

Foraging patterns of Rafinesque's big-eared bat in upland forests managed with prescribed fire

Authors: Johnson, Joseph S., Lacki, Michael J., and Fulton, Shelby A.

Source: Journal of Mammalogy, 100(2) : 500-509

Published By: American Society of Mammalogists

URL: <https://doi.org/10.1093/jmammal/gyz039>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.



Foraging patterns of Rafinesque's big-eared bat in upland forests managed with prescribed fire

JOSEPH S. JOHNSON,* MICHAEL J. LACKI, AND SHELBY A. FULTON

Department of Biological Sciences, Ohio University, Athens, OH 45701, USA (JSJ)

Department of Forestry and Natural Resources, University of Kentucky, Lexington, KY 40546, USA (MJL)

Kentucky State Nature Preserves Commission, Frankfort, KY 40601, USA (SAF)

* Correspondent: jjohnson@ohio.edu

Fire is an important natural disturbance recently reintroduced into many North American ecosystems, spurring questions regarding how fire affects forest wildlife. Bats are an ecologically significant group within North American forests, and the diversity of this group includes species that may benefit or suffer negative impacts from habitat changes initiated by prescribed fires. To determine how fire affects a rare bat species that specializes on gleaning moths from forest vegetation, we studied home ranges and nocturnal habitat selection in Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) in an upland forest ecosystem where small-scale, low-to-moderate intensity prescribed burning occurs in spring. We found home ranges of big-eared bats to be notably small ($\bar{x} = 169$ ha; $n = 41$), not different in size among sexes and reproductive classes, and located nonrandomly on the landscape. Home ranges of females were located farthest from riparian areas, whereas home ranges of males were farthest from burned forests. Home ranges of lactating and postlactating females were closer to burned forests than expected, but no group of females had home ranges located closer to or farther from burned forests relative to unburned forests. All groups used habitats randomly within home ranges. Moth abundance and diversity (number of families) were lowest in riparian habitats, indicating that habitat selection by female bats at the landscape, but not home range, scale was influenced by prey availability. Results indicate that low-to-moderate intensity prescribed fires weakly affected the foraging patterns of Rafinesque's big-eared bats in upland forest ecosystems, provided burned forests exist in a matrix of unburned or less-frequently burned forest stands that support a diverse and abundant lepidopteran prey base.

Key words: Chiroptera, *Corynorhinus rafinesquii*, disturbance ecology, fire ecology, habitat selection, home range, Lepidoptera, moths, prescribed burning

The study of spatial and temporal habitat use by animals has a rich empirical and theoretical history (Burt 1943; Johnson 1980; Van Moorter et al. 2016). Ecologists and land stewards charged with conserving critical habitats for rare or otherwise important animal species have always valued such studies, which are increasingly complicated by environmental change and the ubiquitous impact of human activities (Hautier et al. 2015; Ruddiman et al. 2015). One of the many ways humans affect the environment is by altering disturbance regimes (Turner 2010). Environmental disturbances, both anthropogenic and otherwise, create spatial and temporal heterogeneity of landscapes (Sousa 1984; White and Jentsch 2001). This in turn influences animal movements, which are products of interactions between animals and their environment, including physical properties

and the availability of food and other resources (Börger et al. 2008).

Wild and prescribed fires are notable disturbance events that are increasing in frequency throughout North America (Ryan et al. 2013). This increase represents a shift in policy among land management agencies, many of which suppressed wildfires throughout much of the 20th century. In parts of the western United States, decades of fire suppression have led to an accumulation of combustible fuels, resulting in high-severity, stand-replacing wildfires (Kilgore and Taylor 1979), while the absence of fire from some eastern ecosystems is associated with a feedback cycle promoting mesophication, decreased stem diameters, and increased stem densities (Nowacki and Abrams 2008). Thus, fire and management of this disturbance

regime affects the structure of the physical environment and the composition of biotic communities. Although prescribed fire has gained popularity as a management tool for returning landscapes to desired historical conditions, as well as for wildlife conservation (Walters 1991; Ryan et al. 2013), there are large gaps in our understanding of how fire affects native wildlife (Pilliod et al. 2003).

The impacts of fire, after decades of suppression, on habitat selection by wildlife appear to be highly context dependent, precluding generalities and demonstrating the need for research specific to individual species and ecosystems (Converse et al. 2006; Fontaine and Kennedy 2012; Pastro et al. 2014). This need applies to bats despite considerable research on effects of fire (reviewed by Perry 2012). Although North American bats are all relatively small (< 40 g), their home ranges can exceed 1,000 ha, encompassing habitats used differently for roosting (daytime) and foraging (nighttime) (Johnson et al. 2007; Lacki et al. 2007; Harvey et al. 2011). Thus, bats are highly mobile and use a variety of habitats that may be affected differently by fire. For roosting, several bat species rely on dead trees, or those with cavities, for shelters, with females forming maternity colonies in especially large trees (Barclay and Kurta 2007). Fires often destroy existing tree roosts while creating others, with the magnitude of these changes varying with the timing, intensity, and frequency of fires (Morrison and Raphael 1993; Bagne et al. 2008; Perry 2012). However, not all bats roost primarily in trees. For species that rely more heavily on structures such as caves and buildings, fires are unlikely to influence roost availability, although buildings may occasionally be vulnerable.

Impacts of fire on foraging habitat of bats are more complex, including potential changes to forest structure and shifts in availability of insect prey (Buchalski et al. 2013). It is widely believed that bats are negatively affected by dense forest vegetation that can impede flight (hereafter, clutter—Brigham et al. 1997). Thus, it is often predicted that bats should respond positively to fire, especially less-maneuverable species (Loeb and Waldrop 2008; Armitage and Ober 2012; Lacki et al. 2017). While some studies have provided support for this prediction (Loeb and Waldrop 2008; Armitage and Ober 2012), others found no differences in bat activity following fires (Lacki et al. 2017). One commonality in these studies is the use of acoustic bat detectors to monitor responses of bats. While bat detectors can cost-effectively sample the activity of bats at various spatial and temporal scales, this methodology has a number of limitations, including difficulties in species-level identification, equating the number of bat calls recorded to numbers of bats, and species detection biases (Hayes 2000). Studies quantifying the effects of fire on insects have also met with inconsistent results, with taxa demonstrating variable responses to fire (Swengel 2001; Thill et al. 2004; Lacki et al. 2009; Armitage and Ober 2012; Perry 2012). Inconsistent trends are not surprising given the variable ecological context of each study, but do highlight room for studies of bat movement in relation to fire management and prey availability to improve our understanding of fire effects.

The uncertainty regarding impacts of fire indicates special care is needed when burning in areas occupied by rare, specialist bat species. One such species is Rafinesque's big-eared

bat (*Corynorhinus rafinesquii*), which is uncommon and considered vulnerable throughout its range (Bayless et al. 2011). Rafinesque's big-eared bat is a moth specialist that often gleans prey directly off vegetation during flight (Hurst and Lacki 1997; Lacki and Ladeur 2001; Johnson and Lacki 2013). Adapted for slow, agile flight (Norberg and Rayner 1987), these bats have small home ranges and typically do not forage far from their roosts (Hurst and Lacki 1999; Menzel et al. 2001; Johnson and Lacki 2013). Thus, abrupt changes to the quality of foraging habitats surrounding roosts could significantly affect these bats. Our purpose was to measure habitat selection of Rafinesque's big-eared bat in a landscape managed with low-to-moderate intensity spring burns (Lacki et al. 2017). We predicted that 1) moth family richness and total abundance would be greatest in forest stands burned in the last 4 years compared to those not treated with prescribed fire; and 2) big-eared bats would select habitats with higher prey abundance and diversity for nocturnal foraging.

