Hard forest edges act as conduits, not filters, for bats

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Abstract:

High levels of bat activity have been reported at forest edges worldwide, but few studies have examined the ecological function of edges as a linear landscape feature. Patterns of association of bats at edges between old and young forest stands (hard edges) could be a result of edges acting as either a semi-permeable barrier or a filter to movement into the forest between different-aged forest stands for bats (or their insect prey), causing an accumulation of bat activity along the edge. Alternatively, edges may be a linear landscape feature similar to roads and riparian corridors that bats use as flight conduits as they move from one place to another. Using ultrasound microphone arrays and recording equipment, we were able to determine flight patterns of bats at hard edges within a landscape of intensively managed loblolly pine (*Pinus taeda*) plantation in eastern North Carolina, USA, during 2009. Across edges and species sampled, bats consistently flew parallel to edges, suggesting that edges act as conduits for bats. Feeding rates of bats at edges were low, further supporting use of edges as conduits for bats that are either flying along edges to move to and from roosting and foraging habitat patches or moving among foraging patches. Continuous edges should be maintained between linear and nonlinear landscape features, especially where known roosting and foraging areas are being connected by an edge.

Keywords: Chiroptera | forest management | intensive forestry | movements | North Carolina | pine plantation | Pinus spp. | wildlife corridor

Article:

In the southeastern United States, intensively managed pine (*Pinus* spp.) forests cover approximately 18 million ha of land (Wear and Greis **2002**). Managed pine forests are

economically and ecologically important, because they account for 60% of timber products produced in the United States (National Commission on Science for Sustainable Forestry **2005**) and total approximately 20% of forests in the southern United States (approx. 18 million ha; Smith et al. **2009**). Clearcut harvesting is a common silviculture practice in forests managed for timber production. This practice often produces an abrupt vegetation transition zone between an older forest stand (closed canopy) and the recently harvested and replanted stand (open canopy), which is a linear landscape feature (Stevens and Husband **1998**). The most obvious linear landscape feature of this transition is a hard forest edge (mid- to late-rotation stands adjacent to younger stands or other open areas; hereafter, "edge"; Fig. **1**). Edges are encouraged by third-party forest certification systems (e.g., Sustainable Forestry Initiative) that ensure adjacent clearcuts are different ages (green-up requirements). Edges provide a mixture of habitat characteristics (habitat structure and plant composition) that forest-, open-, and edge-adapted species may use. Edges between mature forest and recent clearcuts can influence species richness, predator–prey interactions, energy transfer, and spatial behaviors (Harris **1988**, Yahner **1988**).

Figure 1. Example of a hard edge in an intensively managed loblolly pine (*Pinus taeda*) forest (Weyerhaeuser Company) in the coastal plain of North Carolina, USA. Photo by Adam Morris.

Bats are the primary nocturnal predator of insects (Crampton and Barclay **1998**), including economically important crop (McCracken et al. **2012**) and forest (Wilson and Barclay **2006**, Lacki and Dodd **2011**) pests. In many forest systems, bats show a high affinity for edges (Verboom and Huitema **1997**; Grindal and Brigham **1998**, **1999**; Hogberg et al. **2002**; Morris et al. **2010**, but see Erickson and West **2003**, Dodd et al. **2012**). Edges are thought to provide suitable foraging habitat, cover, and linear landmarks for navigation for foraging and commuting bats (Racey and Swift **1985**, Verboom and Huitema **1997**, Hein et al. **2009**). Depending on wing morphology and echolocation structure, some bats are more or less suited to the cluttered vegetation that emerges at forest edges (Fenton **1990**). For bats that use forest edges, there may be particular echolocation strategies, such as alternating frequencies, used for foraging on prey located therein (Ratcliffe et al. **2011**).

In an intensively managed forest in the coastal plain region of North Carolina, USA, Morris et al. (**2010**) reported that presence of hard edges was the best predictor of overall bat activity, including foraging activity, for most bat species. In addition, bat activity at edges and open areas was greater than bat activity in other managed stand types (Morris et al. **2010**). Similarly, several species of bats were more active along the edges of residual forest patches within clearcut-harvested areas in Alberta, Canada (Hogberg et al. **2002**).

