Use of forest edges by bats in a managed pine forest landscape

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Abstract:

Forest edges often have increased species richness and abundance (edge effect) and affect spatial behaviors of species and dynamics of species interactions. Landscapes of intensively managed pine (*Pinus* spp.) stands are characterized by a mosaic of patches and linear forest edges. Managed pine forests are a primary landscape feature of the southeastern United States, but the effects of intensive management on bat communities are poorly understood. Insectivorous bats are important top predators in nocturnal forest food webs. We examined bat foraging behavior along forest edges and in 4 structurally distinct stand types (open-canopy pine, prethinned pine, thinned pine, and unmanaged forest) within a managed pine forest in the coastal plain of North Carolina, USA. During May–August, 2006 and 2007, we recorded echolocation calls using Pettersson D240X bat detectors linked to digital recorders at 156 sites. We also sampled nocturnal flying insects at each site using Malaise insect traps. We used negative binomial count regression models to describe bat foraging behavior relative to forest edges, stand types, and prey availability. Although some species showed affinities for certain stand types and prey items, bat activity patterns were most strongly related to forest edges. Edges were used extensively by 6 aerial-hunting bat species, but avoided by *Myotis* species. Forest edges function similarly to natural forest gaps, by providing foraging opportunities for aerial-hunting bat species. Therefore, the maintenance of forest edges in managed pine landscapes may enhance foraging habitat for aerial-hunting bat species.

Keywords: acoustic sampling | bat activity | count data | echolocation | edge effects | forest edges | forest management | intensive forestry | negative binomial distribution | North Carolina

Article:

The coastal plain of North Carolina, USA, is largely composed of forested wetlands that have been converted for agricultural uses and managed timberlands (Guldin and Wigley 1998, Schultz

1999, National Commission on Science for Sustainable Forestry [NCSSF] 2005). Managed pine (*Pinus* spp.) forests are economically important to the southeastern United States, accounting for 60% of the timber products made in the United States (NCSSF 2005) and comprising 20% of southern United States forests in 2007 (18 million ha; Smith et al. 2009). In eastern North Carolina, management of planted forests, due to regular harvesting, creates a mosaic of forest patches in different seral stages (Kuusipalo and Kangas 1994, Watts and Wilson 2005). The juxtaposition of heterogeneous patches creates large amounts of forest edge (Guldin and Wigley 1998). The most prominent and conspicuous forest edges within managed pine landscapes occur at the boundaries between mid- to late-rotation forest stands and young forest stands or other open areas (hard edges).

Edges are a unique microhabitat because they encompass the interface of 2 vegetation types (Forman and Godron 1981, Matlack 1994) and there is considerable evidence that they increase species richness and abundance (edge effect; Leopold 1933, Yahner 1988, Fagan et al. 1999, Ewers and Didham 2006). Edge effects have been reported for mammals (Menzel et al. 1999), birds (Berry 2001), and herpetofauna (Schlaepfer and Gavin 2001). The increased diversity along edges may be accompanied by an increase in herbivory and predator–prey interactions (Donovan et al. 1997, Cadenasso and Pickett 2000). Spatial configuration of edges within a landscape can have varying effects on species and interspecific interactions (Yahner 1988; Fagan et al. 1999; Cadenasso and Pickett 2000, 2001; Herlin 2001). Although many species are abundant along edges, other species are restricted to undisturbed interior habitat and avoid edges (Yahner 1988, Fraver 1994, Ewers and Didham 2006). Therefore, it is important to examine the species-level effects of generating numerous forest edges across landscapes.

Although insectivorous bats are important nocturnal predators in pine forest landscapes, effects of intensive pine management on bat communities are not well understood (Miller et al. 2003, Wigley et al. 2007; but see Miller 2003, Elmore et al. 2005, Menzel et al. 2005, Miles et al. 2006, Hein et al. 2008*a*). Bats have been observed using forest edges for commuting and foraging (Clark et al. 1993, Walsh and Harris 1996, Grindal and Brigham 1999, Hogberg et al. 2002), and some species use canopy gaps created by natural or anthropogenic disturbances (Crome and Richards 1988, Wunder and Carey 1996, Fenton et al. 1998). Bats are also known to forage along the top of the forest canopy (Kalcounis et al. 1999, Menzel et al. 2000). Bats may use edges and gaps to avoid navigating through structurally complex habitat (Clark et al. 1993, Kusch et al. 2004).

Bat species are suited to forage within certain habitats because of their wing morphology and echolocation call structure (Aldridge and Rautenbach 1987, Norberg and Rayner 1987, Fenton 1990, Fenton et al. 1998). Additionally, bats' choice of foraging habitat is likely influenced by both the diversity and abundance of available insect prey (Verboom and Spoelstra 1999, Kusch et al. 2004, Meyer et al. 2004). It remains unclear whether bats select foraging areas based on available prey, or if this is secondary to the constraints imposed by structural characteristics of foraging areas.

Given the amount of land under intensive pine management in the southeastern United States and general lack of information on bat ecology within these systems, we need to better understand the response of bat communities to intensive silviculture. Few previous studies have examined

the use of forest edges by bats (but see Grindal 1996, Grindal and Brigham 1999, Hogberg et al. 2002). Therefore, we examined foraging behavior of bats in an intensively managed pine landscape specifically to assess the use of hard forest edges. We also examined the effects of stand structure and potential prey occurrence on bat foraging activity. We tested the null hypotheses that overall bat activity (both species specifically and for the community as a whole) and feeding activity were unrelated to forest edges, stand structure, and availability of insects.