MATERIALS AND METHODS

Study areas.—We conducted our study in Mammoth Cave National Park, Kentucky, United States (37.2072° N, 86.1319° W). Forests regenerating over agricultural use predating establishment of the National Park cover the majority of the area, which is surrounded by a landscape heavily fragmented by human use. Mammoth Cave National Park contains a number of forest communities found on soils ranging from xeric to mesic (Olson and Noble 2005). These communities can be broadly classified as deciduous, coniferous, and mixed coniferous-deciduous forests, and a small amount of prairie and open areas. Species typically found in deciduous forests include chestnut oak (*Quercus prinus*), post oak (*Q. stellata*), chinkapin oak (*Q. muehlenbergii*), blackjack oak (*Q. marilandica*), white oak (*Q. alba*), black oak (*Q. velutina*), pignut hickory (*Carya glabra*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and American sycamore (*Platanus occidentalis*). Species found in coniferous forests are more limited and include Virginia pine (*Pinus virginiana*) and eastern red cedar (*Juniperus virginiana*). Mixed forests typically include both coniferous species along with red maple (*A. rubrum*), tulip poplar (*Liriodendron tulipifera*), and sweetgum (*Liquidambar styraciflua*). Numerous small drainages to the Green River, which runs through the southern portion of the park, cut through limestone and sandstone bedrock creating a topographically diverse landscape. This erosion of limestone bedrock is responsible for creating the Mammoth Cave system, as well as the creation of hundreds of smaller caves, which are used by Rafinesque's big-eared bats during summer and winter (Johnson et al. 2012; Johnson and Lacki 2014). Big-eared bats in the park also roost in building attics, concrete structures, sandstone rock shelters, and large, hollow live trees.

Remains of ancient plant material found in caves within the park indicate open woodlands and savannahs existed before European settlement, warranting restoration of a portion of upland forests to these historical conditions (Olson and Noble 2005). Fire was reintroduced to Mammoth Cave in 2002, when

11 ha of forest were burned during a prescribed treatment near the northwestern boundary of the park. Larger tracts were burned in 2004 (approximately 246 ha) and 2005 (approximately 233 ha) before the use of fire increased between 2007 and 2010, when a total area of > 5,300 ha was burned.

Capture and radiotelemetry.—All methods were approved by the University of Kentucky's Institutional Animal Care and Use Committee (UK IACUC No. A3336-01), the National Park Service (NPS IACUC No. 2011-30) and follow the American Society of Mammalogist's guidelines for use of wild animals in research (Sikes et al. 2016). We captured bats in mist nets (Avinet, Inc., Dryden, New York) placed over forest roads, ponds, and nearby known day-roosts of Rafinesque's big-eared bats during the summers (May–September) of 2009–2011. We recorded the age, sex, reproductive condition, and body mass of all bats captured, and selected adult male and female Rafinesque's big-eared bats for study. We determined the age of bats (adult versus juvenile) by examining epiphyseal-diaphyseal fusions of long bones in the wing, determined female reproductive condition (nonreproductive versus pregnant, lactating, or postlactating) based on the presence of a fetus or teat condition, and determined male reproductive condition (scrotal versus nonscrotal) based on swelling of the epididymides (Brunet-Rossini and Wilkinson 2009; Racey 2009). When possible, we affixed 0.42-g radio-transmitters (model LB-2N and LB-2N-T, Holohil Systems, Ltd., Carp, Ontario, Canada) between the shoulder blades of adult males and females using surgical adhesive (Torbot, Cranston, RI; Perma-Type, Plainville, Connecticut). Transmitters weighed 2.8–5.3% ($\bar{x} = 4.1\%$) of the body mass of tagged bats.

We tracked bats to their day-roosts every day to study diurnal roosts (reported in Johnson and Lacki 2014) and during the evening to assess habitat selection during nightly foraging bouts. To achieve the latter, we biangulated nighttime locations of bats for 5 h following sunset on 64 evenings between 2009 and 2011. Radiotagged bats were tracked for 2–5 ($\bar{x} = 3.5$) nights each. For each biangulation, we simultaneously collected directional bearings from two field personnel stationed in different locations. We did not triangulate locations because the complex topography of our study area limited the range of radio signals to < 500 m and limited the number of locations from which signals could be detected, making it impractical to collect a third azimuth from a location that was distinct from the other two. Because of this limited range, we moved nighttime telemetry stations throughout the evening, effectively following bats across the landscape. Because big-eared bats had small home ranges, we were able to track them along hiking trails and roads, allowing us to follow bats to specific habitat patches. We calculated the error distance of biangulations as 157 m using transmitters in known locations.

We biangulated bats at 2-min intervals based on consideration of our study objectives and knowledge of our study species (Kernohan et al. 2001). Bats in our study often made relatively quick commutes between foraging areas, and we found that locating bats at longer intervals resulted in losing signals on bats without indication of their destinations,

reducing our ability to follow bats and document high-use areas. Thus, we attempted to repeatedly locate a single bat at 2-min intervals for 10 min (five locations), after which time we would attempt to locate other radiotagged bats. To reduce the biasing effects of “burst sampling,” we did not generate > 5 locations for a bat within 30-min. We used Schoener's ratio (Schoener 1981) to determine the extent of autocorrelation in these data, yielding a t^2/r^2 value of 1.4. Thus, our data contained moderate autocorrelation (Swihart and Slade 1997). We did not reduce our data set in an attempt to eliminate autocorrelation (sensu Swihart and Slade 1985) as the cost of using moderate autocorrelation is low (Swihart and Slade 1997) while eliminating locations for the sake of complete independence reduces biological relevance of telemetry data when determining animal home ranges (De Solla et al. 1999). Similarly, eliminating moderately autocorrelated data may result in the loss of data reflecting selection of specific habitat patches, such as in the case of bats foraging for brief periods before stopping to night-roost.

Home ranges and habitat selection.—We discarded five biangulated points that were located > 1 km from either observer's position because this was well beyond the maximum reception distance that we observed while tracking bats to day-roosts, indicating error during tracking or data recording. Using the remainder of our locations, we generated 95% (hereafter, home range) and 50% (hereafter, core area) probability areas using the fixed kernel method with least squares cross-validation (Worton 1989). Locations of day-roosts were included in kernel estimates, with each roost used as a single location regardless of the frequency of its use to avoid skewing kernel estimates with daytime locations that bats would often visit every day, sometimes for several weeks. We only calculated kernel areas for bats with ≥ 30 locations, based on our previous analysis of the effect of sample size (Johnson and Lacki 2011). We compared the size of home ranges and core areas among sex and reproductive classes of bats using one-way analysis of variance (ANOVA). Scrotal ($n = 4$) and nonscrotal ($n = 4$) males were grouped together for this and all other analyses due to small sample sizes for each group. The significance threshold of these and all other statistical analyses was set to $P \leq 0.05$.

