

Nocturnal activity patterns of northern myotis (*Myotis septentrionalis*) during the maternity season in West Virginia (USA)

JOSHUA B. JOHNSON^{1,3}, JOHN W. EDWARDS¹, and W. MARK FORD²

¹West Virginia University, Division of Forestry and Natural Resources, Box 6125, Morgantown, WV 26506, USA

²U.S. Geological Survey, Virginia Cooperative Fish and Wildlife Research Unit, Virginia Polytechnic Institute and State University, 106 Cheatham Hall, Blacksburg, VA 24061, USA

³Corresponding author: E-mail: j-johnson3@juno.com

Nocturnal activity patterns of northern myotis (*Myotis septentrionalis*) at diurnal roost trees remain largely uninvestigated. For example, the influence of reproductive status, weather, and roost tree and surrounding habitat characteristics on timing of emergence, intra-night activity, and entrance at their roost trees is poorly known. We examined nocturnal activity patterns of northern myotis maternity colonies during pregnancy and lactation at diurnal roost trees situated in areas that were and were not subjected to recent prescribed fires at the Fernow Experimental Forest, West Virginia from 2007 to 2009. According to exit counts and acoustic data, northern myotis colony sizes were similar between reproductive periods and roost tree settings. However, intra-night activity patterns differed slightly between reproductive periods and roost trees in burned and non-burned areas. Weather variables poorly explained variation in activity patterns during pregnancy, but precipitation and temperature were negatively associated with activity patterns during lactation.

Key words: Anabat, bats, *Myotis septentrionalis*, night-roosting, northern myotis, West Virginia

INTRODUCTION

Temperate bat species are nocturnal and exhibit nightly and seasonal activity patterns that vary among species and individuals (Hirshfield *et al.*, 1977; Anthony *et al.*, 1981). During summer nights, bat roost-emergence activity commonly peaks immediately after sunset and can continue for several hours (Kunz, 1973; Barclay, 1982). Typically, a lesser activity peak occurs before sunrise as bats return to their diurnal roosts after foraging (Kunz, 1973). During the night, bats roost at intervals, either at their diurnal roosts or at night-roosts nearer their foraging areas (Adam and Hayes, 2000; Johnson *et al.*, 2002; Daniel *et al.*, 2008).

Females of many bat species form maternity colonies in anthropogenic (e.g., buildings) and/or natural (e.g., tree or snag) structures (Barbour and Davis, 1969; Lewis, 1995). During the maternity season, particularly during the lactation period, females return to their diurnal roosts several times during the night to nurse their young (Henry *et al.*, 2002; Ormsbee *et al.*, 2007). Activity at diurnal roosts at night typically is greater during

lactation than during pregnancy (Henry *et al.*, 2002).

Northern myotis (*Myotis septentrionalis*) is a small (5–8 g) insectivorous bat in the eastern United States and Canada (Caceres and Barclay, 2000). They typically roost in tree cavities or under exfoliating bark of snags or live trees, where they form maternity colonies of < 100 individuals during summer (May–July) (Caceres and Barclay, 2000). Moreover, many of these species exhibit fission-fusion societies during the maternity season whereby individuals switch roost trees about every other day (Caceres and Barclay, 2000; Garroway and Broders, 2007). Little research has examined activity patterns at non-anthropogenic roost sites or activity patterns of northern myotis maternity colonies (Barclay and Cash, 1985; Barclay, 1989; Hickey and Fenton, 1996; Broders *et al.*, 2006). Also, possible effects of increased solar exposure to roost trees following forest disturbances, including partial-harvesting or prescribed fire, on nocturnal bat activity patterns at diurnal roost trees remains uninvestigated (Boyles and Aubrey, 2006; Johnson *et al.*, 2009). Forest disturbances result in gaps in the forest canopy, allowing

increased amount of solar exposure to reach roost trees (Johnson *et al.*, 2009). Increased solar exposure and consequent increase in roost temperatures could result in increased energetic demands on individual females during pregnancy and on growth rates of young during lactation periods (Tuttle, 1975; Boyles and Aubrey, 2006; Ruczyński, 2006). Therefore, intra-night activity levels at roost trees in disturbed areas conceivably should be greater than at roost trees in undisturbed areas. Also, energetic demands on females should be greater during lactation, resulting in higher intra-night activity at roosts than during pregnancy (Henry *et al.*, 2002; Ormsbee *et al.*, 2007). Weather also may influence intra-night activity levels of maternity colonies, but may differ between reproductive periods. Females may avoid foraging during inclement weather, resulting in decreased activity levels during rain, high wind, or low temperatures (Ormsbee *et al.*, 2007).