Patterns of association of bats at edges could be a result of 2 mechanisms. In either case, these mechanisms attribute ecological function; edges can act as either a filter or a conduit for flying bats over the course of a night (see fig. 1 in Hess and Fischer **2001** for definitions). For species that are adapted to foraging in open areas, hard edges may create a semi-permeable barrier or filter to movement into the forest for bats, or their insect prey, causing an accumulation of bat activity along the edge. This accumulation at the edge that acts as a filter is due to either the physical barrier itself or the preferred foraging habitat type that the edge provides. Alternatively, for species that forage in either open or cluttered habitat conditions, edges may be a linear landscape feature similar to roads and riparian corridors that bats use as flight conduits as they move from one place to another (Law and Chidel **2002**). If bats use edges as conduits, edges may provide connectivity between foraging and roosting areas. Although it is well-documented that bats do use edges, it is not clear whether activity along edges is a result of the edge acting as either a filter or a conduit. Distinguishing between these 2 alternatives is important because, if bats are using edges as conduits, then landscape-level planning can incorporate continuous edges to increase connectivity for bats within landscapes.

Using ultrasound microphone arrays and recording equipment, we determined whether the mechanism to explain high bat activity is a result of the edge acting as a filter or a conduit. Each alternative is associated with particular flight patterns. If bats are filtered by hard edges, the flight vector of individual bats should be perpendicular to the hard edge as bats travel from the open toward mature forest. Conversely, if bats use edges as conduits, the flight vector of individual bats should be parallel to the edge.

STUDY AREA

Our study was conducted in eastern North Carolina (Lenoir County), USA, within a landscape of intensively managed loblolly pine (*P. taeda*) plantation owned and managed by Weyerhaeuser Company. The surrounding region was rural and consisted of sandy bottomland forest with a mosaic of agricultural and managed pine forest patches (see Marshall et al. **2012** for more on site description). Bats in intensively managed loblolly pine plantations in eastern North Carolina have been well-studied, with the most common species including open-landscape-adapted species such as red (*Lasiurus borealis*), big brown (*Eptesicus fuscus*), evening (*Nycticeius humeralis*), and tricolored (*Perimyotis subflavus*) bats (Vindigni et al. **2009**, Morris et al. **2010**, M. C. Kalcounis-Rueppell, unpublished data).

METHODS

Experimental Design

Between June and September 2009, we established 10 4-channel microphone arrays (Ultrasound Gate USG; Avisoft, Berlin, Germany) along 7 different hard edges over the field season to determine whether bats flew parallel or perpendicular to edges. Microphone arrays were set up sequentially through the season because we only had equipment for one microphone array. The 7 edges ranged from approximately 88 m to 1,328 m in length and represented the edges available to bats in the study area. Edges consisted of mid- to late-rotation stands planted from 1972 to 1975 adjacent to younger stands planted in 2008. There was approximately a 15–25-m height difference between stands.

We placed 2 microphones on both sides of a hard edge (Fig. **2**; hereafter, referred to as an edge-array). Specifically, 2 microphones were on the side of the older forest stand (closed canopy) and 2 were on the side of the recently harvested and replanted stand (open canopy; Fig. **2**). Thus, edge-arrays were rectangular in shape, approximately 6 m × 17 m (average values of 10 arrays), with the longer length running parallel to the edge (Fig. **2**). On average, edge-arrays were set up 126.80 ± 198.32 m (range = 20–557 m) from the closest end of sampled edges. On 2 of the longest edges, edge-arrays were set up more than once, at different points along the edge. On one of these edges, 2 edge-arrays were set up with 934 m between them and on the other of these edges, 3 edge-arrays were set up with 854 m between the furthest 2 arrays and 106 m between the closest 2 arrays.
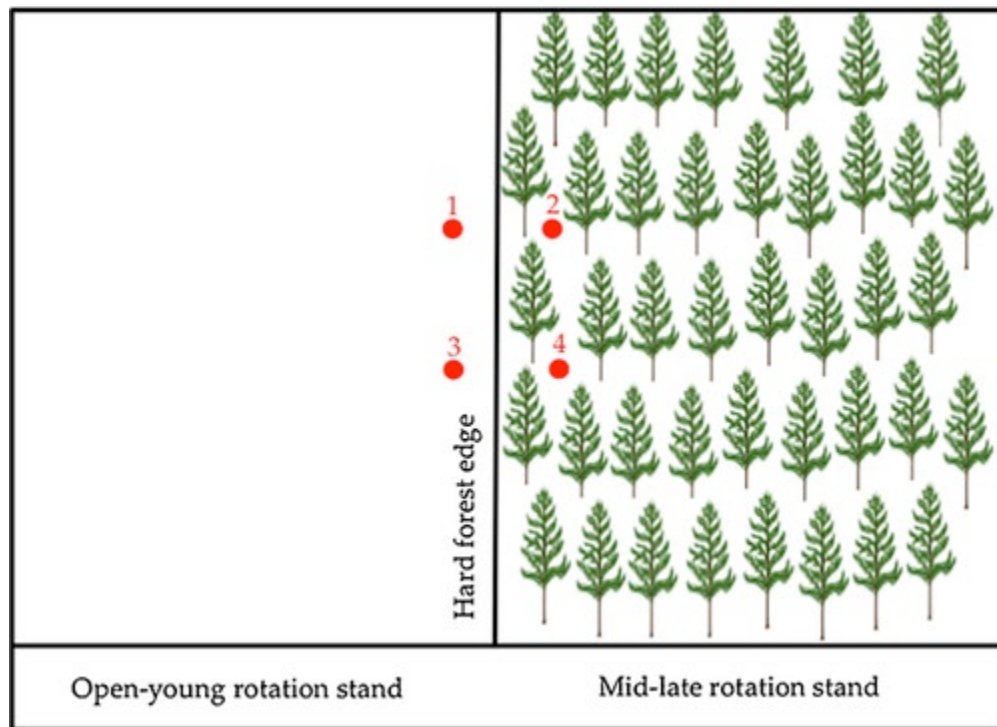