To assess our prediction on foraging patterns, we measured nighttime habitat selection at two scales: placement of home ranges on the landscape (second-order selection) and use of habitats within home ranges (third-order selection—Johnson 1980). We analyzed habitat selection using the Euclidean distance method, which determines if locations are found closer to or farther from available habitats than expected based on random patterns (Conner and Plowman 2001; Conner et al. 2003). This method was ideally suited for our data because it compares minimum distances between estimated animal locations and nearby habitats patches to minimum distances between random locations and those habitats. It is robust to moderate telemetry error and thus does not require modeling of error distributions (Conner et al. 2003). The Euclidean distance method also takes patch size and shape into account. For third-order selection, we generated a number of random locations within each bat home range that was equal to the number of telemetry locations used

to estimate that area. For second-order selection, we created four “study areas” within the park and generated 1,000 random locations within each area. These study areas corresponded to four big-eared bat colonies that did not occupy similar roosts and did not have overlapping home ranges (Fig. 1). We defined each area by buffering telemetry locations by a 3-km distance and drawing a minimum convex polygon around this area. We chose 3 km because we observed several bats traveling up to 3 km between roosts on consecutive days during > 700 days of observation (daytime telemetry methods are described in Johnson and Lacki 2014). Based on this large data set of movements, we concluded that areas within 3 km of any telemetry location were available for big-eared bats to establish as part of their home range, but that areas outside of this buffer were unlikely to be visited and their inclusion could produce spurious correlations. We compared mean distances between telemetry locations and available habitats to mean distances between random locations and habitats using a multivariate analysis of variance (MANOVA) for both spatial scales. We compared use of each habitat type using pairwise *t*-tests with a Holm–Bonferroni adjustment when the MANOVA was significant, and ranked habitats as closest to farthest from bat locations.

We included four habitat types in our distance analysis, obtaining spatial habitat data from the 2001 National Land-cover Database (Homer et al. 2004) and supplementing these data with spatial data on burned habitats provided by National Park Service (Fig. 2). Habitats were unburned deciduous forests (51% of the combined study area), unburned mixed coniferous and deciduous forests (16%), deciduous and mixed forests burned within the last 10 years (2002–2010; 25%), and riparian

zones (1%). Although prescribed fire was reintroduced to the park in 2002, 92% of the area burned before the end of our study was burned between 2007 and 2010. We grouped burned areas together regardless of their age because prescribed fires were relatively small, averaging 252 ha, and occurred in isolated areas within the park each year. As a result, each study area contained stands burned in different years. Thus, grouping burned stands together was necessary to avoid spurious habitat selection results stemming from rarity of each year’s burn. Similarly, we elected to combine burned deciduous forests with burned mixed forests. Despite not including year since burn as a variable in our analysis, examination of telemetry locations in relation to relatively recent and older burns revealed similar nocturnal behaviors. Agricultural areas, grasslands, human developments, and forested wetlands were not included in the analysis because they were rare (collectively < 7%). Habitat edges were not included in our analysis because the types of edges known to influence nocturnal foraging, edges between forested and nonforested habitats, were uncommon in the park (Morris et al. 2010). Riparian areas were included in our analyses despite their low overall cover because these were prominent features found in the areas surrounding the four bat colonies. We based these riparian areas on perennial streams in the study area, which were limited to large river corridors such as the Green River, and excluded smaller headwaters. The relatively small portion of the study areas extending past the boundary of the national park was treated the same as habitats within the park.

Prey diversity and abundance.—We measured total moth abundance and family richness across habitats to determine the effect of prescribed fire on big-eared bat prey. We sampled moths



Fig. 1.—Generalized locations of our four study areas (circled areas) within Mammoth Cave National Park. Map at bottom left shows the location of the park within Kentucky, United States. Exact locations are obscured to protect the species and vulnerable habitats.

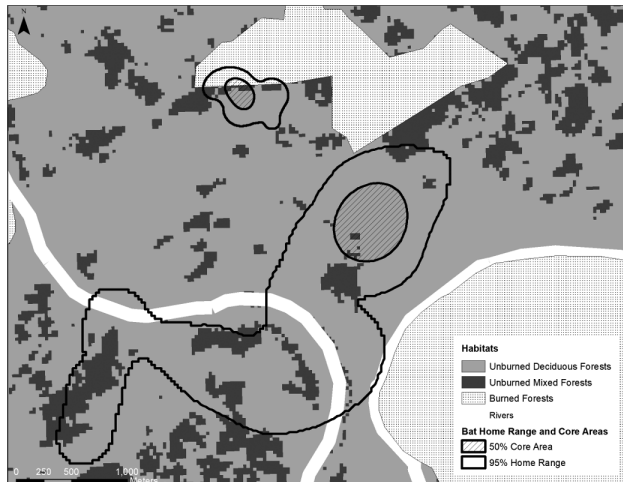


Fig. 2.—Home range and core areas for a postlactating female (smaller range) and male (larger range) Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) determined by radiotelemetry in Mammoth Cave National Park, Kentucky, United States. Bats were tracked concurrently and displayed differing use of a forest stand burned the previous year. Locations are not provided in order to protect the species and vulnerable habitats.

using black light traps containing a jar of ethyl acetate during 17 evenings from 2009 to 2011. We only sampled insects on nights when we collected nighttime telemetry data and similarly limited insect collections to 5 h following sunset. On these evenings, we deployed one black light trap in each habitat, ≥ 50 m from the nearest edge to ensure insects collected were representative of the habitat sampled. We emphasize that these were edges between different forest communities, and not edges between forested and nonforested communities known to be important for bat foraging (Morris et al. 2010). We established three sets of sampling locations, each containing all four habitats, throughout the park to account for variation within habitats. Following collection, we identified all moths to the family level, including the recently defined families within Noctuoidea (LaFontaine and Schmidt 2010), and enumerated the number of moths belonging to each family. Moths with wingspans < 10 mm that could not be identified to family were classified as micro-lepidoptera. We compared the total number of moths captured as well as the number of moth families (family richness), using micro-lepidoptera as a single family, among habitats with a one-way ANOVA. We applied a log transformation to abundance data and a square root transformation to diversity data to meet assumptions of normality prior to analysis. We compared the number of captured moths belonging to commonly observed families among habitats using Kruskal–Wallis tests because these data could not be transformed to meet the assumptions of parametric tests. Where significant differences were found, we used Dunn's multiple comparison tests. For this analysis, we defined commonly observed families as families with > 100 captures, but excluding groups where $> 20\%$ of the total observations came from a single sample.

