Management and Conservation Article

Evening Bat Summer Roost-Site Selection on a Managed Pine Landscape

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ABSTRACT Creation and maintenance of forested corridors to increase landscape heterogeneity has been practiced for decades but is a new concept in intensively managed southern pine (*Pinus* spp.) forests. Additionally, more information is needed on bat ecology within such forest systems. Therefore, we examined summer roost-site selection by evening bats (*Nycticeius humeralis*) in an intensively managed landscape with forested corridors in southeastern South Carolina, USA, 2003–2006. We radiotracked 53 (26 M, 27 F) adult evening bats to 75 (31 M, 44 F) diurnal roosts. We modeled landscape-level roost-site selection with logistic regression and evaluated models using Akaike's Information Criterion for small samples. Model selection results indicated that mature ($\geq$40 yr) mixed pine–hardwood stands were important roost sites for male and lactating female evening bats. Upland forested corridors, comprised of mature pine or mixed pine–hardwoods, were important roosting habitats for males and, to a lesser extent, lactating females. Male roosts were farther from open stands and lactating female roosts were farther from mid-rotation stands than randomly selected structures. Our results suggest roost structures (i.e., large trees and snags) in mature forests are important habitat components for evening bats. We recommend maintaining older (>40 yr old) stand conditions in the form of forest stands or corridors across managed landscapes to provide roosting habitat. Furthermore, our results suggest that an understanding of sex-specific roost-site selection is critical for developing comprehensive guidelines for creating and maintaining habitat features beneficial to forest bats. (JOURNAL OF WILDLIFE MANAGEMENT 73(4):511–517; 2009)

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Within the southeastern United States, proportion of timberlands in planted pine (*Pinus* spp.) has increased from approximately 2 million acres in 1953 to >12.1 million ha in 1999 (Wear and Greis 2002). In 2007, planted pine accounted for approximately 20% of southern forests (U.S. Department of Agriculture Forest Service 2008). Forest product companies in the region often manage planted stands using even-aged systems with short rotations to meet demand for forest products (Wigley et al. 2007). However, when rotations are short, availability of large snags and older trees, often used by forest-roosting bats, can be limited within planted stands (Allen et al. 1996). To balance sustainable economic value and ecological objectives, companies under sustainable forestry programs are expected to provide landscape-level habitat diversity (Wigley et al. 2007). One approach to maintaining a variety of forest structure and composition across managed landscapes is retention of corridors comprised of late-successional forest stands.

Use of forested corridors in conservation strategies has been in practice for decades (Wilson and Willis 1975). Corridors are often maintained to preserve native flora and fauna, reduce erosion, enhance aesthetics, and facilitate wildlife movement (Hobbs 1992). Bats likely use linear landscape features such as corridors as navigational references, foraging areas, and protection from wind and predators (Limpens and Kapteyn 1991, Verboom and Huitema 1997, Estrada and Coates-Estrada 2001). Corridors comprised of mature forest also may provide structures (i.e., tall, large-diam trees, snags) used as day-roosts by forest-dwelling bats. Previously, Hein et al. (2008) found foliage-roosting Seminole bats (*Lasiurus seminolus*) selected forested corridors for summer roost sites in southeastern South Carolina. However, influence of forested corridors on roost-site selection by cavity-roosting bats remains unknown.

Evening bats (*Nycticeius humeralis*) are a common cavity-roosting species found throughout the southeastern United States (Watkins 1972). Previous summer studies have provided insight regarding small-scale (i.e., tree- and plot-level) characteristics of evening bat tree roosts (Menzel et al. 1999, 2000, 2001; Boyles and Robbins 2006; Miles et al. 2006). Large scale (i.e., landscape-level) features affecting evening bat roost-site selection are poorly understood (but see Miles et al. 2006). Furthermore, information regarding differences in roost-site selection between gender and reproductive condition is limited. Therefore, our goal was to examine influence of landscape-level features, including forested corridors, on evening bat roost-site selection, by sex and reproductive condition, within an intensively managed pine landscape.

STUDY AREA

We conducted our research on 41,365 ha owned and managed by MeadWestvaco Corporation in southeastern South Carolina, USA. The study area was located in the Lower Coastal Plain physiographic province and was characterized by flat topography (slopes <2%) and elevations ranging from 20 m to 30 m above mean sea-

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level. Summers were warm and humid with monthly temperatures and precipitation averaging 27° C and 18.6 cm, respectively (National Oceanic and Atmospheric Administration 2002).