Figure 2. Illustration of a 4-channel microphone array located along edges within a managed pine forest (Weyerhaeuser Company) in Lenoir Company, North Carolina, USA, 2009. Red circles indicate location of each microphone in the array.

We attached each microphone array to a laptop computer powered by an external battery. We set microphone arrays to record all full-spectrum sound (sonic, ultrasonic, and harmonics) between

10 kHz and 250 kHz. Each array consisted of 4 microphones (Emkay ultrasound microphones; Avisoft). We attached each microphone to vegetation via a velcro strip approximately 2 m above the ground. We powered on edge-arrays at dusk and powered them off at dawn. We conducted edge-array surveys at the same edge-array for 1–5 nights, aiming for 3 nights of recording at each edge-array site. Edge-arrays were set up according to an approved animal care protocol (University of North Carolina at Greensboro Institutional Animal Care and Use Committee no. 09–10).

We saved data from edge-array surveys to an external hard drive. Using echolocation call-sequence data recorded from the edge-array, we determined position of incoming echolocation call sequence relative to edges, based on time of arrival of the first call in an echolocation sequence at each microphone in the array. We analyzed echolocation call-sequence data with SASLabPro (Avisoft). We did not use any filtering processes to discard either files or background noise from our recordings. Rather, we examined each 4-channel file to determine whether the file was appropriate for analysis. Thus, we manually ensured that the recording was of a bat instead of other biological or non-biological noise, such as insects and birds or wind and rain, respectively.

We selected approximately 100 high-quality echolocation call sequences from each edge-array site, on 3 nights of recording, for analyses. A high-quality sequence was a sequence where we had a clear recording of a single echolocating bat without background noise that masked the echolocation calls. We selected high-quality echolocation call sequences for analyses by manually scanning through recordings of a particular night and choosing echolocation call sequences recorded at the beginning (1 hr after dusk), middle (around midnight), and end of nights (1 hr before dawn), until we had analyzed approximately 100 echolocation call sequences/night. For some nights, we analyzed <100 high-quality echolocation call sequences because it was difficult to find high-quality recordings due to insect noise. For some nights, we analyzed >100 high-quality echolocation call sequences because there was an abundance of high-quality recordings.