RESULTS

Home ranges and habitat selection.—We radiotagged 59 adult Rafinesque's big-eared bats and collected > 30 nighttime

locations ($\bar{x} = 38 \pm 2.0$ SE) on 41 of these bats. We tracked pregnant females between 13 May and 4 June, lactating females between 11 June and 2 July, and postlactating females between 13 July and 28 August, of each year. Nonreproductive females and males were tracked throughout the entire period. Home range ($F_{4,36} = 1.7$, $P = 0.18$) and core area ($F_{4,36} = 1.0$, $P = 0.41$) estimates did not differ among sex and reproductive classes (Fig. 3). Home range estimates ranged from 14 to 480 ha ($\bar{x} = 170$ ha, $SE = 19$). Core area estimates ranged from 1.1 to 88 ha ($\bar{x} = 25$ ha, $SE = 3.0$).

To assess our prediction on big-eared bat foraging, we assessed second- and third-order selection separately for males and each female reproductive class. Second-order use differed from random use for all groups, but with differing patterns of selection (Table 1). Some groups were located significantly closer to burned forests than expected by chance, but no group was located farther from burned forests than expected. Home ranges of pregnant (Wilk's $\lambda = 0.01$, $F = 90.1$, $P < 0.01$) and nonreproductive (Wilk's $\lambda = 0.001$, $F = 536$, $P = 0.002$) females were closer to mixed and deciduous forest types than riparian areas, but no closer to or farther from burned forests than any other habitat. Those of lactating females (Wilk's $\lambda = 0.02$, $F = 50.7$, $P < 0.001$) were closer to burned and mixed forests than riparian areas. Home ranges of postlactating females (Wilk's $\lambda = 0.10$, $F = 16.6$, $P = 0.001$) were located closer to burned forests than riparian areas. Finally, home ranges of males (Wilk's $\lambda = 0.004$, $F = 245$, $P < 0.001$) were located closer to deciduous and mixed forests than burned forests and closer to riparian areas than burned forests. Third-order use did not differ from random use for any group (pregnant females: Wilk's $\lambda = 0.16$, $F = 3.8$, $P = 0.15$; lactating females: Wilk's $\lambda = 0.401$, $F = 1.9$, $P = 0.25$; postlactating females: Wilk's $\lambda = 0.38$, $F = 2.9$, $P = 0.11$; nonreproductive females: Wilk's $\lambda = 0.18$, $F = 2.3$, $P = 0.33$; males: Wilk's $\lambda = 0.42$, $F = 1.4$, $P = 0.38$).

Prey diversity and abundance.—We collected 19,139 moths belonging to 25 families (Apatelodidae, Cossidae, Cosmopterigidae, Crambidae, Drepanidae, Epipyropidae, Elachistidae, Erebidae, Euteliidae, Gelechiidae, Geometridae, Lasiocampidae, Limacodidae, Megalopygidae, Mimallonidae, Noctuidae, Notodontidae, Oecophoridae, Pterophoridae, Pyralidae, Saturniidae, Sphingidae, Tortricidae, Yponomeutidae, and Zygaenidae) plus micro-lepidopterans. One black light trap placed in a riparian area failed and was excluded from analyses. To assess our prediction that a greater abundance and diversity (at the family level) of Lepidoptera would be found in forests treated with prescribed fire, we compared moth captures among habitat types. Moth family richness ($F_{3,63} = 3.2$, $P = 0.03$) and overall abundance of moths ($F_{3,63} = 5.3$, $P < 0.01$) differed among habitats, with lesser moth abundance and family richness observed in riparian areas (Fig. 4). Of the 25 moth families that we identified, six families plus micro-lepidopterans met our standard for commonly observed families. Of these groups, the total number of Erebidae, Geometridae, Notodontidae, and micro-lepidoptera differed among habitats (Table 2). Erebidae, Notodontidae, and micro-lepidopterans were captured in greater numbers in deciduous, mixed, and burned forests than in riparian areas. Geometridae were also captured in greater

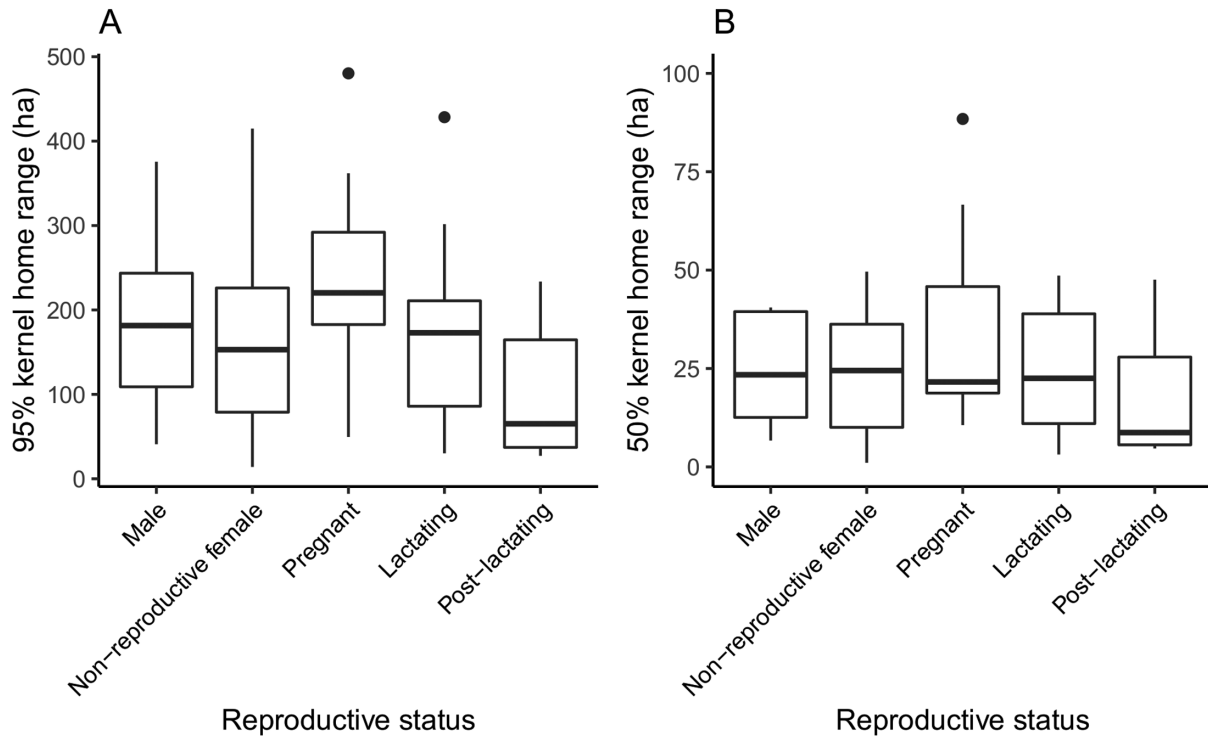


Fig. 3.—Home range (A) and core area (B) estimates did not vary among sexes and reproductive classes of Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) radiotracked in Mammoth Cave National Park, Kentucky, United States, during the summers of 2009–2011. In each panel, boxes contain the interquartile range separated by the median, and observations outside 1.5 times the interquartile range are denoted with a closed circle.

Table 1.—Landscape-scale (second-order) habitat selection by Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) in Mammoth Cave National Park, Kentucky, United States, radiotracked during the summers of 2009–2011. Numbers in brackets are sample sizes. Numbers in parentheses are quotients of the mean distance between telemetry locations and each habitat type divided by mean distances between random locations and each habitat type, plus *SE*. Numbers < 1.0 indicate that bats were located closer to a habitat type than were random locations. Within rows, home ranges are located significantly closer or farther from habitats not sharing common letters ($P < 0.05$). Habitats followed by an * indicate home ranges were located significantly closer to these habitats than random.