Our objectives were to determine if northern myotis activity at diurnal roost trees differed between pregnancy and lactation reproductive phases; and to examine the influence of weather on activity patterns. Also, we additionally attempted to determine if differences in northern myotis activity existed between roost trees in areas subjected to prescribed fire and those in non-burned areas. Consistent with the knowledge that there are increased energetic demands on females during lactation, we predicted that intra-night activity would be greater during lactation period than during pregnancy period. Similarly, because of increased roost temperatures and energetic demand on females at roost trees in burned areas, we predicted that intra-night activity would be greater at roost trees in burned areas than at roost trees in non-burned areas. Lastly, we predicted that inclement weather, e.g., rain, would negatively affect (reduce) bat activity.

MATERIALS AND METHODS

Study Area

We conducted our research at the Fernow Experimental Forest (FEF) in Tucker County, West Virginia. The FEF is a 1,900 ha experimental forest managed by the U.S. Forest Service, Northern Research Station, and is located in the Unglaciated Allegheny Mountains subsection of the Appalachian Plateau Physiographic Province (Kochenderfer *et al.*, 2007). Elevations range from 530 to 1,100 m. Elklick Run, a 2.4-km fourth-order stream, roughly bisects FEF east to west. Approximately 5.5 km of dendritic intermittent and permanent streams feed into Elklick Run and incise the steep slopes and plateau-like ridgetops (Madarish *et al.*, 2002). Mean annual precipitation at FEF is 145.8 cm, ranging from 9.7 cm in October to

14.4 cm in June. Mean annual temperature is 9.2°C, ranging from -18.0°C in January to 20.6°C in July (Kochenderfer, 2006). Vegetation at the FEF is a mosaic of second- and third-growth, mixed-mesophytic and northern hardwood forest that has been managed by even (patch clearcut)- and uneven (single-tree selection)-aged silviculture since the mid-20th century, or has been left undisturbed following initial harvesting in the Elklick watershed from 1903 to 1911 (Schuler and Fajvan, 1999; Schuler, 2004). In spring 2007 to 2009, prescribed fire treatments were conducted in three management compartments totaling ca. 146 ha on FEF. The three management compartments were burned for one day during each treatment using a strip head fire technique, ignited with hand-held drip torches. Actual flame heights and combustion varied from dying out to > 3.5 m high in some spots, due to variability in leaf litter, slope, and aspect. Additionally, 48, 20-m radius plots were randomly located in each of the three management compartments, and all overstory or midstory trees, other than oak or hickory, were herbicided or girdled (T. M. Schuler, personal communication).

Radio Telemetry

To capture bats, we erected mist nets (Avinet, Inc., Dryden, New York) over stream corridors, small pools, skidder trails, and service roads from late-May to mid-July 2007–2009. For each captured bat, we determined species, sex, age, weight, forearm length, and reproductive condition. We used Skin Bond® (Smith and Nephew, Largo, Florida) surgical cement to affix a 0.35-g radio transmitter (Model LB-2N; Holohil Systems Ltd., Carp, Ontario, Canada) between the scapulae of captured female northern myotis. Bat capture and handling protocols were approved by the Animal Care and Use Committee of West Virginia University (Protocol Number No. 08-0504) and followed the guidelines of the American Society of Mammalogists (Animal Care and Use Committee, 1998). We used a radio receiver and 3-element Yagi antenna (Wildlife Materials, Inc., Murphysboro, Illinois) to locate diurnal roost trees.