STUDY AREA

We conducted our study on Weyerhaeuser Company's 4,000-ha Parker Tract, an intensively managed loblolly pine (*Pinus taeda*) landscape in the coastal plain of North Carolina. The Parker Tract was composed primarily (76.1%) of even-aged stands of loblolly pine in various stages of growth. In addition, since 1997, 956 ha of the Parker Tract have been natural hardwood stands. Typical silviculture of intensively managed stands included clear-cut harvest at 27–35 years followed by site preparation, planting of loblolly pine seedlings on a wide (6.1-m) row spacing, vegetation control, fertilization, thinning, and harvest. We classified stands into 3 pine types (young open-canopy, prethinned, thinned) and a single hardwood type (unmanaged forest). Young, open stands had been clear-cut and replanted on average 7.8 years previously (range 0–15 yr old) and had a mixture of herbaceous and woody vegetation. Prethinned stands contained mid-age pines ($\bar{x}$ = 19.6, range 14–24 yr) with closed canopies and sparse understory vegetation (180 trees/ha). When pine stands reach a certain height, they are commercially thinned. This heavy thinning involves the removal of trees until the target density of 50 trees/ha is attained. Thinned stands averaged 28.2 years (range 25–33 yr) and had open canopy structure, which allowed development of understory and midstory vegetation. Unmanaged stands were dominated by red maple (*Acer rubrum*) and red bay (*Persea borbonia*) and are referred to as coastal hardwood swamp (Wilson et al. 2000). These 4 stand types were common across the Parker Tract, with many edges due to the mosaic patterning of patches. Within this landscape, water occurred in numerous narrow ditches and several small man-made ponds (Vindigni et al. 2009). There were no streams or streamside management zones within the landscape, so all edges occurred at borders between stand types. Hard forest edges occurred between older forested stands (prethinned, thinned, or unmanaged) and young open-canopy stands. Hard edges were the most extreme type of edge and represented the most dramatic structural discontinuity within the landscape.

METHODS

Acoustic Sampling

At each sampling site (see below), we deployed 2 ultrasonic bat detectors (Pettersson D240X full spectrum bat detectors; Pettersson Elektronik AB, Uppsala, Sweden) to record echolocation calls from dusk until dawn. The first bat detector was coupled to a digital recorder (Sony Memory Stick Voice Recorder; Sony Electronics Inc., San Diego, CA) and operated in heterodyne mode (Parsons et al. 2000). Heterodyne recordings cannot reliably be used to identify species, but do provide an index of bat activity (counts of bat echolocation sequences). Heterodyne recordings also allow identification of echolocation sequences used for feeding because of the presence or absence of feeding buzzes (distinct sounds that bats make as they approach and attempt to

capture an insect; Griffin et al. 1960). From heterodyne recordings, we obtained counts of bat echolocation sequences and counts of feeding echolocation sequences. We used the second detector in time-expanded mode to record full-spectrum echolocation calls to an iRiver digital recorder (iRiver ifp; Reigncom Ltd., Seoul, Korea). Our time-expansion recording involved a recording delay in which we recorded sounds at a tenth of actual speed to capture a high-resolution sonogram of each bat vocalization (Parsons et al. 2000). We recorded 1.7-second segments of sound, which took 17 seconds to process and record. This spectral resolution allows identification of bat species from sonograms but does not allow continuous sampling due to the recording delay. We uploaded recorded sound files to a computer and analyzed them using Sonobat 2.5 sound analysis software (Sonobat, Arcata, CA). We manually identified echolocation sequences to species groups using a reference call library (Kalcounis-Rueppell et al. 2007). Our reference call library contained calls recorded at our study site (see below) and calls recorded previously in the southeastern United States. We discarded calls that did not contain search-phase echolocation pulses. We grouped echolocation sequences from bats of the genus *Myotis* (northern long-eared bat [*M. septentrionalis*] and southeastern myotis [*M. austroriparius*]) because of their similar call structure.

We recorded echolocation calls of bats during June and July of 2006 and from May to June 2007. We used stand maps to locate hard edges. Each night, we randomly selected 2 sampling locations in nonadjacent stands or along hard edges, constraining stand location based on travel distance between stands. We chose forest interior sites at least 100 m from any edges or roads. To sample along forest edges, we placed detectors in open stands within 50 m of bordering forested stands, with microphones pointed parallel to the stand border. We positioned these sampling locations (referred to hereafter as edge sites) so as to maximize detection range in the open area directly adjacent to the forest edge. We housed detectors in plastic boxes with small holes cut around the microphone. We stacked these plastic boxes within a large wooden box for weather protection, and positioned these 1–2 m above ground level, tied around trees or metal poles using elastic cords. We oriented detectors to 45 degrees above horizontal and pointed them toward canopy openings to limit effects of vegetation on sound propagation (Patriquin et al. 2003) and to record maximum number of bats (Weller and Zabel 2002).

Due to the limited availability of appropriate stands in each forest class, we sampled some stands ($n = 16$) on multiple nights. However, we placed bat detectors in novel locations in stands each night. All sampling locations were at least 50 m apart, and we sampled no stands >6 times. Due to this approach, we assumed that sampling sites within stands were independent. We feel this was justified given that 1) bats forage in response to micro-site conditions (e.g., complexity of vegetation) that can be heterogeneous within stands, and 2) the range of detection (approx. 50 m) is small compared to stand size ($\bar{x} = 31.1$ ha for $n = 129$ stands).

Bat and Insect Capture Methods

We captured bats using mist nets opportunistically over small ponds and ditches within the mosaic landscape. We captured bats for species verification and to record reference calls. We fitted captured bats with light tags or followed them with a spotlight as we released them to record echolocation calls. We recorded calls at the study site because echolocation call structure can vary geographically (O'Farrell et al. 2000). All animal handling followed the guidelines of

the University of North Carolina at Greensboro Institutional Animal Care and Use Committee Protocol 06-11.

