Exploring the "nutrient hot spot" hypothesis at trees used by bats

JOSEPH E. DUCHAMP,* DALE W. SPARKS, AND ROBERT K. SWIHART

Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907, USA (JED, RKS)
Center for North American Bat Research and Conservation, Department of Biology, Indiana State University, Terre Haute, IN 47809, USA (DWS)
Present address of JED: Department of Biology, Indiana University of Pennsylvania, Indiana, PA 15705, USA
Present address of DWS: Environmental Solutions and Innovations, 781 Neeb Road, Cincinnati, OH 45233, USA

* Correspondent: jduchamp@iup.edu

Temperate bat species are well-known predators of nocturnal insects; however, their role in forest nutrient cycling is unclear. We tested the "nutrient hot spot" hypothesis, which suggests that colonial bats should create nutrient peaks in and around their roosts via guano deposits. We measured the mass and nitrogen content of guano deposited outside of roosts occupied by maternal colonies of 2 tree-roosting species, *Myotis septentrionalis* and *M. sodalis*. We assessed whether these measures were related to date, species, and bat abundance using least-squares regression. We then compared the expected amount of nitrogen deposited over a maternity season to the expected annual amount of nitrogen mineralized by a forest. Mass of guano deposited increased with bat abundance and corresponded to periods of parturition and lactation. Nitrogen mineralization near a large roost of bats can be 380% of that due to decay of leaf litter. Such nutrient peaks could influence patterns of forest vegetation by impacting growth of herbaceous plants and development of tree seedlings, and the magnitude of these effects should increase in nutrient-poor areas. DOI: 10.1644/08-MAMM-A-308R2.1.

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Bats may be unique among mammals in terms of their impact on nutrient cycling and redistribution in forests. Bats often forage substantial distances from where they roost. Insectivorous bats can consume large quantities of insects during nightly foraging bouts (Kurta et al 1989; Whitaker 1995; Whitaker and Clem 1992). Depending on the locations of foraging and roosting habitats, bats potentially could import nutrients from nonforested to forested habitats or redistribute nutrients from lowland to upland areas.

Many herbivorous mammals play a role in nutrient redistribution, but only in grassland ecosystems do they appear to increase long-term nutrient availability. In grassland ecosystems both small mammals (Clark et al. 2005) and large ungulates (McNaughton 1985) positively influence nitrogen availability through urine and fecal deposits. However, herbivores in forest ecosystems tend to decrease long-term nitrogen availability to plants by selective browsing that favors plant species adapted to low soil nutrients (Feeley and Terborgh 2005; Pastor et al. 1993). The shift in plant communities toward these species causes a greater depression in overall nitrogen availability than the short-term gains caused by fecal deposits (Pastor et al. 1993).

The 2 patterns of bat guano deposition theorized by Pierson (1998) describe bats acting as potential "nutrient pepper shakers" or generators of "nutrient hot spots" and have distinct ecological implications. The nutrient pepper shaker hypothesis predicts a diffuse effect that bats could have by defecating during foraging bouts. Little information has been collected on actual bat defecation during flight. Brigham et al. (2002) collected almost no guano when sampling with elevated screens along flight paths of bats. Over the course of 4,352 trap nights, only 5 fecal pellets were collected. Thus, it seems that defecation during flight may be sporadic and spread over a large area, with a correspondingly diffuse effect on the distribution of nutrients in forests that is difficult to quantify.