The area was intensively managed for loblolly pine (*Pinus taeda*) sawtimber and consisted of even-aged stands in various successional stages (see detailed description below). Plantation stands typically were clearcut at approximately 20–25 years of age. Silvicultural practices included site preparation and planting of clearcut stands, 1 or 2 commercial thinnings, and vegetation management via fire, mechanical, and chemical treatments. At the time of our study, MeadWestvaco employed a unique forest management system, known as Ecosystem-Based Forestry, designed to increase heterogeneity of wildlife habitat (Constantine et al. 2005). This approach maintained a system of approximately 100–200-m-wide corridors comprised of mature forests within a mosaic of younger plantation stands. Three types of corridors were present: visual corridors along public roads, upland corridors retained to maintained connectivity among habitats, and water-quality corridors buffering streams and poorly drained sites (i.e., streamside management zones [SMZs]). Generally, visual and upland corridors were mature pine or mixed pine–hardwood and water-quality corridors were hardwood stands. Corridors constituted 11% of the total study area and were interspersed throughout a mosaic of plantation stands from 0 years to 22 years old.

METHODS

Capture and Radiotelemetry

We captured evening bats from late May through mid-August 2003–2006 using mist nets set over 9 randomly selected ponds. Ponds were located in open areas, adjacent to roads, and distributed throughout the study area. We recorded mass (g), forearm length (mm), sex, reproductive condition (Racey 1988), and relative age (Anthony 1988) of captured bats. We attached 0.43-g (Biotrack, Wareham, Dorset, United Kingdom) or 0.33-g (Blackburn Transmitters, Nacogdoches, TX) radiotransmitters to the back of adult evening bats using Skin Bond (Pfizer, Largo, FL) or Torbot (Torbot Group, Cranston, RI) adhesive. Radiotransmitter load (M: $\bar{x} = 3.6\%$, range = 2.5–4.9%; F: $\bar{x} = 2.9\%$, range = 1.9–3.8%) was <5% body mass (Aldridge and Brigham 1988). We held bats for 20 minutes to allow adhesive to set and released them at point of capture. We conducted animal capture and handling under University of Georgia Institutional Animal Care and Use Committee guidelines (IACUC no. 2003-10029-ml).

We located day-roosts using radiotelemetry receivers (TRX 2000S; Wildlife Materials, Inc., Murphysboro, IL) and 3-element Yagi antennas. We tracked bats daily, when possible, beginning the day after capture until radiotransmitters failed or were recovered. Roosts located the day after capture were typical of roosts located on subsequent days. We focused tracking efforts on new bats or those with fewer identified roosts. We conducted evening emergence counts, when possible, to verify roost location and determine colony size within roosts. Counts began 30 minutes prior to sunset and continued until bats were no longer visible. We recorded roost locations using a Global Positioning System unit. We differentially corrected coordinates using Pathfinder software (Trimble Navigation, Sunnyvale, CA) and imported them into a Geographic Information System (GIS) for analysis. For each roost, we recorded tree species and type of roost structure (live tree or snag). We determine age of stand in which roost was located from stand inventory GIS layers.

Habitat Variables

We quantified factors potentially influencing evening bat roost-site selection at the landscape scale. We defined 6 stand types available across the study area: open, closed, mid-rotation, mature pine, mixed pine–hardwood, and hardwood (C. Muckenfuss, MeadWestvaco Corporation, personal communication). Open stands included clearcut and regenerating stands ≤5 years old, fields, and wildlife openings (i.e., food plots). Closed stands were dense, prethinned pine stands (6–11 yr) with complete canopy closure. Mid-rotation pine and pine–hardwood stands were 12–22 years old with almost complete canopy closure. Silvicultural prescriptions (i.e., burning, thinning) often occurred in these stands, creating a more open canopy. Mature pine stands consisted of upland pine (>75% pine basal area) stands ≥23 years old. Mixed pine–hardwood stands were mature stands (≥23 yr) containing >25% and <75% pine basal area located on poorly developed soils. Hardwood stands (<25% pine basal area) typically were ≥50 years old and associated with riparian zones (SMZs) or areas of poorly drained soils. Approximately 25% of the study area consisted of open habitat, 15% closed, 33% mid-rotation, 6% mature pine, 10% pine–hardwood, 8% hardwood, with the remaining 3% in water and anthropogenic structures.