We used passive Malaise traps to sample flying and terrestrial insects at sites simultaneously sampled with bat detectors (see Kalcounis-Rueppell et al. 2007). We preserved captured insects in 95% ethanol solution. We identified insects to order using a dissecting microscope and taxonomic keys (Arnett 2000). We included insect orders with 25 or more total captures (over both years) in our analyses. To test for differences in insect abundances across stand types and edge sites, we used a series of analysis of variance tests on counts of insect captures (total, and by order). To examine where differences existed, we conducted post hoc multiple comparison tests, using Tukey's method to control the experiment-wise Type I error rate.

Regression Analysis

We used a series of count regression models to test the null hypotheses that overall bat activity (counts of bat echolocation sequences), bat feeding activity (counts of echolocation sequences containing a feeding buzz), and bat species activity (counts of echolocation sequences identified to a given species) were not related to stand type, edge sites, or availability of insects. We used count regression models because response variables in the form of counts (nonnegative integers) often violate assumptions of distribution of parametric modeling techniques (Vincent and Haworth 1983, White and Bennetts 1996) and may be skewed due to a high frequency of zero-counts (Cunningham and Lindenmayer 2005, Martin et al. 2005). We modeled counts of bat echolocation sequences using Poisson (Vincent and Haworth 1983), negative binomial (Bliss and Fisher 1953, White and Bennetts 1996), zero-inflated Poisson, and zero-inflated negative binomial regression models (Lambert 1992, Cunningham and Lindenmayer 2005). We evaluated the fit of these 4 distributions for each response variable using probability-count plots and Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC) scores (Akaike 1973) as described by Sileshi (2006).

Once we determined the most appropriate count model, we used forest stand type (open, prethinned, thinned, unmanaged) and stand location (edge, interior) as categorical (indicator) variables, and counts of insects (total, and by order) as continuous model predictors. This approach allowed simultaneous testing of effects of location and prey availability on bat foraging behavior. We also tested the significance of 2 covariates (daily mean temp [°C] and daily mean precipitation [cm]) to try to resolve some temporal variation in bat activity. We evaluated hierarchical candidate models based on significance ($\alpha = 0.05$) of parameter estimates and their AIC and BIC scores. We fit and analyzed all regression models using PROC COUNTREG and PROC GENMOD procedures in SAS 9.1 (SAS Institute, Cary, NC).

RESULTS

We sampled 154 sites on 78 nights in open ($n = 27$), prethinned ($n = 26$), thinned ($n = 28$), and unmanaged ($n = 27$) stands and forest edge sites ($n = 46$) occurring at borders of prethinned ($n = 12$), thinned ($n = 20$), and unmanaged ($n = 14$) stands. We captured 14,614 individual insects from 18 orders (Diptera [$n = 12,456$], Homoptera [$n = 797$], Lepidoptera [$n = 564$], Hymenoptera [$n = 254$], Coleoptera [$n = 179$], Collembola [$n = 169$], Hemiptera [$n = 55$],

Orthoptera [$n = 40$], Thysanoptera [$n = 36$], Trichoptera [$n = 24$], Neuroptera [$n = 16$], Psocoptera [$n = 14$], Blattaria [$n = 4$], Megaloptera [$n = 2$], Dermaptera [$n = 1$], Diplura [$n = 1$], Mantodea [$n = 1$], and Isoptera [$n = 1$]). We caught 142 bats of 5 species (red bat [*Lasiurus borealis*; $n = 79$], big brown bat [*Eptesicus fuscus*; $n = 20$], evening bat [*Nycticeius humeralis*; $n = 40$], eastern pipistrelle [*Perimyotis subflavus*; $n = 2$], and Rafinesque's big-eared bat [*Corynorhinus rafinesquii*; $n = 1$]). We analyzed approximately 950 hours of heterodyne recordings that contained 19,986 bat echolocation sequences, including 1,909 feeding buzzes. We analyzed >100,000 time-expanded sound files that contained 6,236 identifiable search-phase calls. We manually identified these sequences to 7 species or species groups (red bat [$n = 3,489$], big brown bat [$n = 1,525$], evening bat [$n = 175$], Brazilian free-tailed bat [*Tadarida brasiliensis*; $n = 526$], hoary bat [*Lasiurus cinereus*; $n = 270$], eastern pipistrelle [$n = 159$], and *Myotis* spp. [$n = 92$]; Table 1).

Table 1. Mean (± SE) number of time-expanded bat echolocation sequences recorded per night for each site type. Data are from acoustic monitoring within an intensively managed pine forest (Weyerhaeuser Parker Tract, NC, USA), during the summers of 2006 and 2007. *Myotis* spp. contains *Myotis septentrionalis* and (or) *Myotis austroriparius*.

	Edges		Open		Prethinned		Thinned		Unmanaged	
Species	$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\bar{x}$	**SE**
Lasiurus borealis	31.48	6.58	8.19	3.06	26.05	15.03	16.04	7.38	35.52	13.35
Eptesicus fuscus	23.98	5.21	2.50	0.81	1	0.74	15.54	11.89	0.41	0.18
Tadarida brasiliensis	8.27	5.70	3.46	2.35	0.95	0.76	1.67	0.69	0.44	0.14
Lasiurus cinereus	4.80	2.96	1.88	1.13	0.19	0.11	0.25	0.15	0	0
Perimyotis subflavus	2.91	1.93	0.31	0.14	0	0	0.17	0.10	0.70	0.53
Nycticeius humeralis	1.66	0.51	0.27	0.16	0.38	0.33	1.63	1.10	1.78	1.16
Myotis spp.	0.10	0.06	0.08	0.05	1.14	0.53	0.46	0.34	1.89	0.43

Table 2. Mean (± SE) number of insects captured per night are shown for each site type. Probability values are from analysis of variance tests that insect abundance did not differ across site types. Uppercase letters denote significant differences indicated by Tukey's post hoc multiple comparison tests. Data are from Malaise trapping within an intensively managed pine forest (Weyerhaeuser Parker Tract, NC, USA), during the summers of 2006 and 2007. Only the most commonly captured insect orders are shown.