Acoustic Monitoring

We used Anabat II (Titley Electronics, Ballina, Australia) broadband, frequency-division, bat detectors to passively monitor for bat echolocation passes, i.e., a series of echolocation pulses, at a random sample of diurnal roost trees during the pregnancy and lactation periods, and at roost trees in burned and non-burned areas (Sasse and Pekins, 1996). We positioned the detectors on the ground with the microphone oriented towards the roost tree exit. The bat detectors were programmed to monitor from one hour prior to sunset to one hour after sunrise. We conducted monitoring at diurnal roost trees on the nights we located radio-telemetered bats at those particular trees. Echolocation passes were recorded to an Anabat CompactFlash storage Zero-Crossing Analysis Interface Module (ZCAIM) and downloaded to a computer for analysis using Analook 4.8p software (Corben, 2001). We used qualitative and quantitative echolocation pass identification methods (Fenton and Bell, 1981; O'Farrell *et al.*, 1999; Murray *et al.*, 2001). We identified echolocation passes of some species by comparing our unknowns to a library comprised of echolocation passes collected from hand-released bats marked with chemiluminescent tags collected throughout the southeastern and mid-Atlantic United States. We only attempted identification of echolocation passes containing at least three pulses. Northern myotis echolocation

passes were distinguished from those of congeners by the characteristic slope ($\Delta \geq 200$ octaves per second) of each pulse. Our identifications were limited to species as no techniques exist to reliably distinguish male/female or adult/juvenile bat echolocation calls. Moreover, quantity of echolocation passes recorded is an index of activity and does not necessarily reflect the quantity of bats being recorded, i.e., one bat can be recorded more than one time (Broders, 2003).

Exit Counts

From early June to mid July, we conducted exit counts at a random set of roost trees in non-burned and burned areas, and during pregnancy and lactation periods. We commenced exit counts approximately one hour before sunset and continued until darkness prevented us from observing emerging bats.

Statistical Analysis

We used Mann-Whitney *U*-tests to compare mean nightly and mean hourly bat passes, defined as the number of echolocation pass sequences recorded, between reproductive periods (pregnancy and lactation) and between roost trees in non-burned and burned areas (Proc Npar1way, SAS Institute, Inc., 2004). Pregnancy and lactation periods were defined by examining the reproductive condition of female northern myotis captured during mist-netting efforts that occurred concurrent with acoustic monitoring of roost trees. We noted if roost trees were located in areas that had recently (2007 and after) been burned or were in areas that had not recently been burned (Johnson *et al.*, 2009). Before making comparisons of mean bat passes among hours following sunset within each reproductive period or each roost tree setting (burned or non-burned), we used a time-series analysis to examine hourly means for temporal autocorrelation (RDCT, 2008). Partial autocorrelation coefficients exceeding 5% confidence limits, i.e., partial autocorrelation (PACF) = |0.59|, were considered significantly autocorrelated (Montgomery *et al.*, 2008). To determine if hourly mean bat passes within nights differed within reproductive periods and within roost tree settings, we performed a 1-way analysis of variance on ranked data (Proc Rank; Proc GLM, SAS Institute, Inc., 2004). Differences among ranked mean bat passes were analyzed using Duncan's New Multiple Range Test.

We examined possible influence of weather variables on bat activity within the pregnancy and lactation periods with Spearman's product moment correlations (Proc Corr, SAS Institute, Inc., 2004). Weather variables included hourly precipitation totals (Precip), daily minimum (MinT) and maximum temperatures (MaxT), and mean hourly temperatures (HrT). We obtained precipitation data, and daily minimum and maximum temperatures from a weather station on the FEF (US Forest Service, unpublished data). Mean hourly temperatures were measured at a random sample of roost trees with StowAway® Tidbit® (Onset Computer Corp., Pocasset, Massachusetts) data loggers that recorded ambient temperature every minute.

We used Mann-Whitney *U*-tests to compare exit counts between roost trees in non-burned and burned areas, and between pregnancy and lactation periods. We used a simple linear regression to evaluate trends in exit counts during summer. We determined if exit counts were correlated with nightly number of echolocation passes recorded by examining Spearman's product moment correlations. Statistical significance for all tests was set at $\alpha = 0.05$.

RESULTS

We radio-tracked 29 female northern myotis (21 pregnant, 8 lactating) to 40 roost trees (28 during the pregnancy period (21 June 2007; 29 May–29 June 2008; 15 June–21 June 2009), 13 during the lactation period (on and after 25 June 2007, 30 June 2008, and 22 June 2009), 1 roost tree was used during both reproductive periods; and 23 in non-burned areas and 17 in burned areas). We acoustically monitored for 52 sample nights (34 during the pregnancy period and 18 during the lactation period; and 27 in non-burned and 25 in burned areas).