In contrast, the nutrient hot spot hypothesis describes the potential for large numbers of bats to produce a peak in nutrients, or a hot spot, by defecating within and in close proximity to the roost tree (Pierson 1998). In tropical systems, defecation by frugivorous bats causes a peak in seed density around roost trees due to the seeds contained in feces (Janzen 1978; Janzen et al. 1976). Additionally, within large old-growth tree roosts in western North America substantial

amounts of guano accumulate within the roost tree itself (Gellman and Zielinski 1996). Tree-roosting bats often roost in several different trees during a single summer, typically revisiting roosts over multiple years (Barclay and Kurta 2007; Betts 1995; Lewis 1995; Sasse and Pekins 1996). Roost trees typically have low amounts of canopy cover and are often senescent or dead (Barclay and Kurta 2007; Kalcounis-Rüppell et al. 2005; Kunz and Lumsden 2003). These conditions create likely sites for young trees to join the upper canopy. If enough guano is deposited near roosts, nutrient peaks are likely to occur where subcanopy trees are competing for dominance.

The objective of our study was to evaluate the potential role of bats for creating nutrient hot spots near roost trees by measuring the amount and timing of nutrient additions. To accomplish this we collected guano at the base of roosts used by female bats and dependent young of 2 species with different abundances and using different structures, northern long-eared myotis (*Myotis septentrionalis*) and Indiana myotis (*M. sodalist*). Our goals were to measure the amount of guano deposited by each species; to measure the percent nitrogen content for guano from each species; to test for effects of species, abundance, and date on the amount of guano deposited and percent nitrogen concentration; and to determine the conditions necessary for bats in a roost to create a nutrient hot spot by comparing roost sites with predicted background levels of nitrogen content resulting from leaf-litter decomposition.

MATERIALS AND METHODS

Study area.—Our study was conducted in central and northern Indiana during May–July from 2002 to 2005 and included bats captured at 10 locations. Upland forests consisted of mixed hardwood stands dominated by species of oak (*Quercus*) and hickory (*Carya*) along with sugar maple (*Acer saccharum*). Bottomland forests were dominated by cottonwood (*Populus deltoides*) and silver maple (*Acer saccharinum*).

Bat capture and radiotelemetry.—Bats were captured in mist nets set across streams and wooded trails and handled in accordance with guidelines of the American Society of Mammalogists (Gannon et al. 2007) and both Purdue University and Indiana State University Institutional Animal Care and Use Committees. Species, mass (g), sex, age, and reproductive status were recorded for each bat captured. Age classes, adult and juvenile, were assessed by fusion of the epiphyseal plate (Anthony 1988; Burnett and Kunz 1982). To locate roost trees occupied by adult females we attached small 0.49-g radio-transmitters (model LB-2; Holohil Systems Ltd., Carp, Ontario, Canada) using nontoxic glue (Skin-Bond; Smith and Nephew, Largo, Florida). We then radiotracked bats to roost locations using a 3-element yagi antenna (Wildlife Materials, Carbondale, Illinois) and telemetry receiver (Communications Specialists, Inc., Orange, California). To confirm the occupancy of a roost and estimate the nightly abundance of bats when we collected

guano we counted bats exiting roosts in the evening. Observations began ≥15 min before sunset and continued until darkness made observations impossible or >10 min passed without an additional emergence or other discernible activity by bats. Additional activity that caused us to extend our observations included noise from within the roost and bats flying near or landing on the roost.

Bat guano collection and measurement.—We collected guano beneath roost entrances using 1×1-m screens 0.5 m above the ground, a design similar to Brigham et al. (2002). Screens were attached to a square frame made of polyvinyl chloride. One to 3 guano screens were set directly beneath roost exit(s) we observed bats using. The number of screens at a roost varied with the number of exits used. We measured guano mass based on the samples from one 1-m^2 quadrat at each roost because this typically captured 70–80% of all pellets. We therefore considered the effective area measured as 1 m^2. Screens were left overnight to collect guano. Guano was gathered on the morning following each emergence, and the screens were checked visually in the evening before sunset to ensure they were clean. Nightly guano collections and emergence counts continued until bats ceased to occupy the roost.