	Edges		Open		Prethinned		Thinned		Unmanaged			
Order	$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\bar{x}$	**SE**	$\bar{x}$	**SE**	**F**	**P**
Diptera	118.07 A	23.30	52.22 B	7.38	82.00 AB	9.19	74.89 AB	11.16	65.46 AB	9.14	2.43	0.050*
Lepidoptera	4.70	0.63	2.26	0.49	4.33	0.82	3.11	0.56	4.00	0.78	2.29	0.063
Homoptera	9.52 A	1.52	4.93 B	1.24	2.04 B	0.35	3.59 B	0.83	3.00 B	0.72	6.85	<0.001*
Hymenoptera	2.13	0.40	2.11	1.21	1.46	0.31	1.48	0.36	0.83	0.26	0.78	0.539
Orthoptera	0.17	0.06	0.15	0.09	0.38	0.12	0.30	0.12	0.46	0.15	1.62	0.172
Thysanoptera	0.26	0.08	0.37	0.17	0.13	0.09	0.19	0.09	0.33	0.17	0.63	0.641
Coleoptera	1.38	0.27	0.93	0.24	1.08	0.25	1.07	0.23	1.46	0.53	0.49	0.743
Hemiptera	0.46	0.14	0.56	0.23	0.25	0.09	0.44	0.16	0.21	0.10	0.74	0.563
All orders	143.59 A	25.07	71.11 B	9.49	93.96 AB	10.04	89.48 AB	12.84	78.46 AB	10.76	2.78	0.029*

* $P < 0.05$.

Total insect abundance differed across site types ($F_{4,143} = 2.78$, $P = 0.029$), and was higher at forest edge sites than in open stands. This difference was driven heavily by Diptera ($F_{4,143} = 2.43$, $P = 0.050$), which accounted for 85% of insects captured. Abundances of Homoptera also differed across site types ($F_{4,143} = 6.85$, $P < 0.0001$), and were highest at edge sites. Although not significant ($F_{4,143} = 2.29$, $P = 0.063$), there was a trend toward higher abundances of Lepidoptera at edge sites than in open stands. Abundances of Hymenoptera, Orthoptera,

Thysanoptera, Coleoptera, and Hemiptera did not differ across stand types or edge sites (Table 2).

Negative binomial regression models for overall bat activity and activity by the 7 species groups consistently gave lower AIC and BIC scores than Poisson or zero-inflated models. Negative binomial models fit the distribution of counts better than Poisson models, due partially to the high frequency of zero-counts (Fig. 1). Significance tests for alpha (the over-dispersion parameter) also supported the use of negative binomial models over Poisson models (Table 3). Therefore, we fit candidate models using negative binomial regression (Tables 4, 5).
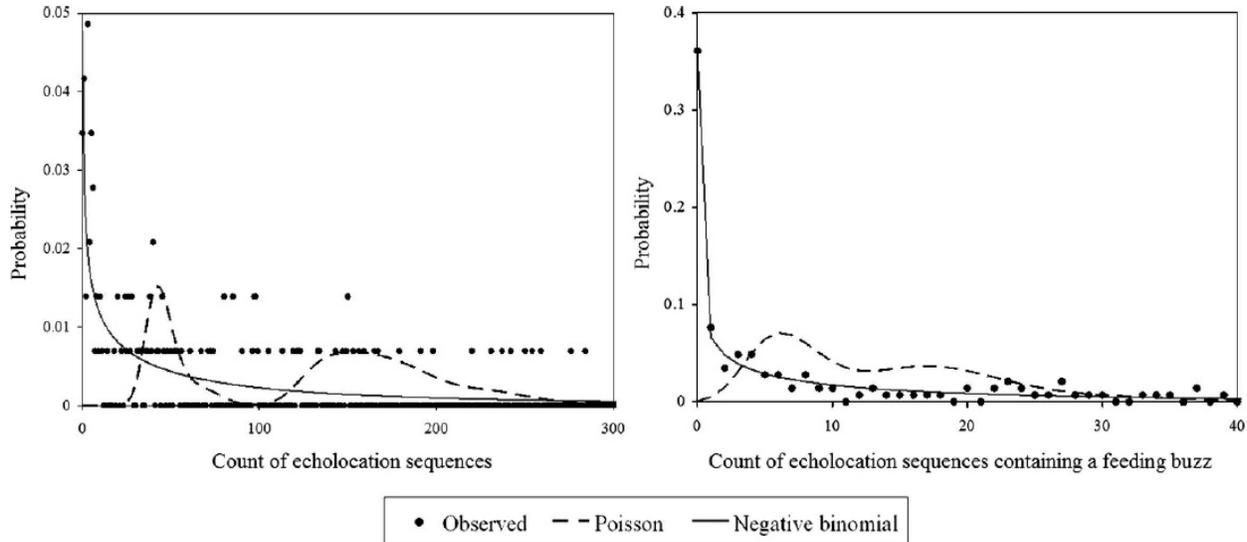
Figure 1. Comparison of model fit for overall bat activity models. We compared Poisson and negative binomial regression models using probability-count plots. Negative binomial models fit well due to large proportion of zero-counts and the highly skewed distribution. Patterns of probability-count plots comparing Poisson and negative binomial regression models for individual species and species groups were similar to patterns for overall bat activity models (data not shown). We collected acoustic data within an intensively managed pine forest (Weyerhaeuser Parker Tract, NC, USA), during the summers of 2006 and 2007.