Sex and reproductive groups	Habitats			
	Closest		Farthest	
Nonreproductive females [6]	Deciduous forests ^{*A} (0.22 ± 0.11)	Mixed forests ^{*A} (0.33 ± 0.05)	Burned forests ^{A,B} (0.73 ± 0.20)	Riparian areas ^B (1.3 ± 0.21)
Pregnant females [7]	Mixed forests ^{*A} (0.24 ± 0.08)	Deciduous forests ^{*A} (0.24 ± 0.13)	Burned forests ^{A,B} (1.0 ± 0.18)	Riparian areas ^B (1.2 ± 0.24)
Lactating females [9]	Burned forests ^{*A} (0.29 ± 0.10)	Mixed forests ^{*A} (0.63 ± 0.12)	Deciduous forests ^{A,B} (0.73 ± 0.23)	Riparian areas ^B (1.0 ± 0.10)
Postlactating females [11]	Burned forests ^{*A} (0.36 ± 0.15)	Mixed forests ^{*A,B} (0.53 ± 0.13)	Deciduous forests ^{*A,B} (0.52 ± 0.15)	Riparian areas ^B (0.96 ± 0.14)
Males [8]	Deciduous forests ^{*A} (0.11 ± 0.03)	Mixed forests ^{*A} (0.23 ± 0.05)	Riparian areas ^B (0.63 ± 0.07)	Burned forests ^C (1.1 ± 0.12)

numbers outside of riparian areas and were captured more in mixed forests than in burned forests.

DISCUSSION

We found that Rafinesque's big-eared bats placed their home ranges nonrandomly throughout a heavily forested landscape, but that habitat selection within home ranges was random. Contrary to our prediction, we did not observe differences in moth diversity or abundance between burned and unburned forest stands. However, we did find partial support for our prediction that

habitat selection would be influenced by moth family diversity and abundance, with female home ranges located farther from riparian areas, where moth abundance and diversity were lowest, than other habitats. Reproductive groups of big-eared bats varied in the placement of their home ranges with respect to burned forests. Lactating and postlactating females placed their home ranges significantly closer to burned areas than expected by chance, although home ranges of no group were significantly closer to burned forests than to unburned forests, and those of males were located farther away from burned areas than other habitats. Together, these results suggest that low-to-moderate

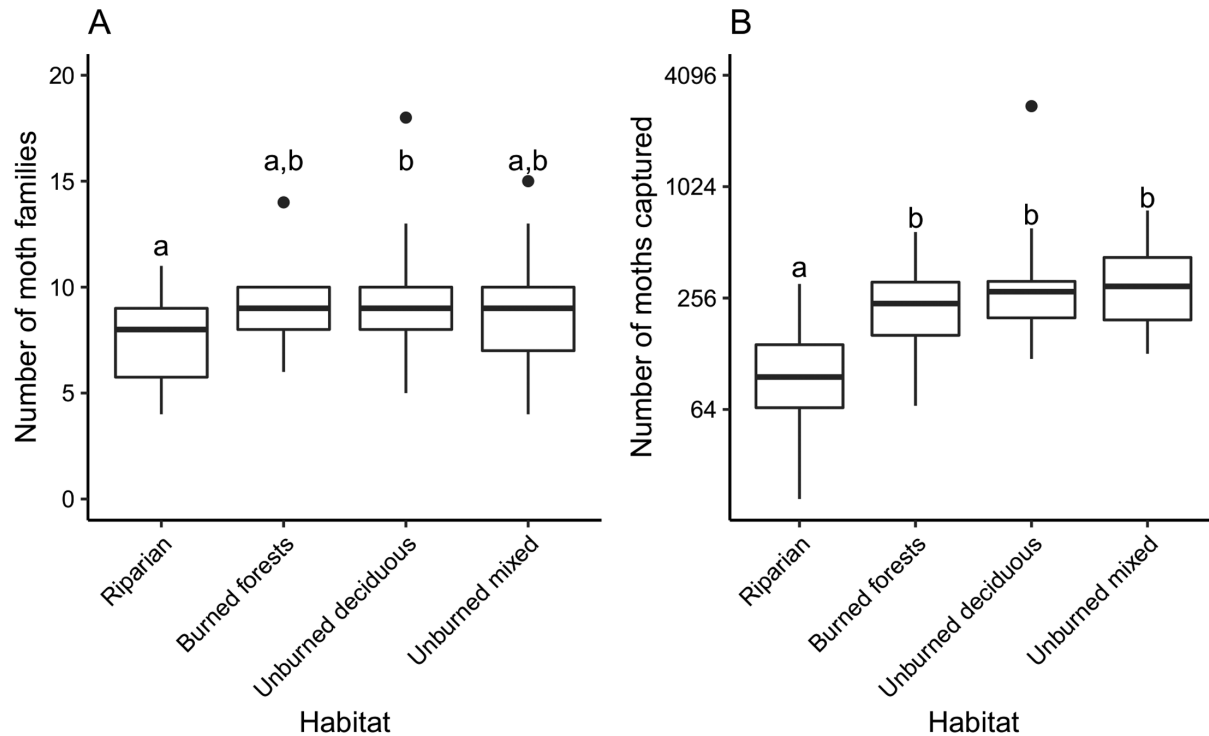


Fig. 4.—The number of moth families (A) and total number of moths (B) captured in black light traps varied among habitats sampled at Mammoth Cave National Park, Kentucky, United States, during the summers of 2009–2011. In each panel, boxes contain the interquartile range separated by the median, and observations outside 1.5 times the interquartile range are denoted with a closed circle. Box and whiskers not sharing common letters are significantly different ($P < 0.05$).

Table 2.—Mean (\pm standard error) number of commonly captured moth families across forest habitat types in Mammoth Cave National Park, Kentucky, United States, during the summers of 2009–2011. Within rows, the numbers of moths captured varied between habitats not sharing common letters ($P < 0.05$).

Family (<i>n</i>)	Riparian	Burned forests	Deciduous forests	Mixed forests
Erebidae (3,441)	16.1 \pm 3.8 ^A	56.8 \pm 14.8 ^B	67.2 \pm 14.5 ^B	63.2 \pm 15.0 ^B
Geometridae (1,699)	10.6 \pm 2.5 ^A	18.2 \pm 2.5 ^B	29.6 \pm 8.9 ^{B,C}	42.1 \pm 7.2 ^C
Noctuidae (1,453)	15.4 \pm 4.5	22.5 \pm 3.6	21.9 \pm 5.5	25.5 \pm 4.8
Notodontidae (433)	1.3 \pm 0.5 ^A	7.7 \pm 1.5 ^B	9.1 \pm 2.6 ^B	7.4 \pm 2.1 ^B
Pyralidae (2,004)	16.7 \pm 3.9	22.5 \pm 4.6	49.7 \pm 17.8	29.9 \pm 6.7
Saturniidae (303)	1.4 \pm 0.7	3.2 \pm 1.0	8.2 \pm 3.9	5.2 \pm 1.5
Micro-lepidoptera (8,322)	32.7 \pm 7.4 ^A	109 \pm 26.4 ^B	191 \pm 107 ^B	159 \pm 45.4 ^B

intensity prescribed fires weakly affect foraging patterns of Rafinesque's big-eared bats occupying forested landscapes supporting a diverse assemblage of moth prey.