Nightly mean bat passes were similar (Mann-Whitney test, $U = 515$, $P = 0.92$) between the pregnancy ($\bar{x} \pm SE = 7.43 \pm 2.10$ echolocation passes, $n = 34$), and lactation periods (7.79 ± 2.51 , $n = 18$). Mean bat passes were similar (Mann-Whitney test, $U = 596$, $P = 0.23$) at roost trees in non-burned (9.48 ± 2.95 , $n = 27$) and burned areas (6.00 ± 2.05 , $n = 25$). Within nights, mean hourly echolocation passes were not serially autocorrelated during the pregnancy (PACF $\leq |0.293|$) or lactation (PACF $\leq |0.362|$) periods, or in non-burned (PACF $\leq |0.322|$) or burned areas (PACF $\leq |0.349|$). Because data were not serially autocorrelated, we considered mean hourly echolocation passes independent data and valid for analysis of variance and multiple comparison procedures. During pregnancy, activity peaked just prior to sunrise, with mean bat passes differing between the 1st, 7th, and 11th hours after sunset (Table 1). During lactation, activity peaked during the 3rd hour after sunset, which differed from all other hours but the 4th and 10th. Among hours between reproductive periods, only the 3rd hour after sunset differed; mean bat passes were higher during lactation (Table 1).

During pregnancy, bat activity was poorly associated with weather variables (Precip: $\rho = -0.013$, MaxT: $\rho = -0.064$, MinT: $\rho = 0.050$, HrT: $\rho = 0.028$). During lactation, bat activity was negatively associated with all weather variables (Precip: $\rho = -0.001$, MaxT: $\rho = -0.347$, MinT: $\rho = -0.195$, HrT: $\rho = -0.003$).

Within non-burned areas, mean hourly bat passes peaked just before sunrise. Mean bat passes during the 10th hour after sunset were higher than other hours except for the 3rd, 4th, and 9th hours (Table 2). Within burned areas, mean hourly bat passes peaked in the 3rd and 4th hours following sunset. Mean bat passes during the 3rd and 4th hours following sunset were similar to all but the 1st and 11th hours following sunset (Table 2). Among hours between non-burned and burned areas, mean passes

TABLE 1. Female *M. septentrionalis* night-roosting activity during pregnancy ($n = 34$ samples at 29 roost trees) and lactation ($n = 18$ samples at 14 roost trees) reproductive periods at the Fernow Experimental Forest, West Virginia, 2007–2009

Hours after sunset	Pregnant		Lactating		P-level
	Mean ¹	SE	Mean ¹	SE	
1	3.32 ^{BC}	0.91	2.17 ^{BC}	0.99	0.119
2	6.82 ^{ABC}	1.93	5.44 ^{BC}	2.05	0.476
3	7.74 ^{ABC}	3.31	19.56 ^A	7.03	0.041
4	8.24 ^{ABC}	4.05	13.28 ^{AB}	4.49	0.054
5	7.35 ^{ABC}	2.37	8.67 ^{BC}	2.84	0.302
6	7.29 ^{ABC}	2.51	7.89 ^{BC}	3.20	0.186
7	6.06 ^{BC}	2.16	6.28 ^{BC}	2.71	0.488
8	7.59 ^{ABC}	2.52	5.67 ^{BC}	2.90	0.228
9	10.85 ^{AB}	3.24	7.00 ^{BC}	3.27	0.436
10	15.47 ^A	4.51	9.50 ^{ABC}	3.58	0.300
11	0.97 ^C	0.71	0.22 ^C	0.22	0.245

¹ — Mean number of echolocation passes detected followed by different capital letters within columns was significantly different according to Duncan's New Multiple Range Test

differed in the 1st, 10th, and 11th hours; mean bat passes were higher at trees in non-burned areas (Table 2).

Exit counts were statistically similar (Mann-Whitney test, $U = 62$, $P = 0.46$) yet greater at roost trees in non-burned (27.2 ± 9.1 bats, range = 2–48 bats, $n = 6$ samples) compared to those in burned (14.1 ± 2.8 bats, range = 1–33 bats, $n = 11$ samples) areas. Exit counts also were statistically similar (Mann-Whitney test, $U = 76$, $P = 0.74$) yet greater during pregnancy (21.1 ± 7.2 bats, range = 1–48 bats, $n = 9$ samples) compared to lactation (16.0 ± 1.5 bats, range = 7–20 bats, $n = 8$ samples) period. Exit counts were not correlated with mean nightly echolocation passes ($\rho = -0.01$, $n = 10$, $P = 0.99$).