Table 3. Model selection criteria for overall bat activity models. Count regression models for total bat activity and feeding activity were compared based on Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC). Patterns of AIC and BIC for individual species and species groups were similar to overall bat activity models (data not shown; see Morris 2008 for details). Data are from acoustic monitoring within an intensively managed pine forest (Weyerhaeuser Parker Tract, NC, USA), during the summers of 2006 and 2007.

Dependent variable	Model distribution[a]	AIC	BIC
No. of echolocation sequences	Poisson	21,861	21,876
	Negative binomial	1,571	1,589
	ZIP	21,412	21,430
	ZINB	1,573	1,594
No. of feeding sequences	Poisson	3,779	3,791
	Negative binomial	884	899
	ZIP	2,658	2,673
	ZINB	886	903

[a] ZINB 5 zero-inflated negative binomial, ZIP 5 zero-inflated Poisson.

Overall bat activity was high along edges and within thinned and unmanaged stands, and was positively correlated with counts of lepidopterans (Table 4). Counts of echolocation sequences

containing feeding buzzes were high along edges and within thinned stands, and were positively related to counts of lepidopterans (Table 4). Models for bat activity and foraging activity yielded similar results because the proportion of echolocation sequences containing a feeding buzz was similar across all stand types and along edges ($\bar{x}$ = 0.10; 95% CI = 0.08–0.13; Fig. 2).
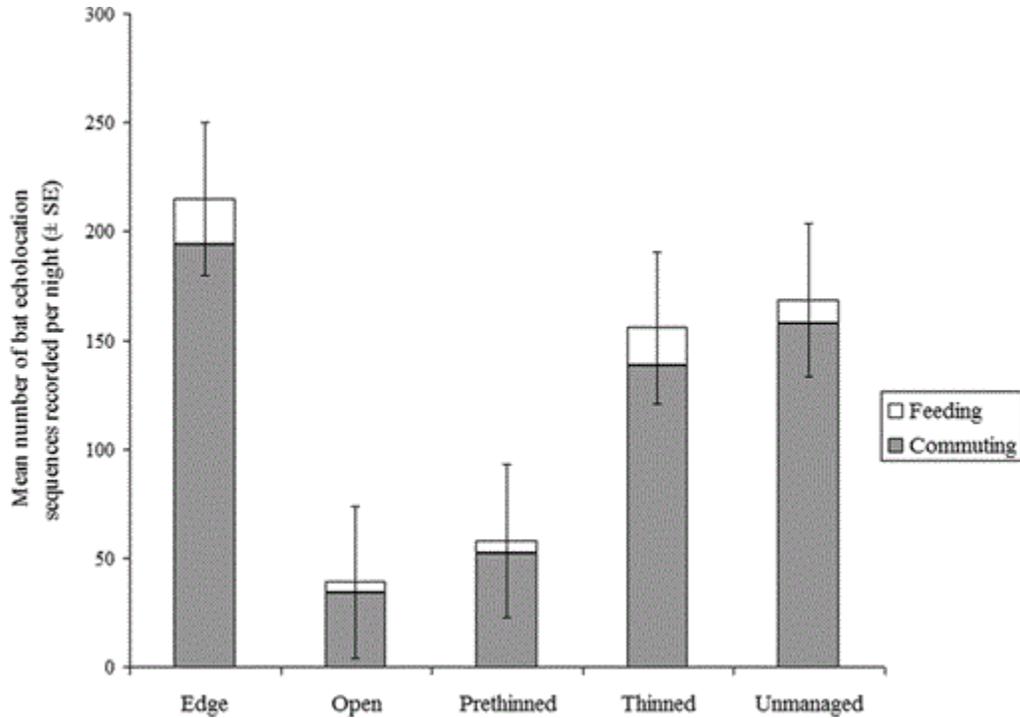
Figure 2. Overall bat activity and feeding activity in stands and along forest edges. Mean number of echolocation sequences recorded per night (±SE) are shown for 4 stand types and along forest edges. We classified echolocation sequences as feeding if they contained a feeding buzz, and commuting if they did not. We collected acoustic data within an intensively managed pine forest (Weyerhaeuser Parker Tract, NC, USA), during the summers of 2006 and 2007.

Table 4. Parameter estimates for overall bat activity and feeding activity regression models. Models describe total bat activity (count of echolocation sequences), and bat foraging activity (count of feeding echolocation sequences) in relation to stand types, forest edges, and insect community. We represented stand types and forest edges with indicator variables. Significance of the over-dispersion parameter alpha implies that the negative binomial model fits better than the Poisson model. We collected data using acoustic monitoring with bat detectors and insect trapping in 4 stand types and along forest edges in an intensively managed pine forest (Weyerhaeuser Parker Tract, Washington County, NC, USA), during the summers of 2006 and 2007.