Home ranges of big-eared bats in our study ($\bar{x} = 170$ ha) were remarkably similar to those reported for western Kentucky (170 ha—Johnson and Lacki 2013), South Carolina (95 ha—Menzel et al. 2001), and southeastern Kentucky (161 ha—Hurst and Lacki 1999). These home ranges are small compared to many North American bat species which, although highly variable, can exceed 1,000 ha (Lacki et al. 2007; Womack et al. 2013; Moore et al. 2017). Given the relatively small size of home ranges, it is not surprising that we found home ranges to be nonrandomly distributed on the landscape. For females, which face the large energetic demands of raising young and entering hibernation with fat reserves sufficient enough to both overwinter and ovulate upon emergence (Kunz et al. 1998), home ranges were located closest to habitat types supporting

the greatest diversity and abundance of moths. Differences in moth abundance and family diversity were primarily driven by captures of moths in the families Erebidae, Geometridae, and Notodontidae, as well as micro-lepidopterans, which were less abundant in riparian areas than other forested habitats. Erebidae, Geometridae, and Notodontidae include species commonly consumed by Rafinesque's big-eared bats in our study area (Dodd et al. 2015). With the exception of the Geometridae, the abundance of these families did not differ among the nonriparian forest types, closely resembling habitat selection in female big-eared bats. While we were able to detect some significant differences with our sampling intensity, considerable variation in the availability of moths exists. Variability within and across years of sampling likely contributed to this variation, and closer examination of seasonal availability of moth prey may further explain habitat selection by big-eared bats throughout their home range.

Although it is not surprising that habitat selection by a specialist predator such as Rafinesque's big-eared bat is influenced by food availability, these results differ from a study of this species in bottomland hardwood forests (Johnson and Lacki 2013). In the seasonally flooded forests in western Kentucky, big-eared bat home ranges were located closer to habitats with greater availability of roosting habitat rather than abundance of prey. In those bottomland hardwood forests, big-eared bats roosted exclusively in large, hollow trees located primarily in a single habitat type on the landscape, whereas in the present study, bats roosted in buildings, caves, and trees that were not associated with a single habitat type (Johnson and Lacki 2014). While it is not possible to directly evaluate the relative influence of roosting habitat and prey availability on habitat selection in these two studies, the possibility that differences in availability of roosting habitat influence local differences in foraging patterns across the range of Rafinesque's big-eared bat merits additional research.

Although abundance of preferred prey influenced habitat selection at the landscape scale, habitat selection at the home range scale was random. Random selection at this scale was partly a result of behaviors such as the length of time bats spent within individual habitat patches, and the time between return visits (Van Moorter et al. 2016). Although we did not quantify the movement patterns of big-eared bats in our study, we made several observations of these phenomena. First, bats typically foraged in the area immediately surrounding their day-roost for 0.5–1 h following their nighttime emergence, after which they would make flights to habitat patches where they would remain for one or more hours. This observation is consistent with the work of Van Moorter et al. (2016), who showed that longer residence times are associated with smaller home ranges. This pattern is also reflected in foraging behaviors of bats in the genus *Corynorhinus*, all of which are slow, agile predators specializing on gleaning moths from vegetation (Lacki and Dodd 2011). We suggest this hunting strategy requires *Corynorhinus* species to spend relatively large amounts of time in a habitat patch and, therefore, partly explains small home ranges in these species. Second, we frequently observed bats returning to their day-roost for short periods before returning to the same habitat patches to resume foraging on the same evening, resulting in short time to return intervals, which are also associated with smaller home ranges (Van Moorter et al. 2016). Bats may roost during the night to digest or cull wings from moths before eating (Lacki and Dodd 2011), and lactating females may return to nurse young (Clark et al. 1993). Thus, small home ranges, and random habitat selection within these areas, are not surprising given the unique ecological morphology and behavior of *Corynorhinus* bats.

Fires may alter the quality of habitat patches, influencing the foraging success or amount of time bats reside there, by reducing clutter or altering the prey community (Buchalski et al. 2013). Concurrent with our study, Lacki et al. (2017) quantified the effect of fire on the density of vegetation at different heights above the forest floor (i.e., clutter) and used ultrasonic bat detectors to measure the response of foraging

bats at Mammoth Cave. While clutter varied with fire severity, acoustic detection rates of bats did not. Other researchers have found positive correlations between bat acoustic activity or occupancy and clutter-reducing forest treatments (Cox et al. 2016; Silvis et al. 2016). However, these studies cannot be directly applied to *Corynorhinus* species given the infrequent use of low-intensity echolocation calls by these bats that are less likely to be detected by both moths and bat detectors (Clement and Castleberry 2011). Our radiotelemetry data indicate that reduction in clutter from fires had a weak influence on foraging patterns in big-eared bats. Although home ranges of reproductive classes of females exhibited much variation around their proximity to burned forests, only males differed in their use of burned versus unburned forest types. Home ranges of males were farther from burned forests than all other habitats, but they were not located significantly farther from burned habitat than expected by chance, and thus there was no indication that males actually avoided burned forests. An explanation for differing patterns of habitat selection between the sexes remains unclear, but this outcome indicates important variables driving habitat selection were not identified in our study design. This may include the number of years that elapsed since application of prescribed fires, or differences in their intensity and impacts on forest vegetation. These variables could not be included due to the modest extent to which fires occurred in our study area, but should be investigated in future studies.

Our study adds to a body of literature describing Rafinesque's big-eared bat as a specialist species. Adapted for slow, maneuverable flight and capable of passively detecting sounds made by moths located on the surface of vegetation, Rafinesque's big-eared bats have relatively small home ranges that are located closest to habitats with the greatest diversity and abundance of moths. Although dietary specialization and small home ranges likely make this big-eared bat vulnerable to disturbance, our research shows that low-to-moderate intensity-prescribed fires only weakly affect the nocturnal habitat selection of this species in the years immediately following prescribed burning. Nevertheless, the tendency of some big-eared bats to establish home ranges relatively far from burned habitats suggests some potential for negative effects of prescribed fire, and care should be taken when applying fire treatments in areas with big-eared bat maternity colonies.

ACKNOWLEDGMENTS

We thank R. Toomey and S. Thomas of the National Park Service for advice and logistical support while working at Mammoth Cave National Park. We thank J. Grider, G. Langlois, C. Farr, D. Frasier, and H. Comstock for assistance in the field. Financial support was provided by the Kentucky Department of Fish and Wildlife Resources and the College of Agriculture, Food, and Environment at the University of Kentucky. This research is connected with a project of the Kentucky Agricultural Experiment Station (KAES no. 18-09-41) and is published with the approval of the Director.