We determined area of potentially available habitat based on ecology of evening bats. We used ArcView 3.2 to create a circular landscape (M: radius = 2.5 km, area = 1,963 ha; F: radius = 3.5 km, area = 3,848 ha) around 9 capture ponds (Taylor 1999). These radii represented maximum distances flown from capture pond to roosts by male and female bats, respectively. Because water sources were limited or ephemeral, bats likely remained close to these ponds (Waldien et al. 2000, Miles et al. 2006). All stand types were available in each landscape in relative proportion to total study area.

We selected random sites from a grid of 250 points within each circular landscape. We selected a number of random sites in each landscape equal to number of roost structures located per capture pond. We updated GIS layers each year with stand and landscape data to control for changes in availability of habitat types among years. We measured distance (m) from each roost and random site to nearest edge or road (de) and to nearest corridor (dcorr). We also measured distances (m) to edge of nearest open (do), closed (dc), mid-rotation (dmr), mature pine (dmp), mixed pine–hardwood (dph), and hardwood (dh) stand. We assigned a value of zero to the stand type in which we found the roost or random site (Conner et al. 2003). Because we used maximum distance traveled from capture pond to roost to define our available landscape, we did not include distance to water in our analysis.

Analysis and Model Development

We conducted correlation analysis to ensure no pairs of variables were highly correlated (Spearman's $r > 0.7$). Prior to model analysis, we separated data by sex and further divided females into reproductive conditions, pregnant (PF), lactating (LF), and nonreproductive (NF). We developed global logistic regression models containing all 8 variables for male and LF bats. We did not create models for PF or NF bats due insufficient sample sizes. We tested global models for goodness-of-fit using the Hosmer–Lemeshow statistic. We also selected 47 of a possible 255 candidate models based on our hypotheses relating roost-site selection to landscape variables. We used the same set of candidate models for male and LF bats. All variables appeared in an equal number of models creating a balanced model set.

Prior to model analysis, we examined spatial and temporal autocorrelation of male and LF data. We fit our global logistic regression models with structure type (roost vs. random) as the binary response and conducted an analysis of variance of residuals using bat or year as the independent variable (Rieman et al. 2006). Our results indicated no significant spatial or temporal autocorrelation for male or LF bats. Because our data were independent, we conducted our analysis, with roost as the experimental unit, using traditional logistic regression techniques (Sokal and Rohlf 1995).

We used log-likelihood for each model to calculate Akaike's Information Criterion for small sample sizes. We calculated Akaike model weights to evaluate and select the most parsimonious model and to predict variable importance (Burnham and Anderson 2002). We created a confidence set of models by including those models with Akaike weights within 10% of the highest value, which is comparable with minimum cutoff point suggested by Royall (1997). We calculated Nagelkerke's R^2 for all models, to assess variation explained by each model contained within the confidence set (Nagelkerke 1991).

We used model-averaging to incorporate model selection uncertainty directly into parameter estimates and standard errors using Akaike weights (Burnham and Anderson 2002). We calculated odds ratios (OR) from averaged parameter estimates. However, because larger or smaller unit changes may be more ecologically interpretable, we calculated scaled OR when appropriate (Hosmer and Lemeshow 2000). We evaluated ecological importance of each variable in the composite model by computing 90% confidence intervals for scaled OR and interpreting magnitude of values within these intervals (Gerard et al. 1998).

We used leave-one-out cross-validation as a means of determining predictive power of our selected model (Neter et al. 1996). We used an estimated probability of presence ≥ 0.5 as the criterion for presence. We conducted all analyses using SAS version 8.0 (SAS Institute, Cary, NC).