We collected guano pellets from screens using tweezers, placed them in a sealed plastic bag, and froze them later that day. Frozen samples were later thawed and placed into a drying oven for 7 days at 60°C. Then samples were weighed and stored in sealed glass jars. Each night's collection at a roost tree was considered a single sample for measuring guano mass. We measured the percent nitrogen content of dried guano samples by combustion with a carbon, nitrogen, and sulfur analyzer (CNS-2000; Leco Corporation, St. Joseph, Michigan). For nitrogen analysis we pooled samples collected from each roost location within the same 2-week period. For carbon, nitrogen, and sulfur analysis we ground the guano into a fine powder using a mortar and pestle. To reduce machine error we performed a drift correction every 5 measurements using sulfamethazine (Leco Corporation) with a standard nitrogen concentration of 20.13%. We conducted 2 trials for each guano sample and then averaged these values.

We analyzed the relationship between guano mass deposited and percent nitrogen content to potentially relevant factors using 2 separate multiple linear regression models in program R (v. 2.2.1; R Foundation for Statistical Computing, Vienna, Austria). The 1st model assessed the relationship between the amount of guano collected and bat abundance, Julian calendar day (Date) or a quadratic transformation of Julian calendar day ($Date^2$), and species. The 2nd model evaluated the relationship between percent nitrogen content of guano and Date, $Date^2$, year, and species. The quadratic transformation of date allowed for a curvilinear relationship to be generated. This type of relationship was examined in case variables changed with events occurring during the middle of the summer, such as parturition and lactation. Year was represented by binary variables for 2004 (Year04; $n = 7$) and 2005 (Year05; $n = 9$), with values of 0 for both variables representing samples from 2002 and 2003 ($n = 4$). Values for guano mass were log-

TABLE 1.—Guano mass (g) deposited nightly beneath roosts, nightly emergence counts, nightly per capita guano mass (g/bat) deposited beneath roosts ($n = 13$ *Myotis septentrionalis*; $n = 32$ *M. sodalis*), and percent nitrogen content of guano ($n = 5$ *M. septentrionalis*; $n = 15$ *M. sodalis*).

Measure	Species	$\bar{X} \pm SD$	Range
Guano mass	*M. septentrionalis*	0.225 ± 0.324	0.000–0.912
	M. sodalis	0.813 ± 1.755	0.003–7.854
No. bats present	*M. septentrionalis*	22.3 ± 16.0	2–55
	M. sodalis	41.5 ± 36.6	3–156
Per capita guano deposits	*M. septentrionalis*	0.012 ± 0.021	0.001–0.063
	M. sodalis	0.015 ± 0.017	0.000–0.059
Percent nitrogen content	*M. septentrionalis*	9.33 ± 0.38	8.94–9.71
	M. sodalis	10.07 ± 0.53	9.45–11.05

transformed to improve conformity with normality assumptions. Values for abundance, Date, and Date^2 were standardized to a mean of 0 and standard deviation of 1. Models containing all possible sets of variables were compared using Akaike's information criterion corrected for small sample size (AIC_c) using program R (version 2.2.1, package wle; R Foundation for Statistical Computing). Models within 2 AIC_c values of the model with the lowest AIC_c value were considered competing models (Burnham and Anderson 2002). All competing models were averaged to summarize parameter estimates and uncertainties into a single additive model (Burnham and Anderson 2002). We represented error in our parameter estimates as 95% confidence intervals (95% *CI*s).

To assess whether the amount of guano deposited at a location might be comparable to pools of forest nutrients we predicted the mass of nitrogen deposited via guano by combining the predicted values of the regression relationships for guano mass and percent nitrogen content over the duration of the maternity season using:

$$\text{nitrogen mass} = \text{guano mass} \times \frac{\text{percent nitrogen}}{100}.$$

We then plotted the predicted mass of nitrogen deposited during a night over a range of observed dates for guano deposits at roosts with 3 different abundances for each species. The abundance values were based on the range of group size we recorded and included the average group size for each species, the largest group size, and the 3rd-smallest group size. Although smaller groups of both species were observed to exit roosts, we felt that predictions based on these small numbers would be trivial. To estimate the total deposits at a roost location we summed our estimates of nitrogen mass for large groups of each species over 2 different time periods, average period of roost occupancy and the entire observation period. Average period of occupancy was calculated based on the number of consecutive days that roosts were occupied (Duchamp 2006).