Using SASLabPro, we examined time of arrival of the first call within a sequence at all 4 microphones to determine difference between arrival times of the same call at the 4 microphones. We then used arrival order to determine position of an incoming echolocation call. If the first call in an echolocation sequence arrived at the 2 microphones at the outside edge of the array (i.e., microphones 1 and 3 in Fig. **2**) and then arrived at the 2 microphones on the inside edge of the forest (i.e., microphones 2 and 4 in Fig. **2**), the bat had to be flying toward the edge from the open area, and we deemed this flight vector to be perpendicular to the edge. If, however, the first call in an echolocation sequence arrived at either of the 2 microphones that crossed the outside-forest and inside-forest side of the array (i.e., microphones 1 and 2 or microphones 3 and 4 in Figs. **2** and **3**), the bat had to be flying along the edge toward either one of these sides of the array, and we deemed this flight vector to be parallel to the edge. If an echolocation call sequence could not be clearly categorized as perpendicular or parallel based on our decision rules (described above), we did not classify the call as either perpendicular or parallel. Further, for every sequence analyzed, we noted whether the bat was feeding based on presence of ≥1 feeding buzz.
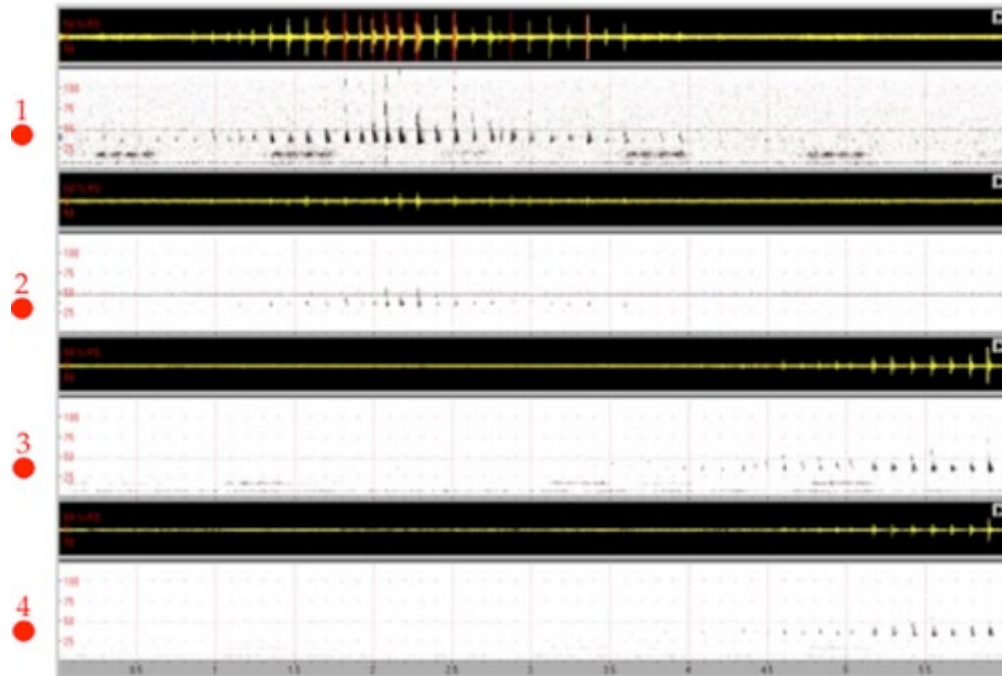
Figure 3. Spectrograph of 4 channels from the microphone array that shows a typical bat echolocation-call-sequence arriving at all 4 microphones. Microphone numbers in this array are as shown in Figure 2. The first call in the echolocation sequence arrived at microphones 1 and 2 and then arrived at microphones 3 and 4. Therefore, the bat had to be flying along the edge toward microphones 1 and 2. This bat had a parallel flight vector relative to the edge. Echolocation call sequence was collected during 2009 using a 4-channel microphone array along edges in Lenoir County, North Carolina, USA, within a managed pine forest landscape (Weyerhaeuser Company).

Because we were interested in bat community use of edges, we did not identify every call sequence to species. However, to ensure that all species responded to the edge array in the same manner, we identified a subset of call sequences to species. We chose a subset of calls for logistic reasons related to availability of computer processing resources. We selected call sequences from 1 night (randomly selected) recorded at 7 edge-arrays (randomly selected) for species analysis. Sequences were identified to species using SonoBat for the US Northeast region v 3.1 (DND Design, Arcata, CA). Sequences from a given night were batch-processed though scrubbing by using default settings in SonoBat Batch Scrubber 5.1.vi. Call sequences that remained post-scrubbing were then analyzed using SonoBat 3 default settings except for the decision threshold, which we varied from 0.9 to 0.7 depending on the night. For a species assignment to be accepted for further analysis it needed to have a species assigned by both consensus and vote in SonoBat for the US Northeast region v 3.1. SonoBat for the US Northeast region v 3.1 is optimized to identify echolocation sequences from bat species in the northeastern United States and was used because 1) there is no southeastern United States version and 2) there is overlap in all of the non-myotid species between North Carolina and the northeast region. Myotid bats rarely use edges in North Carolina (Morris et al. **2010**).