DISCUSSION

Nocturnal activity patterns of female northern myotis at diurnal roost trees was largely unaffected by reproductive period or roost tree setting. Exit counts and mean nightly bat passes both indicated that northern myotis colony sizes were similar between reproductive periods and between roost trees in burned and non-burned areas. Though not statistically significant, exit counts revealed that roost trees in non-burned areas generally had larger colonies than those in burned areas. This may be due to roost trees in burned areas having higher internal temperatures due to increased solar exposure, possibly reducing need for thermal advantages of larger colony sizes (Barclay and Kurta, 2007). Similarly, exit counts during pregnancy also were greater, though statistically similar, than during lactation period, which is consistent with our observation of declining colony sizes over the course of

summer, and possibly due to group fission dynamics (Garraway and Broders, 2007). Colony sizes we documented were slightly less than others recorded in West Virginia (Menzel *et al.*, 2002) and Nova Scotia (Garraway and Broders, 2007), but were similar to those recorded in New Hampshire (Sasse and Pekins, 1996) and Michigan (Foster and Kurta, 1999). We concluded data collection prior to juvenile volancy, which occurs approximately 21 days after parturition (Krochmal and Sparks, 2007), thus negating influences of their activity on comparisons. During pregnancy, intra-night activity patterns of northern myotis steadily increased before sunrise, probably as bats were returning from foraging (Henry *et al.*, 2002). A lack of activity peak after sunset during pregnancy may have been due to a gradual emergence of the colonies. Energetic demands during lactation may necessitate prompt foraging after sunset, resulting in more concentrated emergence activity (Anthony and Kunz, 1977; McWilliam, 1989). However, we did not observe a peak in activity of lactating bats until the 3rd hour following sunset, probably as bats were returning from their first foraging bout to nurse their young (Henry *et al.*, 2002). Thereafter, females may have intermittently emerged and returned from foraging to nurse their young, resulting in similar activity levels throughout the night until a small peak just before sunrise as more bats returned for diurnal roosting (Henry *et al.*, 2002). During pregnancy, it is common for female bats to use night-roosts that are not their diurnal roosts (Henry *et al.*, 2002; Murray and Kurta, 2004).

Energetic demands of different reproductive periods on female bats are well-documented, and can be affected by weather conditions and insect availability (Anthony *et al.*, 1981; Barclay, 1982; Hickey

TABLE 2. Female *M. septentrionalis* night-roosting activity at roost trees in non-burned ($n = 27$ samples at 23 roost trees) and burned ($n = 25$ samples at 17 roost trees) areas of the Fernow Experimental Forest, West Virginia, 2007–2009

Hours after sunset	Non-burned		Burned		P-level
	Mean ¹	SE	Mean ¹	SE	
1	4.81 ^{BC}	1.14	0.88 ^B	0.46	0.006
2	9.74 ^{BC}	2.42	2.68 ^{AB}	1.09	0.086
3	14.70 ^{AB}	5.51	8.72 ^A	3.49	0.829
4	11.59 ^{ABC}	5.08	8.24 ^A	3.32	0.643
5	9.48 ^{BC}	2.95	6.00 ^{AB}	2.05	0.574
6	9.74 ^{BC}	3.05	5.08 ^{AB}	2.37	0.147
7	8.41 ^{BC}	2.63	3.68 ^{AB}	1.97	0.063
8	9.70 ^{BC}	3.06	3.92 ^{AB}	2.14	0.122
9	13.74 ^{AB}	3.90	4.96 ^{AB}	2.43	0.125
10	21.52 ^A	5.56	4.64 ^{AB}	1.69	0.030
11	1.37 ^C	0.89	0.00 ^B	0.00	0.026