RESULTS

Sixteen female bats were tracked to 20 roost locations where a total of 45 guano samples were collected (Table 1). Based on the

TABLE 2.—Best 5 linear regression models predicting a) guano mass and b) percent nitrogen content. Models were ranked according to Akaike's information criterion corrected for small sample size (AIC_c—Burnham and Anderson 2002). Values for guano mass were log-transformed to improve conformity to normality assumptions. All possible sets of variables were compared using program R (version 2.2.1, package wle). See text for definition of variables.

AIC_c	ΔAIC_c	Adjusted R^2	Variables in model
a)			
157.82	0.00	0.51	Abundance, Date, Date^2
158.46	0.64	0.52	Abundance, Date, Date^2, Species
159.24	1.43	0.47	Abundance, Date
160.62	3.50	0.47	Abundance, Date, Species
161.22	4.68	0.42	Abundance
b)			
30.32	0.00	0.34	Species, Year04
31.47	1.14	0.38	Species, Year04, Date^2
33.08	2.75	0.30	Species, Year04, Year05
33.10	2.77	0.30	Species, Year04, Date
34.47	4.14	0.34	Species, Year04, Date, Date^2

distance between roosts, bats likely came from at least 3 colonies of *M. sodalis* (minimum distance between roost trees of separate colonies = 11 km), and 6 colonies of *M. septentrionalis* (minimum distance between roost trees of separate colonies = 12 km). The amount of guano deposited at a roost during a night ranged from 0 to 7.85 g (Table 1). Negligible amounts were deposited during the day. Among the potential regression models explaining variation in guano mass, 3 nested models emerged with ΔAIC_c values < 2 and were considered competing models (Table 2a). The competing models were averaged to produce a final model with parameters that described guano mass captured throughout the summer, based on group size in the roost and species ($F_{4,40} = 14.13$, $P < 0.001$, $R_a^2 = 0.56$; Table 2a). The amount of guano deposited was related positively to the number of bats occupying a roost (1.102, 95% *CI* = 0.669–1.536, $P < 0.001$) and increased with Julian date (0.532, 95% *CI* = 0.113–0.949, $P = 0.014$). An increase in guano mass in mid-season was not statistically significant (-0.252, 95% *CI* = 0.794–0.290, $P = 0.365$). *M. sodalis* and *M. septentrionalis* did not differ in the amount of guano deposited beneath roosts (0.158, 95% *CI* = -0.397–0.714, $P = 0.578$).