LITERATURE CITED

- ARMITAGE, D. W., AND H. K. OBER. 2012. The effects of prescribed fire on bat communities in the longleaf pine sandhills ecosystem. *Journal of Mammalogy* 93:102–114.
- BAGNE, K. E., K. L. PURCELL, AND J. T. ROTENBERRY. 2008. Prescribed fire, snag population dynamics, and avian nest site selection. *Forest Ecology and Management* 255:99–105.
- BARCLAY, R. M., AND A. KURTA. 2007. Ecology and behavior of bats roosting in tree cavities and under bark. Pp. 17–59 in *Bats in forests: Conservation and management* (M. J. Lacki, J. P. Hayes, and A. Kurta, eds.). Johns Hopkins University Press, Baltimore.
- BAYLESS, M. L., M. K. CLARK, R. C. STARK, B. S. DOUGLAS, AND S. M. GINGER. 2011. Distribution and status of eastern big-eared bats (*Corynorhinus* spp.). Pp. 13–25 in *Conservation and management of eastern big-eared bats: a symposium* (S. C. Loeb, M. J. Lacki, and D. A. Miller, eds.). U.S. Forest Service, General Technical Report SRS-145.
- BÖRGER, L., B. D. DALZIEL, AND J. M. FRYXELL. 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters* 11:637–650.
- BRIGHT, R. M., S. D. GRINDAL, M. C. FIRMAN, AND J. L. MORISSETTE. 1997. The influence of structural clutter on activity patterns of insectivorous bats. *Canadian Journal of Zoology* 75:131–136.
- BRUNET-ROSSINNI, A. K., AND G. S. WILKINSON. 2009. Methods for age estimation and the study of senescence in bats. Pp. 315–325 in *Ecological and behavioral methods for the study of bats* (T. H. Kunz and S. Parsons, eds.). 2nd ed. Johns Hopkins University Press, Baltimore, Maryland.
- BUCHALSKI, M. R., J. B. FONTAINE, P. A. HEADY, 3rd, J. P. HAYES, AND W. F. FRICK. 2013. Bat response to differing fire severity in mixed-conifer forest California, USA. *Plos ONE* 8:e57884.
- BURT, W. H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24:346–352.
- CLARK, B. S., D. M. LESLIE, AND T. S. CARTER. 1993. Foraging activity of adult female Ozark big-eared bats (*Plecotus townsendii ingens*) in summer. *Journal of Mammalogy* 74:422–427.
- CLEMENT, M. J., AND S. B. CASTLEBERRY. 2011. Comparison of survey methods for Rafinesque's big-eared bats. Pp. 147–158 in *Conservation and management of eastern big-eared bats: a symposium* (S. C. Loeb, M. J. Lacki, and D. A. Miller, eds.). U.S. Forest Service, General Technical Report SRS-145.
- CONNER, L. M., AND B. W. PLOWMAN. 2001. Using Euclidean distances to assess nonrandom habitat use. Pp. 275–290 in *Radio tracking and animal populations* (J. J. Millspaugh and J. M. Marzluff, eds.). Academic Press, San Diego, California.
- CONNER, L. M., M. D. SMITH, AND L. W. BURGER. 2003. A comparison of distance based and classification based analyses of habitat use. *Ecology* 84:526–531.
- CONVERSE, S. J., G. C. WHITE, K. L. FARRIS, AND S. ZACK. 2006. Small mammals and forest fuel reduction: national-scale responses to fire and fire surrogates. *Ecological Applications* 16:1717–1729.
- COX, M. R., E. V. WILLCOX, P. D. KEYSER, AND A. L. VANDER YACHT. 2016. Bat response to prescribed fire and overstory thinning in hardwood forest on the Cumberland Plateau, Tennessee. *Forest Ecology and Management* 359:221–231.
- DE SOLLA, S. R., R. BONDURIANSKY, AND R. J. BROOKS. 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. *Journal of Animal Ecology* 68:221–234.
- DODD, L. E., M. J. LACKI, J. S. JOHNSON, AND L. K. RIESKE. 2015. Prey size and dietary niche of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*). *Southeastern Naturalist* 14:685–696.
- FONTAINE, J. B., AND P. L. KENNEDY. 2012. Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. Fire-prone forests. *Ecological Applications* 22:1547–1561.
- HARVEY, M. J., J. S. ALTENBACH, AND T. L. BEST. 2011. *Bats of the United States and Canada*. Johns Hopkins University Press, Baltimore, Maryland.
- HAUTIER, Y., D. TILMAN, F. ISBELL, E. W. SEABLOOM, E. T. BORER, AND P. B. REICH. 2015. Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science* 248:336–340.
- HAYES, J. P. 2000. Assumptions and practical considerations in the design and interpretation of echolocation-monitoring studies. *Acta Chiropterologica* 2:225–236.
- HOMER, C., C. HUANG, L. YANG, B. WYLIE, AND M. COAN. 2004. Development of a 2001 national land-cover database for the United States. *Photogrammetric Engineering & Remote Sensing* 70:829–840.
- HURST, T. E., AND M. J. LACKI. 1997. Food habits of Rafinesque's big-eared bat in southeastern Kentucky. *Journal of Mammalogy* 78.
- HURST, T. E., AND M. J. LACKI. 1999. Roost selection, population size, and habitat use by a colony of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*). *American Midland Naturalist* 142:363–371.
- JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- JOHNSON, J. S., AND M. J. LACKI. 2011. Foraging and roosting ecology of Rafinesque's big-eared bat at the northern edge of the range. Pp. 129–138 in *Conservation and management of eastern big-eared bats: a symposium* (S. C. Loeb, M. J. Lacki, and D. A. Miller, eds.). U.S. Forest Service, General Technical Report SRS-145.
- JOHNSON, J. S., AND M. J. LACKI. 2013. Habitat associations of Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) and their lepidopteran prey in bottomland hardwood forests. *Canadian Journal of Zoology* 91:94–101.
- JOHNSON, J. S., AND M. J. LACKI. 2014. Effects of reproductive condition, roost microclimate, and weather patterns on summer torpor use by a vespertilionid bat. *Ecology and Evolution* 4:157–166.
- JOHNSON, J. S., M. J. LACKI, AND M. D. BAKER. 2007. Foraging ecology of long-legged myotis (*Myotis volans*) in north-central Idaho. *Journal of Mammalogy* 88:1261–1270.
- JOHNSON, J. S., M. J. LACKI, S. C. THOMAS, AND J. F. GRIDER. 2012. Frequent arousals from winter torpor in rafinesque's big-eared bat (*Corynorhinus rafinesquii*). *Plos ONE* 7:e49754.
- KERNOHAN, B. J., R. A. GITZEN, AND J. J. MILLSPAUGH. 2001. Analysis of animal space use and movements. Pp. 125–166 in *Radio tracking and animal populations* (J. J. Millspaugh and J. M. Marzluff, eds.). Academic Press, San Diego, California.
- KILGORE, B. M., AND D. TAYLOR. 1979. Fire history of a sequoia-mixed conifer forest. *Ecology* 60:129–142.
- KUNZ, T. H., J. A. WRAZEN, AND C. D. BURNETT. 1998. Changes in body mass and fat reserves in pre-hibernating little brown bats (*Myotis lucifugus*). *Ecoscience* 5:8–17.
- LACKI, M. J., S. K. AMELON, AND M. D. BAKER. 2007. Foraging ecology of bats in forests. Pp. 83–127 in *Bats in forests: Conservation and management* (M. J. Lacki, J. P. Hayes, and A. Kurta, eds.). Johns Hopkins University Press, Baltimore, Maryland.
- LACKI, M. J., D. R. COX, L. E. DODD, AND M. B. DICKINSON. 2009. Response of northern bats (*Myotis septentrionalis*) to prescribed fires in eastern Kentucky forests. *Journal of Mammalogy* 90:1165–1175.
- LACKI, M. J., AND L. E. DODD. 2011. Diet and foraging behavior of *Corynorhinus* in eastern North America. Pp. 39–52 in