We used a chi-square test of independence or Fisher's exact text (for cells with values of <5) to test the null hypothesis that the proportion of bats flying parallel to or perpendicular to edges did

not differ from random expectations. The random expectation for the chi-square analysis was 50% parallel flight sequences and 50% perpendicular flight sequences. It is possible that longer edges may direct flight parallel along edges more readily than shorter edges. It is also possible that the probability of detecting a bat at any one point along the edge is higher if a bat is flying parallel to the edge than if it is flying perpendicular to the edge because a bat flying parallel will be recorded on an edge-array set anywhere along the edge, whereas a bat flying perpendicular will only be recorded if the edge-array is located along the edge at the site where it hits the edge. Therefore, we tested whether edge length (m) was related to number of parallel calls we recorded for an array with a simple linear regression. We determined edge length by overlaying Global Positioning System coordinates from each array in Google Earth (2012; **earth.google.com**) and measuring length of forest edge where each array was located. Our rejection criterion was set at $P < 0.05$. Results are presented as mean ± 1 standard deviation. All statistical analyses were completed in R (R Core Team **2012**).
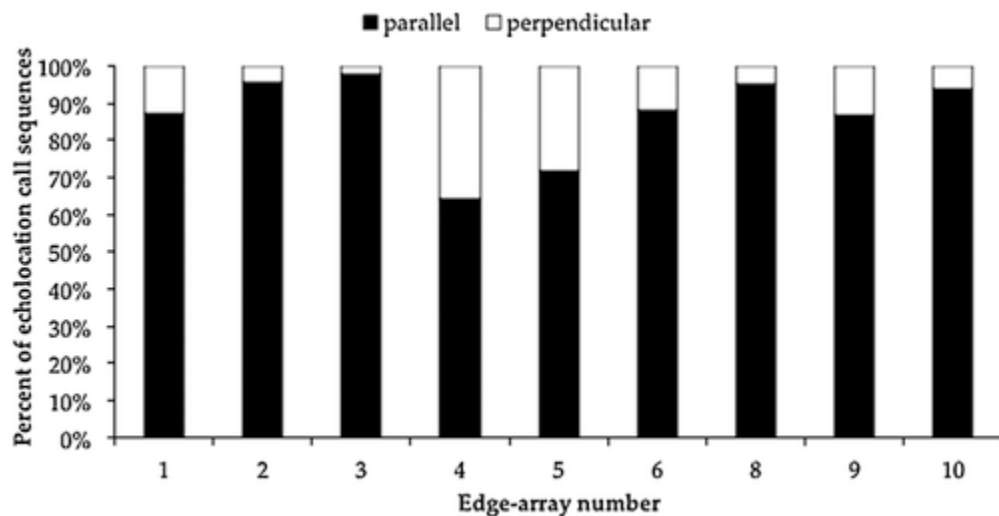

Figure 4. Percent of bat echolocation calls identified as parallel or perpendicular relative to 9 hard forest edge-arrays. Acoustic data were collected during 2009 using a 4-channel microphone array along 6 hard edges in Lenoir County, North Carolina, USA, within a managed pine forest landscape (Weyerhaeuser Company). Call sequences analyzed for each edge: Edge 1 ($n = 461$), Edge 2 ($n = 1,184$), Edge 3 ($n = 709$), Edge 4 ($n = 304$), Edge 5 ($n = 164$), Edge 6 ($n = 496$), Edge 8 ($n = 280$), Edge 9 ($n = 275$), Edge 10 ($n = 268$).

RESULTS

We sampled 10 edge-array sites over 44 nights (2.79 ± 0.67 nights/array) and recorded 481 hours and 129,763 echolocation call-sequence files. We discarded all data from edge-array 7 due to excess ultrasound noise from a power inverter that decreased call quality. Therefore, we included 9 edge-arrays in our analyses. We analyzed 5,085 echolocation call sequences. On average, we analyzed 565.00 ± 326.68 (min. = 204, max. = 1,476) echolocation call sequences/edge-array ($n = 9$ edge arrays). On average, we analyzed 202.20 ± 151.62 (min. = 81, max. = 539) echolocation call sequences/night ($n = 25$ nights). On average, we were not able to assign parallel or perpendicular flight to $17.32 \pm 10.57\%$ (min. = 5.63, max. = 41.54) of echolocation call

sequences/edge-array site. Not including the unassigned calls, there were 4,141 echolocation call sequences that could be assigned as either being parallel or perpendicular flight.