Percent total nitrogen across all guano samples was 9.93% $\pm$ 0.57% *SD* with measurements ranging from 8.94% to 11.05% (Table 1). Among the potential regression models for describing variation in nitrogen concentration, 2 nested models emerged as competing models (Table 2b). These were averaged and resulted in a final model that described guano mass varying between species, by year, and throughout the summer ($F_{3,16} = 4.10$, $P = 0.025$, $R_a^2 = 0.33$; Table 2b). Percent nitrogen was lower in samples collected in 2004 relative to other years (-0.509, 95% *CI* = -0.930– -0.087, $P = 0.020$) and in samples collected beneath *M. sodalis* roosts (0.575, 95% *CI* = 0.110–1.041, $P = 0.017$). A seasonal peak in percent nitrogen was not significant (-0.053, 95% *CI* = -0.217–0.112, $P = 0.266$).
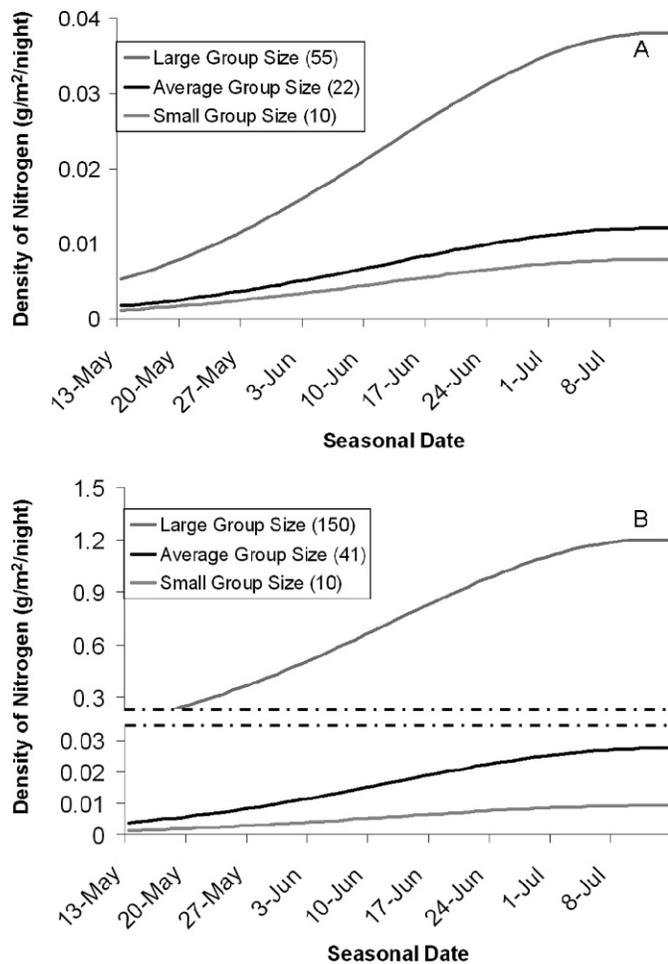
FIG. 1.—Predicted seasonal variation in density of deposited nitrogen (g/m² per night) beneath roost trees for 3 different group sizes of A) *Myotis septentrionalis* and B) *M. sodalis*. Predictions are based on combined values from model-averaged regression equations estimating the amount of guano and concentration of nitrogen.

Combining predictions from models for percent nitrogen and guano mass yielded substantial variation in the predicted mass of nitrogen deposited outside roosts during the maternity season for each species (Figs. 1A and 1B). For *M. septentrionalis*, the mass of nitrogen deposited by large (55), average (22), and small groups (10) was predicted to be 12% (1.46 g/m², 95% CI = 0–8.73 g/m²), 4% (0.46 g/m², 95% CI = 0–9.22 g/m²), and 3% (0.30 g/m², 95% CI = 0–11.05 g/m²), respectively, of the upper range of annual net nitrogen mineralization in the region (12 g/m²—Fan et al. 1998). In contrast to the lower range (2 g/m²—Fan et al. 1998) of annual net nitrogen mineralization, these values were 73%, 23%, and 15%, respectively, for the different group sizes. Over an average period of roost occupancy for *M. septentrionalis* (2 days) we predicted the mass of guano deposited by large groups of bats would be only 4% (0.08 g/m², 95% CI = 0–1.73 g/m²) of the lower value during the middle to late portions of the maternity season. For large (150), average (41), and small (10) groups of *M. sodalis* the predicted mass of nitrogen deposited beneath an occupied roost over the entire observation period was 380% (46.04 g/m², 95% CI = 14.47–77.61 g/m²), 9% (1.05 g/m², 95% CI = 0–10.42 g/m²),

and 3% (0.36 g/m², 95% CI = 0–11.11 g/m²) of the upper range of annual net nitrogen mineralization (Fan et al. 1998) and 2,300%, 52%, and 18% respectively, relative to the lower range. Over an average period of roost occupancy (7 days) for large populations of *M. sodalis*, mass of nitrogen deposits were expected to be 67% (8.39 g/m², 95% CI = 0–18.86 g/m²) of this upper value and 400% of the lower range of annual net nitrogen mineralization (2.00 g/m²) during the middle to late portions of the maternity season.