RESULTS

We radiotracked 26 adult male and 27 adult female (7 PF, 15 LF, 5 NF) evening bats to 31 and 44 (11 PF, 24 LF, 9 NF) individual roost trees, respectively. Evening bats roosted in 9 tree species including American elm (*Ulmus americana*), bald cypress (*Taxodium distichum*), Carolina ash (*Fraxinus caroliniana*), hickories (*Carya* spp.), loblolly pine, red maple (*Acer rubrum*), swamp tupelo (*Nyssa biflora*), sweetgum (*Liquidambar styraciflua*), and water oak (*Quercus nigra*). Loblolly pine (8 M, 7 PF, 6 LF, 2 NF) and red maple (7 M, 1 PF, 8 LF, 2 NF) were used most commonly. Roost types included tree cavities (24 M, 4 PF, 14 LF, 7 NF), fork-topped loblolly pines (4 M, 7 PF, 8 LF), live trees (2 M, 2 LF, 1 NF), and exfoliating bark (1 M). Mean stand age of roost locations was 46.9 ± 3.7 ($\bar{x} \pm$ SE) years, 48.1 ± 3.7 years, 37.4 ± 6.9 years, and 50.9 ± 5.4 years for male, LF, PF, and NF evening bats, respectively. Evening bats roosted in 4 stand types: mid-rotation (6 M, 6 PF, 2 LF, 1 NF), mature pine (4 M, 1 PF, 6 LF, 2 NF), mixed pine–hardwood (13 M, 4 PF, 14 LF, 5 NF), and hardwood (8 M, 0 PF, 2 LF, 1 NF). Male evening bats (roosts = 12) used corridor stands more often than did females (roosts = 8; 2 PF, 4 LF, 2 NF).

Eighty-nine percent of males ($\bar{x} = 0.81$ km, range = 0.1–2.5 km) and 84% of females ($\bar{x} = 1.2$ km, range = 0.2–3.5 km) roosted ≤ 1.5 km from point of capture. Male bats always roosted individually, whereas females roosted alone or in colonies. Although 5 trees were used by 2 radiotagged females, we only used the trees once for analysis. We located 33 maternity colonies, 15 in fork-topped trees and 18 in tree cavities. Colony size varied by structure type, with smaller colonies located in fork-topped trees (4–27 bats) and larger colonies in tree cavities (≥ 22 bats). Four cavity trees contained >50 bats, 2 of which had >100 bats. Male bats often remained in the same roost for the life of the radiotransmitter whereas female bats often switched roosts daily. However, radiotransmitters typically were attached to bats ≤ 3 days. Thus, we were unable to calculate roosting home ranges for male and female evening bats because few bats were tracked to ≥ 3 roosts.

Spearman tests showed no correlation among habitat variables for male and LF bats. Our results indicated no significant spatial (M: $F_{25,36} = 0.35$, $P = 0.997$; LF: $F_{14,33} = 0.7$, $P = 0.761$) or temporal (M: $F_{3,58} = 0.32$, $P = 0.811$; LF: $F_{3,44} = 0.53$, $P = 0.662$) autocorrelation. The global model provided an adequate fit to the data for male (Hosmer–Lemeshow goodness-of-fit [GOF] statistic = 7.771, df = 8, $P = 0.456$) and LF (Hosmer–Lemeshow GOF statistic = 4.995, df = 8, $P = 0.758$) bats, respectively.

The best approximating model for male roost-site selection incorporated distance to nearest corridor and distances to nearest open and mixed pine–hardwood stands (Table 1) with a 68.5% probability (Table 2). This model was 8.8 times more likely than the next best-approximating model, which contained distances to nearest open and mixed pine–hardwood stands. The confidence set of models included the top 2 models with a sum of Akaike weights

Table 1. Means and standard errors of 8 habitat variables measured at male, lactating female (LF), pregnant female (PF), and nonreproductive female (NF) evening bat summer roost and random structures in the Lower Coastal Plain, South Carolina, USA, 2003–2006.