Variable	Parameter	Estimate	SE	t	P
No. of echolocation sequences	Intercept	3.478	0.227	15.29	<0.001
	Edge	1.481	0.268	5.52	<0.001
	Thinned	1.241	0.318	3.91	<0.001
	Unmanaged	1.245	0.337	3.70	<0.001
	Lepidoptera	0.089	0.035	2.58	0.010
	Alpha	1.652	0.176	9.37	<0.001
No. of feeding sequences	Intercept	1.459	0.305	4.79	<0.001
	Edge	1.132	0.350	3.24	0.001
	Thinned	1.016	0.425	2.39	0.017
	Lepidoptera	0.112	0.053	2.09	0.037
	Alpha	3.208	0.430	7.46	<0.001

Table 5. Parameter estimates for negative binomial models of bat species activity. Models describe bat species activity (count of time-expanded echolocation sequences) in relation to stand types, forest edges, and insect community. We represented stand types and forest edges with indicator variables. Significance of the over-dispersion parameter alpha implies that the negative binomial model fits better than the Poisson model. We collected data using acoustic monitoring with bat detectors and insect trapping in 4 stand types and along forest edges in an intensively managed pine forest (Weyerhaeuser Parker Tract, NC, USA), during the summers of 2006 and 2007. *Myotis* spp. contains *Myotis septentrionalis* and (or) *Myotis austroriparius*.

Species	Parameter	Estimate	SE	t	P
Lasiurus borealis	Intercept	2.118	0.315	6.73	<0.001
	Edge	0.765	0.377	2.03	0.043
	Unmanaged	0.917	0.461	1.99	0.046
	Lepidoptera	0.139	0.052	2.67	0.008
	Alpha	3.732	0.473	7.88	<0.001
Eptesicus fuscus	Intercept	−7.941	2.788	−2.85	0.004
	Temperature	0.103	0.038	2.71	0.007
	Edge	3.444	0.428	8.05	<0.001
	Open	1.043	0.510	2.04	0.041
	Thinned	2.865	0.508	5.64	<0.001
	Alpha	3.357	0.513	6.54	<0.001
Tadarida brasiliensis	Intercept	0.748	0.358	2.09	0.037
	Edge	1.365	0.572	2.39	0.017
	Unmanaged	−1.559	0.729	−2.14	0.033
	Alpha	8.642	1.627	5.31	<0.001
Lasiurus cinereus	Intercept	−3.432	0.587	−5.84	<0.001
	Open	3.424	0.683	5.01	<0.001
	Edge	2.825	0.579	4.88	<0.001
	Lepidoptera	0.273	0.063	4.35	<0.001
	Alpha	4.438	1.090	4.07	<0.001
Perimyotis subflavus	Intercept	−2.030	0.372	−5.45	<0.001
	Edge	1.887	0.547	3.45	<0.001
	Diptera	0.004	0.002	2.42	0.016
	Alpha	5.795	1.802	3.22	0.001
Nycticeius humeralis	Intercept	−1.142	0.509	−2.24	0.025
	Edge	1.648	0.691	2.38	0.017
	Thinned	1.628	0.813	2.00	0.045
	Unmanaged	1.717	0.784	2.19	0.028
	Alpha	9.034	2.099	4.30	<0.001
Myotis spp.	Intercept	0.446	0.281	1.59	0.112
	Thinned	−1.226	0.548	−2.24	0.025
	Open	−3.011	0.836	−3.60	<0.001
	Edge	−2.821	0.634	−4.45	<0.001
	Alpha	3.138	0.967	3.25	0.001

Stand type (Fig. 3) and distribution of insect prey had species-specific effects on bat foraging behavior (Table 5). Six bat species exhibited substantially higher activity along forest edges than in forest interiors (Fig. 4; Table 5). Activity of red bats was positively related with forest edges, unmanaged stands, and counts of lepidopterans (Table 5). Activity of big brown bats was high along edges, in thinned and open stands, and was positively correlated with mean temperature (Table 5). Activity of Brazilian free-tailed bats was high along edges but low in unmanaged stands (Table 5). Activity of hoary bats was high along edges and in open stands and positively correlated with counts of lepidopterans (Table 5). Activity of eastern pipistrelles was high along edges and was positively related to abundance of dipterans (Table 5). Activity of evening bats

