Research Article

Multi-Scale Roost-Site Selection by Evening Bats on Pine-Dominated Landscapes in Southwest Georgia

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Abstract

*Bats likely incorporate multi-scale criteria when selecting roost sites, which may change across different landscapes. During summers 2002 and 2003, we used radiotelemetry to investigate day-roost selection of evening bats (*Nycticeius humeralis*) at multiple scales in mature longleaf (*Pinus palustris*; natural) and intensively managed loblolly pine (*P. taeda*; managed) landscapes in the Gulf Coastal Plain of Georgia, USA. We used Akaike's Information Criterion (AIC) to evaluate models describing roost-site selection at the tree, plot, stand, and landscape scales. Evening bats on the natural site selected day-roosts based on tree, plot, and landscape characteristics, but bats on the managed site selected day-roosts only at the tree and plot scale. We hypothesize that greater availability of roosting structures (i.e., abundant large trees and snags) throughout the natural site allowed evening bats to select day-roosts that had favorable landscape characteristics (i.e., closer to water and foraging sites), possibly providing benefits from reduced commuting costs. On the managed site, the relatively young age structure of stands resulted in less-abundant roosting structures throughout the landscape, resulting in selection only at the tree and plot scales. Evening bats appeared to select day-roosts that provide energetic benefits when landscape conditions permitted, however, replicated studies are needed to examine the relationship between energetics and roost availability. Land management on pine landscapes of the southeastern United States that promotes large trees, retention of snags, and an open midstory appears to provide abundant roost structures for evening bats. On managed landscapes, roost sites for evening bats may be provided by retention of forked-topped pines in managed stands and by allowing maturation and senescence of trees in set-aside areas, such as streamside management zones, to promote snag and cavity formation.* (JOURNAL OF WILDLIFE MANAGEMENT 70(5):1191–1199; 2006)

Key words

evening bat, forest management, Georgia, loblolly pine, longleaf pine, Nycticeius humeralis, *pine plantation,* Pinus palustris, Pinus taeda, *roost-site selection.*

Because of the importance of roost sites to bats (Kunz 1982) and the hypothesis that lack of suitable roost sites may limit bat populations (Humphrey 1975), roost studies traditionally have been important components of bat research (Miller et al. 2003). Studies on roost selection by forest bats generally have indicated that cavity- and bark-roosting bats select trees that are taller, have a larger diameter at breast height (dbh), have a more open canopy, are found in stands with greater snag density, and are closer to water than surrounding trees (Kalcounis-Rüppell et al. 2005). However, most of these studies have limited inferential scope because they only investigated characteristics at the small spatial scale (i.e., roost tree) or only investigated roost selection in a single forest condition, which may not accurately represent roost selection by the same species in other forest conditions or in different landscapes (Miller et al. 2003). For example, Waldien et al. (2000) found that western long-eared myotis (*Myotis evotis*) selected large snags when capture locations were surrounded by mature forest, but they selected stumps when capture locations were surrounded by intensively managed forests. Had inference been drawn with only one of the forest conditions present, conclusions would have been misleading. Such studies highlight the need to conduct roost-selection studies across a range of landscape conditions.

The longleaf pine (*Pinus palustris*) forest ecosystem of the southeastern United States historically covered an estimated 37 million ha, but currently covers <1.2 million ha (Landers et al. 1995). The decline has been attributed to a variety of factors, including clearing for agricultural uses, conversion to other forest types, and disruption of natural fire regimes. Historically, abundant large trees and lightning-strike-created snags in longleaf forests likely provided habitat for cavity- and bark-roosting bats. Conversely, the area covered by managed pine plantations in the southeastern United States is estimated at about 12 million ha, or 15% of the total forested land area (Wear and Greis 2002), and is expected to remain relatively constant over the next 2 decades (National Commission on Science for Sustainable Forestry 2005). Although research has demonstrated the general conservation value of managed pine stands in the Southeast for a variety of species, including use by bats (e.g., Wigley et al., in press), intensive management of these forests may limit development of large trees and snags across the landscape and could limit opportunities for cavity- and bark-roosting bats.