¹ — Mean number of echolocation passes detected followed by different capital letters within columns was significantly different according to Duncan's New Multiple Range Test

and Fenton, 1996). During pregnancy, weather variables were not strong predictors of bat activity in our study. Energetic demands of bats during pregnancy are less than that during lactation. Consequently, bat foraging strategies likely differ between the two reproductive periods (Speakman and Thomas, 2003). We can reasonably expect weather variables to have less influence on bat activity during the pregnancy period. Similar to our findings, lactating little brown myotis (*Myotis lucifugus*) activity has been shown to be negatively correlated with minimum nightly temperatures (Anthony *et al.*, 1981). During cooler nights, insect activity decreases, causing bats to forage less, and thus remain in roost trees to conserve energy (Anthony *et al.*, 1981; Hickey and Fenton, 1996). Moreover, cooler nightly temperatures may necessitate females spending more time in their roost trees to maintain internal roost temperatures that foster juvenile growth and survival (Tuttle, 1975). Because bats spent more time in their roosts on cooler nights, we detected fewer echolocation passes on these nights.

Despite creating numerous suitable roost areas with an abundance of potential diurnal roost trees exposed to greater solar radiation (Johnson *et al.*, 2009), the effects of prescribed fire also had little effect on the nocturnal activity patterns of northern myotis maternity colonies. At roost trees in both non-burned and burned areas, intra-night activity showed peaks (although not significant in all cases) three hours after sunset and again just before sunrise, probably as bats were returning after their first foraging bout and for diurnal roosting, respectively (Henry *et al.*, 2002). Although overall mean bat passes were similar between roost trees within non-burned and burned areas, there were few hourly

differences during the emergence and entrance periods. Contrary to our predictions, activity during these hours was greater at roost trees in non-burned areas than in burned areas. It is possible that the increased solar exposure at roost trees in burned areas would negatively affect colony size because occupancy of fewer individuals would be necessary to maintain favorable roost temperatures (Johnson *et al.*, 2009). However, according to exit counts and acoustic data, there were no statistically significant differences in colony size between roost tree settings. Prescribed fire in our study area resulted in canopy gaps over roost trees, resulting in increased temperatures at roost trees (Johnson *et al.*, 2009). Nightly temperatures did not differ between roost trees in non-burned and burned areas. Also, we would expect the increase in solar exposure to increase energetic demands, similar to that experienced during lactation, which would result in a more concentrated emergence. Indeed, trends in nightly bat activity patterns during lactation and at roost trees in burned areas were similar. Canopy gap sizes were more variable at roost trees in burned areas than in non-burned areas (Johnson *et al.*, 2009), possibly resulting in less-concentrated emergence events at roost trees throughout the burned areas. This phenomenon could be influenced by a combination of factors, including relatively high variation in energetic demand at roost trees in burned areas compared to those in non-burned areas, or more simply, variation in perceived twilight times at roost trees in burned areas. Emergence times may be influenced physiognomically in that activity may be more concentrated in intact forest canopies, or more variable at trees in burned areas due to variation in canopy gap size and distribution, but this is unclear

and merits further investigation. Bat emergence times typically are highly correlated with sunset, but can be shifted earlier during cloudy evenings (McWilliam, 1989). Varying light conditions at roost trees in burned areas may have been significant enough to delay or advance emergence times to different hourly bins, i.e., 1st or 2nd hour after sunset.