DISCUSSION

Consistent with the nutrient hot spot hypothesis, we found considerable concentrations of guano deposited by both *M. septentrionalis* and *M. sodalis* directly beneath roost exits. The amount of guano deposited varied most strongly with abundance, but it also increased independently during the middle to late stages of the maternity season corresponding with increased flight activity by female adults during lactation (Murray and Kurta 2004) and the 1st foraging trips by juveniles. During this period bats exhibit increased activity outside of roosts at dusk and dawn (Humphrey et al. 1977). Additionally, foraging by juveniles often occurs in short bouts close to the roost (Humphrey et al. 1977). Thus, behavioral changes by the bats likely contribute to seasonal changes in the amount of guano deposited.

Differences between the 2 species regarding the nitrogen concentration within guano, although statistically significant, probably are not ecologically significant. Differences were <1%, with greater differences in overall nitrogen deposition beneath a roost likely to occur due to the amount of guano in relation to group size and roost fidelity (Duchamp 2006). *M. sodalis* occurred in larger groups within roosts and tended to occupy sites for 7 consecutive days compared to 2 days for *M. septentrionalis* (Duchamp 2006). These differences should produce different patterns of nutrient deposition, with *M. sodalis* leaving a stronger nitrogen footprint at fewer roosts, whereas nitrogen contributions of *M. septentrionalis* should be smaller but spread among more trees.

Amounts of nitrogen we recorded within our 1-m² sampling units beneath roosts housing large groups of bats are comparable to the annual amount mineralized per 1 m² during the decomposition of forest litter (Fan et al. 1998). Guano deposits at roosts thus likely serve as a local nutrient pulse and could influence vegetation patterns within forests. Temporary and localized nutrient peaks are typical in temperate forests, and many herbaceous plant species are adapted to exploit this resource variability (Farley and Fitter 1999). Nitrogen influxes also can alter soil chemistry, decomposition rates of leaf litter, and soil respiration (Agren et al. 2001; Bowden et al. 2004; Frey et al. 2004; McClaugherty et al. 1985). Additionally, elevated nutrient levels, combined with the propensity of bat roosts to be located in forest openings (Barclay and Kurta 2007; Kalcounis-Rüppell et al. 2005; Pierson 1998), should favor the development of seedlings from early-successional tree species (Bazzaz and Miao 1993) and also could offset the level of intraspecific competition in high-density seed shadows of parent trees.

Our study is the 1st quantitative attempt to assess the ecological role of bats in temperate forest nutrient dynamics. Depending on the amount of guano deposited, roost sites could provide temporary peaks in soil nutrients during early and mid-summer. Based on our results, nutrient peaks are to occur most likely at roosts used by large groups of bats during lactation and postlactation periods. We expect these deposits to be most important in nutrient-poor areas such as uplands and more northern forests (Farley and Fitter 1999). Guano from birds is an effective and traditional fertilizer that tends to mineralize in 3–14 days, depending on conditions (Hadas and Rosenberg 1992). Based on the long history of bat guano serving the same function as a high-quality, naturally occurring fertilizer (Hutchinson 1950; Kunz and Lumsden 2003), we predict a similar time line for nitrogen mineralization. Annual influxes of nitrogen of just 5 g/m^2 per year have measurable impacts on soil respiration and microbial communities that process soil nutrients (Bowden et al. 2004; Frey et al. 2004). Therefore, roosts experiencing perennial use by large groups of bats should exhibit observable effects on the surrounding soil. Further work is needed to determine the amount of nitrogen that is made available in the soil from deposited guano; if the forest soil surrounding large, upland roost locations is distinct from the surrounding soil; what, if any, response occurs from the plant and microbial community; and whether guano deposits within large cavity roosts interact with the nutrient levels of surrounding soils before and after collapse of the tree.

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