	M (n = 31)				LF (n = 24)				PF (n = 11)				NF (n = 9)			
	Roost		Random		Roost		Random		Roost		Random		Roost		Random	
Variable	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
dcorr[a]	255	43	477	58	319	72	481	61	459	97	520	185	261	78	243	86
de	61	11	80	13	54	11	93	16	89	19	60	21	73	18	29	8
do	283	46	165	44	114	21	131	39	285	82	404	131	205	58	153	50
dc	556	108	474	90	896	157	667	106	352	151	474	134	162	33	554	179
dmr	212	54	210	39	295	59	183	41	139	53	112	41	141	40	159	88
dmp	448	69	420	70	301	51	495	87	670	102	608	129	509	124	723	210
dph	182	37	422	66	125	41	483	74	259	77	399	138	157	68	429	127
dh	1,234	175	1,303	167	1,249	193	1,218	166	1,747	216	1,312	258	2,077	315	637	245

[a] dcorr = distance (m) to nearest corridor, de = distance (m) to nearest edge or road, do = distance (m) to open stand, dc = distance (m) to closed stand, dmr = distance (m) to mid-rotation stand, dmp = distance (m) to mature pine stand, dph = distance (m) to pine–hardwood stand, dh = distance (m) to hardwood stand.

of 0.763 indicating a 76.3% chance that one of these models was the best approximating model based on our data and set of candidate models. There was insufficient evidence to consider remaining models as plausible explanations for roost-site selection. Distance to nearest corridor and distance to nearest mixed pine–hardwood stand were negatively related, and distance to nearest open stand was positively related with site selection (Table 3). The other 5 distance measures had model-averaged 90% confidence intervals that included zero, indicating they provided little information regarding roost-site selection. Distance to nearest mixed pine–hardwood stand had the highest importance value, followed by distance to nearest corridor and distance to nearest open stand. The composite model contained 3 variables whose scaled OR were precise (90% CI did not include 1; Table 4). Roost sites were 9% less likely to occur for every 25-m increase in distance to nearest mixed pine–hardwood stand and 9% more likely for every 25-m increase in distance to nearest open stand. Odds of a roost occurring decreased by 8% for every 25-m increase in distance from nearest corridor. We evaluated model performance for male roost-site selection using the top model from our confidence set. The top model incorrectly predicted 18% of used sites as random and 24% of random sites as roosts. Based on our classification rates, our top model classified 75% of roosts and 84% of random sites correctly.

Table 2. Variables, number of parameters in the model (K), Akaike's Information Criterion adjusted for small sample size (AIC$_c$), difference of AIC$_c$ between a model and the model with the lowest AIC$_c$ (ΔAIC$_c$), model weights (w_i), and Nagelkerke's R^2 values for the confidence set of models we used to predict evening bat summer roost-site selection relative to forested corridors on an intensively managed loblolly pine landscape in the Lower Coastal Plain, South Carolina, USA, 2003–2006.

Model	K	AIC$_c$	ΔAIC$_c$	w_i	R^2
M					
dcorr do dph[a]	4	71.310	0	0.685	0.418
do dph	3	75.663	4.352	0.078	0.315
Lactating F					
dmr dph	3	48.318	0	0.354	0.538
dcorr dmr dph	4	49.149	0.831	0.234	0.563
de dmr dph	4	50.554	2.236	0.116	0.540
dmp dph	3	51.800	3.482	0.062	0.478
dcorr dmp dph	4	52.557	4.296	0.043	0.506
dcorr dph dh	4	52.614	4.855	0.041	0.505

[a] dcorr = distance (m) to nearest corridor, do = distance (m) to open stand, dph = distance (m) to pine–hardwood stand, dmr = distance (m) to mid-rotation stand, de = distance (m) to nearest edge or road, dmp = distance (m) to mature pine stand, dh = distance (m) to hardwood stand.

The best approximating model for LF roost-site selection incorporated distance to nearest mid-rotation stand and distance to nearest mixed pine–hardwood stand (Table 1) with a 35.4% probability (Table 2). This model was 1.5 times more likely than the next best-approximating model, which contained the same parameters plus distance to nearest corridor. The confidence set of models included the top 6 models with a sum of Akaike weights of 0.85. Distance to nearest mixed pine–hardwood stand was negatively related and distance to nearest mid-rotation stand was positively related with site selection (Table 3). All other distance measures had model averaged 90% confidence intervals that included zero. Distance to nearest mixed pine–hardwood stand had the highest importance value, followed by distance to nearest mid-rotation stand. The composite model contained 2 variables whose scaled OR were precise (Table 4). Lactating female evening bats were 17% more likely to select a site for every 25-m decrease in distance to nearest mixed pine–hardwood stand. Roost sites were 11% less likely to occur for every 25-m decrease in distance from nearest mid-rotation stand. Our top model for lactating female evening bat roost-site selection incorrectly predicted 18% of used sites as random and 23% of random sites as roosts. Based on our classification rates, our top model classified 75% of roosts and 83% of random sites correctly.