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LITERATURE CITED

- ADAM, M. D., and J. P. HAYES. 2000. Use of bridges as night roosts by bats in the Oregon coast range. *Journal of Mammalogy*, 81: 402–407.
- ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy*, 79: 1416–1431.
- ANTHONY, E. L. P., and T. H. KUNZ. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology*, 58: 755–786.
- ANTHONY, E. L. P., M. H. STACK, and T. H. KUNZ. 1981. Night roosting and the nocturnal time budget of the little brown bat, *Myotis lucifugus*: effects of reproductive status, prey density, and environmental conditions. *Oecologia* (Berlin), 51: 151–156.
- BARBOUR, R. W., and W. H. DAVIS. 1969. *Bats of America*. University Press of Kentucky, Lexington, 312 pp.
- BARCLAY, R. M. R. 1982. Night roosting behavior of the little brown bat, *Myotis lucifugus*. *Journal of Mammalogy*, 63: 464–474.
- BARCLAY, R. M. R. 1989. The effect of reproductive condition on the foraging behavior of female hoary bats, *Lasiurus cinereus*. *Behavioral Ecology and Sociobiology*, 24: 31–37.
- BARCLAY, R. M. R., and K. J. CASH. 1985. A non-commensal maternity roost of the little brown bat (*Myotis lucifugus*). *Journal of Mammalogy*, 66: 782–783.
- BARCLAY, R. M. R., 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. Lacki, J. Hayes, and A. Kurta, eds.). The Johns Hopkins University Press, Baltimore, 329 pp.
- BOYLES, J. G., and D. P. AUBREY. 2006. Managing forests with prescribed fire: implications for a cavity-dwelling bat species. *Forest Ecology and Management*, 222: 108–115.
- BRODERS, H. G. 2003. Another quantitative measure of bat species activity and sampling intensity considerations for the design of ultrasonic monitoring studies. *Acta Chiropterologica*, 5: 235–241.
- BRODERS, H. G., G. J. FORBES, S. WOODLEY, and I. D. THOMPSON. 2006. Range extent and stand selection for roosting and foraging in forest-dwelling northern long-eared bats and little brown bats in the Greater Fundy Ecosystem, New Brunswick. *Journal of Wildlife Management*, 70: 1174–1184.
- CACERES, M. C., and R. M. R. BARCLAY. 2000. *Myotis septentrionalis*. *Mammalian species* 634:1–4.
- CORBEN, C. 2001. *Analook*. Version 4.8p. Computer software. IBM.
- DANIEL, S., C. KORINE, and B. PINSHOW. 2008. Central-place foraging in nursing, arthropod-gleaning bats. *Canadian Journal of Zoology*, 86: 623–626.
- FENTON, M. B., and G. P. BELL. 1981. Recognition of species of insectivorous bats by their echolocation calls. *Journal of Mammalogy*, 62: 233–243.
- FOSTER, R. W., and A. KURTA. 1999. Roosting ecology of the northern bat (*Myotis septentrionalis*) and comparisons with the endangered Indiana bat (*Myotis sodalis*). *Journal of Mammalogy*, 80: 659–672.
- GARROWAY, C. J., and H. G. BRODERS. 2007. Nonrandom association patterns at northern long-eared bat maternity roosts. *Canadian Journal of Zoology*, 85: 956–964.
- HENRY, M., D. W. THOMAS, R. VAUDRY, and M. CARRIER. 2002. Foraging distances and home range of pregnant and lactating little brown bats (*Myotis lucifugus*). *Journal of Mammalogy*, 83: 767–774.
- HICKEY, M. B. C., and M. B. FENTON. 1996. Behavioural and thermoregulatory responses of female hoary bats, *Lasiurus cinereus* (Chiroptera: Vespertilionidae), to variations in prey availability. *Ecoscience*, 3: 414–422.
- HIRSHFELD, J. R., Z. C. NELSON, and W. G. BRADLEY. 1977. Night roosting behavior in four species of desert bats. *Southwestern Naturalist*, 22: 427–433.
- JOHNSON, J. B., M. A. MENZEL, J. W. EDWARDS, and W. M. FORD. 2002. Gray bat night-roosting under bridges. *Journal of the Tennessee Academy of Science*, 77: 91–93.
- JOHNSON, J. B., J. W. EDWARDS, W. M. FORD, and J. E. GATES. 2009. Roost tree selection by northern myotis (*Myotis septentrionalis*) maternity colonies following prescribed fire in a Central Appalachian Mountains hardwood forest. *Forest Ecology and Management*, 258: 233–242.
- KOCHENDERFER, J. N. 2006. Fernow and the Appalachian hardwood region. Pp. 17–39, in *The Fernow watershed acidification study* (M. B. Adams, D. R. DeWalle, and J. L. Horn, eds.). Springer, Dordrecht, Netherlands, 279 pp.
- KOCHENDERFER, J. N., M. B. ADAMS, G. W. MILLER, and J. D. HELVEY. 2007. Factors affecting large peakflows on Appalachian watersheds: lessons from the Fernow Experimental Forest. USDA Forest Service, Research Paper NRS-3, Northeastern Research Station, Newtown Square, Pennsylvania, 24 pp.
- KROCHMAL, A. R., and D. W. SPARKS. 2007. Timing of birth and estimation of age of juvenile *Myotis septentrionalis* and *Myotis lucifugus* in west-central Indiana. *Journal of Mammalogy*, 88: 649–656.
- KUNZ, T. H. 1973. Resource utilization: temporal and spatial components of bat activity in central Iowa. *Journal of Mammalogy*, 54: 14–32.