Of our 4,141 echolocation call sequences, >90% were from bats flying parallel ($n = 3,738$) rather than perpendicular ($n = 403$) to edges. This distribution of flight vectors differed from random expectations, with more bats flying parallel and fewer bats flying perpendicular than expected (only considering call sequences that were classified: $\chi^2 = 406.21$, df $= 8$, $P < 0.001$, Fig. **4**; considering all call sequences including unclassified sequences: $\chi^2 = 615.00$, df $= 16$, $P < 0.001$, with random expectation of 33.33% in each group). Our result was not biased by edge length because there was no correlation between number of parallel flight vectors and length of edge ($r = -0.13$, df $= 7$, $P = 0.57$).

Species we identified were as expected and included big brown, tricolored, red, silver-haired (*Lasionycteris noctivagans*), evening, and hoary bats (*Lasiurus cinereus*). Only one hoary bat was identified (flying parallel) so it is not included in our species-level analysis. When considering echolocation sequences identified to species, the distribution of flight vectors differed from random expectations, with more bats flying parallel and fewer bats flying perpendicular than expected for all species (Fisher's exact $P = 0.002$; Fig. **5**). Within each species, the result was the same for big brown (Fisher's exact $P < 0.001$; Fig. **5**), tricolored (Fisher's exact $P < 0.001$; Fig. **5**), red (Fisher's exact $P < 0.001$; Fig. **5**), silver-haired (Fisher's exact $P = 0.02$; Fig. **5**), and evening (Fisher's exact $P = 0.03$; Fig. **5**) bats, with more bats flying parallel and fewer bats flying perpendicular than expected.
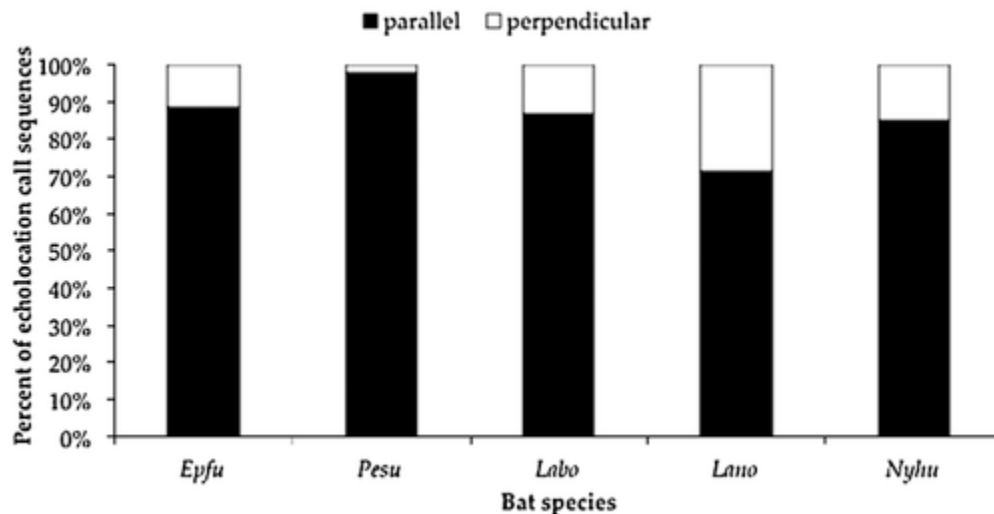

Figure 5. Percent of bat echolocation calls identified as parallel or perpendicular relative to bat species at hard forest edge-arrays. Acoustic data were collected during 2009 using a 4-channel microphone array along 6 hard edges in Lenoir County, North Carolina, USA, within a managed pine forest landscape (Weyerhaeuser Company). Total call sequences identified for each species: *Epfu* (*Eptesicus fuscus*, $n = 16$), *Pesu* (*Perimyotis subflavus*, $n = 94$), *Labo* (*Lasiurus borealis*, $n = 86$), *Lano* (*Lasionycteris noctivagans*, $n = 10$), *Nyhu* (*Nycteceius humeralis*, $n = 18$).

Rate of feeding within our classified echolocation call sequences was low, with only 2% (93) containing feeding buzzes. The feeding rate differed ($\chi^2 = 4.89$, df $= 1$, $P = 0.03$) between bats,

with parallel ($n = 77$ feeding buzzes; 2% rate of feeding) and perpendicular flight vectors ($n = 16$ feeding buzzes; 4% rate of feeding).