- Conservation and management of eastern big-eared bats: a symposium (S. C. Loeb, M. J. Lacki, and D. A. Miller, eds.). U.S. Forest Service, General Technical Report SRS-145.
- LACKI, M. J., L. E. DODD, N. S. SKOWRONSKI, M. B. DICKINSON, AND L. K. RIESKE. 2017. Relationships among burn severity, forest canopy structure and bat activity from spring burns in oak-hickory forests. *International Journal of Wildland Fire* 26:963–972.
- LACKI, M. J., AND K. M. LADEUR. 2001. Seasonal use of lepidopteran prey by Rafinesque's big-eared bats (*Corynorhinus rafinesquii*). *The American Midland Naturalist* 145:213–217.
- LAFONTAINE, J. D., AND B. C. SCHMIDT. 2010. Annotated checklist of the Noctuoidea (Insecta, Lepidoptera) of North America north of Mexico. *Zookeys* 40:1–239.
- LOEB, S. C., AND T. A. WALDROP. 2008. Bat activity in relation to fire and fire surrogate treatments in southern pine stands. *Forest Ecology and Management* 255:3185–3192.
- MENZEL, M. A., J. M. MENZEL, W. M. FORD, J. W. EDWARDS, T. C. CARTER, J. B. CHURCHILL, AND J. C. KILGO. 2001. Home range and habitat use of male Rafinesque's big-eared bats (*Corynorhinus rafinesquii*). *The American Midland Naturalist* 145:402–408.
- MOORE, P. R., T. S. RISCH, D. K. MORRIS, AND V. ROLLAND. 2017. Habitat use of female gray bats assessed using aerial telemetry. *Journal of Wildlife Management* 81:1242–1253.
- MORRIS, A. D., D. A. MILLER, AND M. C. KALCOUNIS-RUEPPELL. 2010. Use of forest edges by bats in a managed pine forest landscape. *Journal of Wildlife Management* 74:26–34.
- MORRISON, M. L., AND M. G. RAPHAEL. 1993. Modeling the dynamics of snags. *Ecological Applications* 3:322–330.
- NORBERG, U. M., AND J. M. V. RAYNER. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences* 316:335–427.
- NOWACKI, G. J., AND M. D. ABRAMS. 2008. The demise of fire and “mesophication” of forests in the Eastern United States. *BioScience* 58:123–138.
- OLSON, R., AND C. NOBLE. 2005. The geological foundation for prescribed fire in Mammoth Cave National Park. *Geodiversity and Geoconservation* 22:22–28.
- PASTRO, L. A., C. R. DICKMAN, AND M. LETNIC. 2014. Fire type and hemisphere determine the effects of fire on the alpha and beta diversity of vertebrates: a global meta-analysis. *Global Ecology and Biogeography* 23:1146–1156.
- PERRY, R. W. 2012. A review of fire effects on bats and bat habitat in the eastern oak region. Pp. 170–191 in *Proceedings of the 4th fire in eastern oak forests conference* (D. C. Dey, M. C. Stambaugh, S. L. Clark, and C. J. Schweitzer, eds.). U.S. Forest Service General Technical Report NRS-P-102.
- PILLIOD, D. S., R. B. BURY, E. J. HYDE, C. A. PEARL, AND P. S. CORN. 2003. Fire and amphibians in North America. *Forest Ecology and Management* 178:163–181.
- RACEY, P. A. 2009. Reproductive assessment of bats. Pp. 249–364 in *Ecological and behavioral methods for the study of bats* (T. H. Kunz and S. Parson, eds.). 2nd ed. Johns Hopkins University Press, Baltimore, Maryland.
- RUDDIMAN, W. F., E. C. ELLIS, J. O. KAPLAN, AND D. Q. FULLER. 2015. Geology. Defining the epoch we live in. *Science* (New York, N.Y.) 348:38–39.
- RYAN, K. C., E. E. KNAPP, AND J. M. VARNER. 2013. Prescribed fire in North American forests and woodlands: History, current practice, and challenges. *Frontiers in Ecology and the Environment* 11:e15–24.
- SCHOENER, T. W. 1981. An empirically based estimate of home range. *Theoretical Population Biology* 20:281–325.
- SIKES, R. S., AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2016. 2016 guidelines of the American society of mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97:663–688.
- SILVIS, A., S. D. GEHRT, AND R. A. WILLIAMS. 2016. Effects of shelterwood harvest and prescribed fire in upland Appalachian hardwood forests on bat activity. *Forest Ecology and Management* 360:205–212.
- SOUSA, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15:353–391.
- SWENGEL, A. B. 2001. A literature review of insect responses to fire, compared to other conservation managements of open habitat. *Biodiversity and Conservation* 10:1141–1169.
- SWIHART, R. K., AND N. A. SLADE. 1985. Testing for independence of observations in animal movements. *Ecology* 66:1176–1184.
- SWIHART, R. K., AND N. A. SLADE. 1997. On Testing for Independence of Animal Movements. *Journal of Agricultural, Biological, and Environmental Statistics* 2:48–63.
- THILL, R. E., D. C. RUDOLPH, AND N. E. KOERTH. 2004. Shortleaf pine-bluestem restoration for Red-cockaded Woodpeckers in the Ouachita Mountains: Implications for other taxa. Pp. 657–671 in *Red-cockaded woodpecker: Road to recovery* (R. Costa and S. J. Daniels, eds.). Blaine, Minnesota.
- TURNER, M. G. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91:2833–2849.
- VAN MOORTER, B., C. M. ROLANDSEN, M. BASILLE, AND J. M. GAILLARD. 2016. Movement is the glue connecting home ranges and habitat selection. *Journal of Animal Ecology* 85:21–31.
- WALTERS, J. R. 1991. Application of ecological principles to the management of endangered species: the case of the redcockaded woodpecker. *Annual Review of Ecology and Systematics* 22:505–523.
- WHITE, P. S., AND A. JENTSCH. 2001. The search for generality in studies of disturbance and ecosystem dynamics. Pp. 399–450 in *Progress in botany*. Springer Berlin, Heidelberg, Germany.
- WOMACK, K. M., S. K. AMELON, AND F. R. THOMPSON III. 2013. Summer home range size of female Indiana bats (*Myotis sodalis*) in Missouri, USA. *Acta Chiropterologica* 15:423–429.
- WORTON, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168.

Submitted 20 April 2018. Accepted 6 February 2019.

Associate Editor was Robert Schooley.