- LEWIS, S. E. 1995. Roost fidelity in bats: a review. *Journal of Mammalogy*, 76: 481–496.
- MADARISH, D. M., J. L. RODRIGUE, and M. B. ADAMS. 2002. Vascular flora and macroscopic fauna on the Fernow Experimental Forest. General Technical Report GTR-NE-291, U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, Pennsylvania, 37 pp.
- MCWILLIAM, A. N. 1989. Emergence behaviour of the bat *Tadarida (Chaerephon) pumila* (Chiroptera: Molossidae) in Ghana, West Africa. *Journal of Zoology (London)*, 219: 698–701.
- MENZEL, M. A., S. F. OWEN, W. M. FORD, J. W. EDWARDS, P. B. WOOD, B. R. CHAPMAN, and K. V. MILLER. 2002. Roost tree selection by northern long-eared bat (*Myotis septentrionalis*) maternity colonies in an industrial forest of the central Appalachian mountains. *Forest Ecology and Management*, 155: 107–114.
- MONTGOMERY, D. C., C. L. JENNINGS, and M. KULAHCHI. 2008. Introduction to time series analysis and forecasting. Wiley-Interscience, Hoboken, New Jersey, 445 pp.
- MURRAY, K. L., E. R. BRITZKE, and L. W. ROBBINS. 2001. Variation in search-phase calls of bats. *Journal of Mammalogy*, 82: 728–737.
- MURRAY, S. W., and A. KURTA. 2004. Nocturnal activity of the endangered Indiana bat (*Myotis sodalis*). *Journal of Zoology (London)*, 262: 197–206.
- O'FARRELL, M. J., B. W. MILLER, and W. L. GANNON. 1999. Qualitative identification of free-flying bats using the Anabat detector. *Journal of Mammalogy*, 80: 11–23.
- ORMSBEE, P. C., J. D. KISER, and S. I. PERLMETER. 2007. Importance of night roosts to the ecology of bats. Pp. 129–151, in *Bats in forests: conservation and management* (M. LACKI, J. HAYES, and A. KURTA, eds.). The Johns Hopkins University Press, Baltimore, 329 pp.
- R DEVELOPMENT CORE TEAM [RDCT]. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- RUCZYŃSKI, I. 2006. Influence of temperature on maternity roost selection by noctule bats (*Nyctalus noctula*) and Leisler's bats (*N. leisleri*) in Białowieża Primeval Forest, Poland. *Canadian Journal of Zoology*, 84: 900–907.
- SAS INSTITUTE, INC. 2004. SAS STAT 9.1 users guide. Version 9.1. SAS Institute, Inc., Cary, North Carolina, 5: 121 pp.
- SASSE, D. B., and P. J. PEKINS. 1996. Summer roosting ecology of northern long-eared bats (*Myotis septentrionalis*) in the White Mountain National Forest. Pp. 91–101, in *Bats and forests symposium* (R. M. R. BARCLAY and R. M. BRIGHAM, eds.). British Columbia Ministry of Forests Working Paper 23/1996, Victoria, Canada.
- SCHULER, T. M. 2004. Fifty years of partial harvesting in a mixed mesophytic forest: composition and productivity. *Canadian Journal of Forest Research*, 34: 985–997.
- SCHULER, T. M., and M. A. FAJVAN. 1999. Understory tree characteristics and disturbance history of a central Appalachian forest prior to old-growth harvesting. USDA Forest Service, Res. Pap. NE-710, Northeastern Research Station, Radnor, Pennsylvania.
- SPEAKMAN, J. R., and D. W. THOMAS. 2003. Physiological ecology and energetics of bats. Pp. 430–490, in *Bat ecology* (T. H. KUNZ and M. B. FENTON, eds.). University of Chicago Press, Chicago, 779 pp.
- TUTTLE, M. D. 1975. Population ecology of the gray bat (*Myotis grisescens*): factors influencing early growth and development. *Occasional Papers of the Museum of Natural History. University of Kansas*, 36: 1–24.

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