DISCUSSION

Evening bats in our study selected roosts in a variety of tree species, structure types, and habitat conditions. Miles et al. (2006) observed similar results for evening bats in southwest Georgia, USA. Because forest conditions frequently change

Table 3. Model-averaged parameter estimates, unconditional standard errors, 90% lower (L) and upper (U) confidence intervals, and importance values for habitat variables included in the confidence set of models examining male and lactating female evening bat summer roost-site selection relative to forested corridors on an intensively managed loblolly pine landscape in the Lower Coastal Plain, South Carolina, USA, 2003–2006.

Variable	Estimate	SE	L 90% CI	U 90% CI	Importance
M					
intercept	1.148	0.682	0.030	2.267	1.000
dph[a]	−0.003	0.001	−0.005	−0.001	0.943
dcorr	−0.003	0.001	−0.005	−8.5E-04	0.871
do	0.003	0.002	9.30E-04	0.006	0.842
dc	4.00E-04	6.40E-04	−6.4E-04	0.002	0.065
dh	−2.2E-04	3.30E-04	−7.6E-04	3.10E-04	0.060
dmp	3.40E-04	8.50E-04	−0.001	0.002	0.052
dmr	−3.1E-05	0.001	−0.002	0.002	0.049
de	−0.003	0.005	−0.011	0.005	0.039
Lactating F					
intercept	1.322	1.041	−0.386	3.030	1.000
dph	−0.006	0.002	−0.010	−0.003	1.000
dmr	0.004	0.002	0.001	0.007	0.724
dcorr	−0.002	0.001	−0.004	3.70E-04	0.385
de	−0.003	0.007	−0.137	0.009	0.179
dmp	0.002	0.002	−0.004	6.20E-04	0.149
dh	−5.2E-04	5.40E-04	−0.001	3.70E-04	0.083
do	0.006	0.005	−0.003	0.014	0.073
dc	2.00E-04	7.80E-04	−0.001	0.002	0.051

[a] dph = distance (m) to pine–hardwood stand, dcorr = distance (m) to nearest corridor, do = distance (m) to open stand, dc = distance (m) to closed stand, dh = distance (m) to hardwood stand, dmp = distance (m) to mature pine stand, dmr = distance (m) to mid-rotation stand, de = distance (m) to nearest edge or road.

on intensively managed landscapes, plasticity in roost selection likely allows evening bats to adjust to variations in forest structure and composition (Waldien et al. 2000, Miles et al. 2006). Similar to Boyles and Robbins (2006), we found evening bats roosting primarily in tree cavities, which typically were located in mature pine, mixed pine–hardwood, and hardwood stands. Mature forest stands provide numerous tall, large-diameter trees in later stages of decay suitable for cavity-roosting bats (Cryan et al. 2001). In mid-rotation and younger mature pine stands (range = 15–34 yr), evening bats typically selected roosts in fork-topped pine trees. Fork-topped trees are frequently used by evening bats, particularly reproductive females, in southeastern managed pine forests and may provide an alternative to older trees (Menzel et al. 2001; Miles et al. 2006; D. A. Miller, Weyerhaeuser Company, unpublished data).

Our model results demonstrate importance of mature mixed pine–hardwood stands for male and LF evening bats

Table 4. Odds ratios (OR), scaled odds ratios, variable unit change, and lower (L) and upper (U) confidence intervals of scaled odds ratios for parameter estimates of habitat variables used to examine male and lactating female evening bat summer roost-site selection relative to forested corridors on an intensively managed loblolly pine landscape in the Lower Coastal Plain, South Carolina, USA, 2003–2006.