was high along edges and in thinned and unmanaged stands (Table 5). In contrast, activities of *Myotis* spp. were negatively related to edges, open stands, and thinned stands (Table 5).
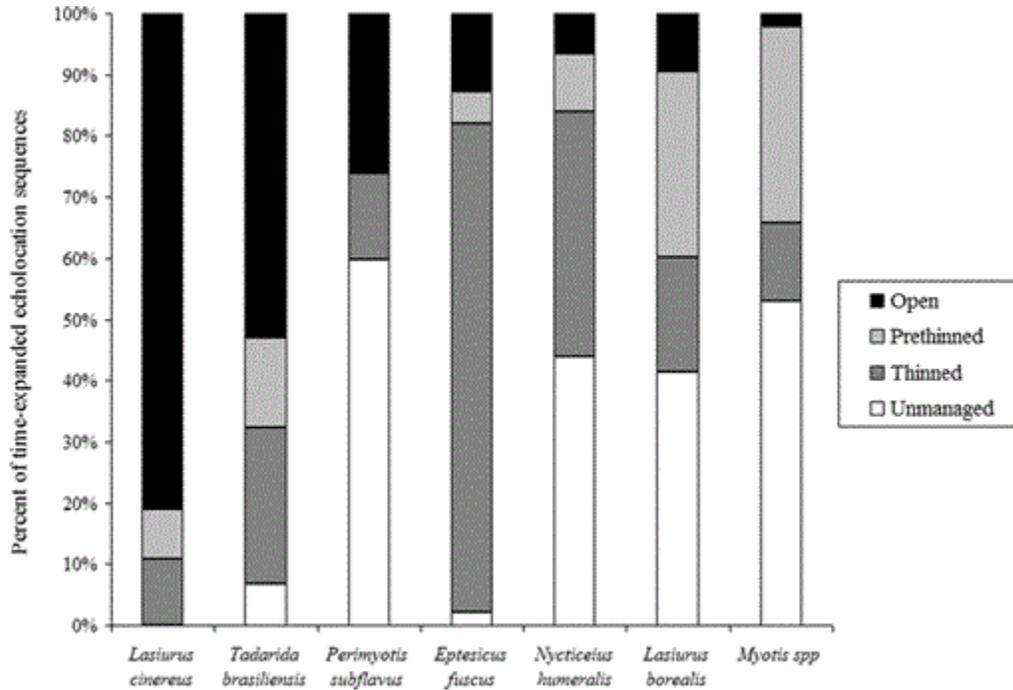
Figure 3. Relative bat activity in forest stand interiors. Percentages of time-expanded bat echolocation sequences recorded within 4 stand types are shown. We collected acoustic data within an intensively managed pine forest (Weyerhaeuser Parker Tract, NC, USA), during the summers of 2006 and 2007.
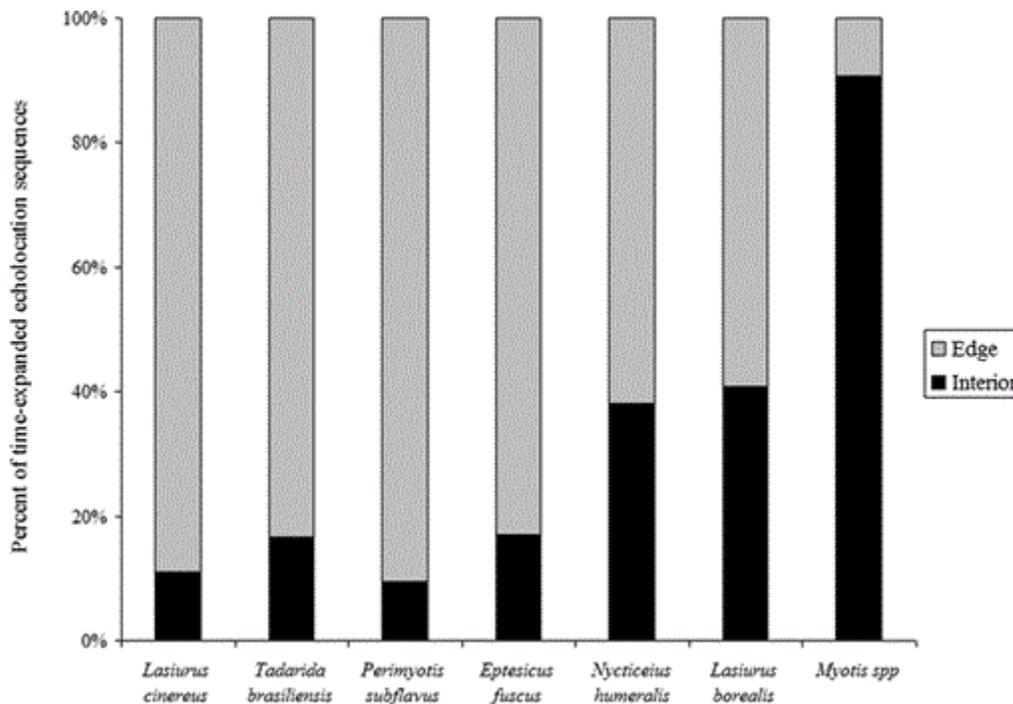
Figure 4. Relative bat activity along forest edges. Percentages of time-expanded bat echolocation sequences recorded along hard forest edges and within stand interiors are shown. We collected acoustic data within an intensively managed pine forest (Weyerhaeuser Parker Tract, NC, USA), during the summers of 2006 and 2007.

DISCUSSION

Using bat detectors and mist netting, we identified more species than we would have with either method alone, due to biases associated with each method (Kuenzi and Morrison 1998). We detected echolocation calls from hoary bats, Brazilian free-tailed bats, and *Myotis* bats, but did not capture these species. Hoary and Brazilian free-tailed bats fly high (Caire et al. 1984, Kalcounis et al. 1999) and are therefore difficult to capture in mist nets. In contrast, we captured one Rafinesque's big-eared bat, but did not record the species ultrasonically, likely because Rafinesque's big-eared bats use low-intensity echolocation calls that are difficult to detect (Murray et al. 1999).

Overall heterodyne-recorded bat activity and foraging activity specifically were high along hard forest edges and within thinned and unmanaged stands. Overall activity was also correlated with counts of lepidopterans. These patterns were likely driven by the most common species we recorded, red and big brown bats (which represent 59% of recorded call sequences). Our species models indicate that patterns observed from heterodyne recordings were not universal across species, that is, species-specific trends were obscured by treating the bat community as a single entity, which is consistent with the conclusion of Patriquin and Barclay (2003).