DISCUSSION

We found that bats in an intensively managed pine landscape in the southeastern United States used hard edges as conduits because, across the bat community, flight patterns were consistently parallel with the forest edge. The bat community we sampled was representative of species known to use edges in the southeastern United States (Morris et al. **2010**). Our results were consistent across edge-arrays and species, suggesting that parallel flight is a general response to hard-edge habitat types and not a response related to bat-species-specific patterns associated with wing shape and/or echolocation call structure.

We suggest that for deciduous and boreal forest types wherein high levels of bat activity occur at forest edges, the conduit mechanism is also a likely explanation. Knowing that linear edges are landscape features that help bats traverse among forest patches improves our ability to increase landscape connectivity and can potentially facilitate efficient bat movements across landscapes. Our results are consistent with studies that have shown bats using other linear features such as wooded corridors, rivers, and tree lines to commute between roosting and foraging habitat, in some cases preferentially over shorter straight-line commutes in open habitat types (Racey and Swift **1985**, Murray and Kurta **2004**). However, we cannot determine whether bats are flying along edges to move to and from roosting and foraging habitat patches or moving among foraging patches. Determining how bats are using habitat patches at ends of the conduit would require tracking individual bats (e.g., radiotelemetry).

Linear landscape features aid in forming acoustic and visual cues to form spatial memory necessary for navigation (Verboom et al. **1999**, Ulanovsky and Moss **2008**). In terms of acoustics, Verboom et al. (**1999**) demonstrated that commuting bats consistently modified their echolocation calls depending on distance from the banks of a channel. Also, in laboratory experiments, bats have been trained to avoid collision with objects in complete darkness, but avoidance declined when said objects were shifted slightly (Jensen et al. **2005**). Additionally, in a homing experiment of bats released at a distance from their cave roost, blindfolded bats were unable to find their way back, whereas ear-plugged bats and control bats were more likely to find the roost (Layne **1967**). These studies indicate combined importance of both acoustics and vision in navigation and orientation and may explain why bats in our study apparently used edges primarily for commuting.

The low incidence of feeding buzzes we recorded at the edge further supports the hypothesis that edges are conduits. Approximately 98% of our echolocation call sequences did not contain a feeding buzz, suggesting that bats were not using edges as foraging habitat. Our observation of low levels of feeding while using edges as a conduit is consistent with observations of bats opportunistically foraging while in commute (Wai-Ping and Fenton **1989**, Verboom and Huitema **1997**). Our observed levels of feeding are lower than the approximately 9.5% value reported by Morris et al. (**2010**) in an intensively managed pine forest in coastal North Carolina. The difference between studies may reflect that our sampling was restricted to hard edges, as opposed to the hard edge, forest interior, and open habitat patches sampled by Morris et al.

(**2010**). When examining insect availability along hard forest edges, compared with forest interior and open habitat patches, Morris et al. (**2010**) reported higher insect availability along forest edges. Thus, in this landscape, hard forest edges may also support temporary, albeit infrequently used, energetic requirements for commuting bats.

It is likely that hard forest edges contribute to orientation and navigation of commuting bats, perhaps between roosting and foraging areas or among foraging areas. Because edges are conduits for bats, continuous edges between nonlinear landscape patches (e.g., stands in intensively managed forests) should be considered. Additional study identifying foraging and roosting patches of bats within managed forest landscapes could provide further insight to improve connectivity between important roosting and foraging habitat components. Lastly, this study only considered the hard edge between mature pine (closed-canopy) and recently harvested and replanted (open-canopy) stands, which represents only one edge type. It remains to be determined whether bats would use the forest edge between a mid-rotation stand next to a mature stand, or the forest edge between a mid-rotation stand and a water source, in the same way.

MANAGEMENT IMPLICATIONS

During forest planning, edge orientation, density, and connectivity should be considered as a possible positive impact on bat communities. This is especially true in cases where preferred bat roosting locations are known and are separated from quality foraging habitat. It may also be important to provide connectivity between multiple foraging areas, if they are known. However, little is known about how most landscapes relate to and affect bat–habitat relationships, so there is a limited basis upon which to make these decisions in most cases. Managers should also consider possible negative impacts of edges on other taxa and seek to achieve a balance between edge-affiliated and interior-affiliated species.

ACKNOWLEDGMENTS

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