector that a bat can be recorded (Schnitzler and Kalko 2001). In contrast, Northern Long-eared Myotis, when present, were more likely to be detected in sites with higher basal area. An increase in Julian date had a positive effect on the probability of detecting Big Brown Bats and Eastern Red Bats, consistent with seasonal activity patterns for these species on the installation (Hauer et al. 2023).

Our study assessed the short-term (<4 years) effects of shelterwood harvest and prescribed fire on use of forests by bats. Over time, managed forests may eventually regenerate to dense forests with a high degree of clutter in the mid- and understories (Guldin et al. 2007), making them less suitable for some species (Blakey et al. 2016). Changes in vegetation structure should be monitored in forested areas that have been thinned or burned because bat use of these areas may change over time (Cox et al. 2016). The effects of overstory thinning and prescribed fire on roosting habitat should also be evaluated and considered when implementing forest management strategies for bats. Overall, we encourage the implementation of occupancy studies alongside forest management actions like this study to further our understanding of how management influences use of forests by different bat species.

Acknowledgments

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