Stand structure had species-specific effects on bat foraging behavior. Our results are consistent with previous data that categorize bats based on their ability to navigate and hunt within various levels of structural complexity. Hoary bats and Brazilian free-tailed bats are considered open-area foragers (Simmons et al. 1979), and were most active in open stands. We also detected big brown bats in open stands, but they are more flexible in foraging behavior (Kalcounis-Rueppell et al. 2007), and also foraged in moderately complex (thinned) stands. Red and evening bats were more tolerant of structural complexity, and foraged in both unmanaged and thinned stands. Thinned stands, particularly recently thinned stands, had a relatively open midstory structure, which may have been conducive for foraging by these species and possibly roosting by red bats (Elmore et al. 2004). Additionally, unmanaged stands may have provided roosting opportunities for bats because of older, larger trees (Elmore et al. 2004, Kalcounis-Rueppell et al. 2005, Miles et al. 2006, Wigley et al. 2007). Bats in the genus *Myotis* consistently foraged within stand interiors and avoided edges. Furthermore, *Myotis* spp. activity was negatively related to open and thinned stands. Northern long-eared bats (*Myotis septentrionalis*) likely comprised a portion of our *Myotis* detections (Morris et al. 2009) and are known to glean prey from substrates (Faure et al. 1993, Ratcliffe and Dawson 2003). This foraging strategy is unlikely to be useful in open areas, and northern long-eared bats have been reported to avoid gaps and open areas (Owen et al. 2003, Patriquin and Barclay 2003). Other bats in the genus *Myotis* may be well suited to forage within structurally complex habitats because they are small and maneuverable in flight (Fenton 1990).

The abundance of insect prey also played a role in determining bat foraging behavior. Insect order variables retained in models were useful in presence of other explanatory variables; that is, they explained significant amounts of variation after we accounted for stand structure. After accounting for site effects, counts of echolocation sequences and echolocation sequences containing feeding buzzes were positively correlated with counts of Lepidoptera. This pattern

was strongest in red and hoary bats, which are known to specialize on Lepidoptera (Whitaker et al. 1997, Carter et al. 2003). In addition, eastern pipistrelles, which eat Diptera (Whitaker et al. 1997, Carter et al. 2003), and may be limited to small prey due to their own small size (Barclay and Brigham 1994), were most active at sites where Diptera were abundant. Models for other species did not contain insect count variables because the effect of insect abundance was not strong after accounting for habitat structure. For example, even though *Myotis* spp. eat Diptera, and Diptera were most common at edge sites, *Myotis* spp. consistently hunted within structurally complex stands. Stand-level structural characteristics were better predictors of bat activity than the abundance of insects. Our models suggest stand-level characteristics are of primary importance and insect availability probably plays a secondary role in shaping bat foraging behavior. In addition, although not specifically addressed by our study, proximity to roosts (Crampton and Barclay 1998) and water sources (Walsh and Harris 1996, Vaughan et al. 1997, Kusch et al. 2004) likely affect bat foraging behavior.

In addition to exhibiting stand-type preferences for foraging, bat species showed strong associations with hard forest edges. Six species (red bats, big brown bats, evening bats, Brazilian free-tailed bats, hoary bats, and eastern pipistrelles) had substantially higher activity along hard edges than in forest interiors. This is consistent with other evidence for high species richness and abundance along edges (edge effects). These 6 bat species are aerial-hawking hunters with varying levels of tolerance for structural complexity (Lacki et al. 2007). Hard forest edges may provide valuable foraging opportunities because they are relatively open. Species that foraged in open areas (Brazilian free-tailed bats, hoary bats, and big brown bats) also had higher activity at edge sites than in open stand interiors. This may be because insect prey, especially dipterans, homopterans, and lepidopterans, were more abundant at edge sites than interiors of open stands. Grindal (1996) and Grindal and Brigham (1999) also found that insect abundance and bat activity were greater along forest edges than in the centers of clear-cuts. Forest edges may function as windbreaks that collect large densities of insects (Pasek 1988, Swystun et al. 2001).

For bats that forage efficiently in open areas, hard forest edges may create a semipermeable barrier to movement by bats into the forest, causing an accumulation of bat activity in the open area directly adjacent to the forest edge. Furthermore, forest edges may redirect the flow of foraging bats parallel to edges. Bats have been observed foraging parallel to forest edges within managed pine landscapes (A. D. Morris, University of North Carolina at Greensboro, unpublished data). In addition to providing foraging habitat, linear forest edges may function as landmarks by which bats orient themselves (Verboom and Huitema 1997, Verboom and Spoelstra 1999). Bats use linear landscape features such as roads and riparian corridors as flight paths (Law and Chidel 2002, Hein et al. 2008*b*), and it is possible that linear forest edges may improve connectivity between foraging areas. This function of forest edges occurs at a broader spatial scale and would require use of alternative methods (e.g., radiotelemetry) to test effectively.

MANAGEMENT IMPLICATIONS

Bats in intensively managed pine forest responded to landscape structure in species-specific ways. Thus, management should attempt to accommodate different foraging strategies. Stand types appeared to be partitioned based on conditions of structural complexity of vegetation.

Maintenance of a variety of cluttered and uncluttered stands, ranging from open areas to closed canopy pine stands, provides foraging areas for bats with various tolerances for structural complexity. The hard forest edges surrounding open stands were exploited by 6 common aerial-hunting bat species. Our results emphasize the importance of hard linear edges to bats within fragmented landscapes as relatively open foraging areas rich in insect prey. Although we did not sample soft forest edges occurring between forested stands of different heights, bats may forage along these edges as well. Maintenance of forest edges within the landscape likely benefits several aerial-hunting bat species. However, interior forest patches are important to other species (northern long-eared bat and southeastern myotis). Unmanaged patches within the landscape should be retained for interior-foraging species and maintenance of suitable roost sites (Kalcounis-Rueppell et al. 2005). The mosaic landscape composed of forested and open stands (and resulting hard forest edges) may be identical to a natural forested landscape, with respect to bat foraging behavior. Forest edges function similarly to natural forest gaps, by providing foraging opportunities for aerial-hunting bats. However, because we did not sample natural pine forest, we do not know how foraging behavior would compare between the managed pine and the historical landscape. Our data suggest that the intensively managed pine landscape may provide suitable foraging habitat for most bat species in the coastal plain of North Carolina.

Acknowledgments

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