Variable	OR	Scaled OR	Unit change	L 90% CI scaled OR	U 90% CI scaled OR
M					
dph[a]	0.997	0.921	25	0.874	0.970
dcorr	0.997	0.932	25	0.888	0.979
do	1.003	1.089	25	1.024	1.159
dc	1.000	1.010	25	0.984	1.037
dh	1.000	0.999	25	0.981	1.008
dmp	1.000	1.008	25	0.974	1.044
dmr	1.000	0.999	25	0.953	1.048
de	0.997	0.973	10	0.897	1.055
Lactating F					
dph	0.994	0.853	25	0.783	0.930
dmr	1.004	1.108	25	1.029	1.194
dcorr	0.998	0.959	25	0.911	1.009
de	0.998	0.975	10	0.872	1.090
dmp	0.998	0.955	25	0.898	1.016
dh	1.000	0.987	25	0.965	1.009
do	1.006	1.149	25	0.932	1.417
dc	1.000	1.005	25	0.973	1.038

[a] dph = distance (m) to pine–hardwood stand, dcorr = distance (m) to nearest corridor, do = distance (m) to open stand, dc = distance (m) to closed stand, dh = distance (m) to hardwood stand, dmp = distance (m) to mature pine stand, dmr = distance (m) to mid-rotation stand, de = distance (m) to nearest edge or road.

on our study area. However, previous studies in other areas have demonstrated evening bats selecting a variety of habitat types for roosting. Menzel et al. (2001) located 93% of evening bats in longleaf pine (*P. palustris*) stands >45 years. Boyles and Robbins (2006) found evening bats roosting exclusively in mature hardwood habitat. Miles et al. (2006) tracked 78% of bats to mature longleaf pine stands (>70 yr) on a natural longleaf pine landscape and 48% to riparian hardwood stands (>50 yr) on an intensively managed pine landscape. Contrary to Miles et al. (2006), we did not find evening bats roosting in riparian hardwood stands. We conclude that across their distribution, evening bats appear to select more mature forests that provide suitable roost structures (i.e., older trees and snags) regardless of specific habitat types available.

Distance to nearest corridor was negatively related to roost-site selection by male evening bats. We found nearly 40% of male evening bat roosts located within upland corridors comprised of pine or mixed pine–hardwood stands. Hein et al. (2008) documented a high proportion of male and female Seminole bat day-roosts in similar corridor stands. Although models containing distance to nearest corridor were included in the confidence set for LF evening bats in our study, model-averaged parameter estimates suggested that corridors were less important for that group. Although male and LF evening bats selected mixed pine–hardwood habitats either in corridors or stands, corridors were used more by males, suggesting that geometric configuration of the stand (linear vs. block) as a selection criterion may differ between sexes.

Compared to random sites, male roosts were located farther from open stands. Previous landscape-level studies on forest bats have reported similar findings (Elmore et al. 2004, Miles et al. 2006). Although bats frequently forage over or near open habitat (Grindal and Brigham 1998, Jung et al. 1999, Patriquin and Barclay 2003, Elmore et al. 2005), selecting roosts offering optimal thermal conditions and protection may outweigh commuting costs (Racey and Swift 1981). Male bats in our study generally exhibited fidelity to diurnal roosts that often were not near open habitats, suggesting that they select for higher quality roosts regardless of distance to foraging sites. Lactating female bats roosted farther from mid-rotation pine stands compared to random sites. Mid-rotation stands likely do not provide suitable structures (i.e., tall, large-diam trees) used as maternity colonies for lactating female bats and their pups. Furthermore, mid-rotation stands may not offer optimal foraging opportunities for bats due to high clutter (Erickson and West 1996).

Differences in selection criteria likely are influenced by distinct physiological demands between male and female bats during summer. Our findings were consistent with recent studies that demonstrated differential roost-selection between sexes (Broders and Forbes 2004, Elmore et al. 2004, Hein et al. 2008) and further emphasize the need for additional sex-specific studies. Although we were unable to model roost-site selection for pregnant or nonreproductive female evening bats, our data suggest differences among these reproductively distinct groups.

MANAGEMENT IMPLICATIONS

Retaining fork-topped trees through harvest rotations likely will increase potential roosting habitat for evening bats on managed pine forests. However, because evening bats typically select roost structures (i.e., snags and cavity trees) associated with mature forests, we also recommend maintaining older forest conditions in the form of stands or corridors across managed landscapes. We acknowledge that managed landscapes represent a diversity of management objectives and approaches. Therefore, caution should be used in applying our results across the range of conditions represented. Additional research is needed to further elucidate bat–habitat relationships across a diversity of intensively managed landscapes (Wigley et al. 2007).

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