We selected the evening bat (*Nycticeius humeralis*), a common forest bat in the southeastern United States, as a model for examining questions relative to day-roost

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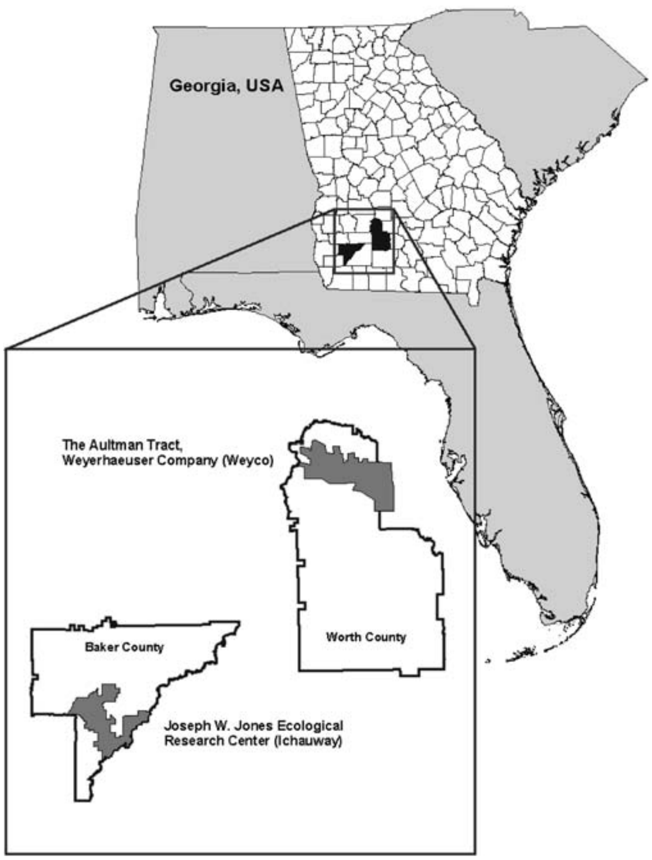

Figure 1. Locations of the Joseph W. Jones Ecological Research Center (natural site) and the Aultman Tract (managed site) study areas in southwestern Georgia, USA, used in an investigation of evening bat roost-site selection in 2002–2003.

selection by bats in pine-dominated landscapes at multiple spatial scales. Evening bats use Spanish moss (*Tillandsia usneoides*; Jennings 1958), exfoliating bark of snags (Jennings 1958, Chapman and Chapman 1990, Menzel et al. 1999, 2001), tree cavities (Menzel et al. 1999, 2001), and buildings (Chapman and Chapman 1990, Wilkinson 1992) as diurnal roosts. Previous studies on the roosting ecology of evening bats have examined roost selection at a small scale (i.e., roost structure and immediate area; Menzel et al. 1999, 2000, 2001). Larger-scale influences on day-roost selection by evening bats remain an unstudied, yet important component of developing effective management strategies for forest-roosting bats. Therefore, our objectives were to examine the influence of scale on evening bat roost-site selection and how selection scale differed between a natural, longleaf pine landscape and an intensively managed pine landscape.

Study Area

We conducted our study in the Upper Coastal Plain physiographic region of southwestern Georgia, USA, between 31°50′ and 31°4′N latitude and 84°40′ and 83°39′W longitude. The region was characterized by hot, humid summers with average daily temperatures of 27°C. Annual precipitation averages 132 cm/year (Goebel et al. 1997).

We selected 2 sites for study; 1 that simulated the historic longleaf condition and 1 that represented an intensively managed pine landscape (Fig. 1). The Joseph W. Jones Ecological Research Center at Ichauway (natural site), in Baker County, Georgia was a 12,000-ha research site managed with biennial prescribed fire to simulate natural disturbance patterns and promote a landscape similar to the historic longleaf pine ecosystem. Longleaf forests, which comprised approximately 68% of the Center's total forested land area, were between 70–90 years old, with individual trees >300 years old scattered throughout the site. Because the forests were naturally regenerated, tree densities in longleaf stands were highly variable. Southern red oak (*Quercus falcata*), sweetgum (*Liquidambar styraciflua*), and other hardwoods commonly occurred within the mature pine forests. Snags, primarily pine, but also hardwoods, also were common in forested areas. Riparian hardwood forests, mixed pine–hardwood forests, and wildlife openings were scattered throughout.

The Aultman Tract (managed site) in Worth County, Georgia, USA was a 14,000-ha area managed by Weyerhaeuser Company with approximately 80% of the forested land area in loblolly pine (*Pinus taeda*) plantations on a 30-year sawtimber rotation. Management for intensively managed pine stands included site preparation and planting, vegetation management, commercial thinning, pruning, and fertilization. Pines typically were planted at 182 trees/ha and thinned to a target density of 55 trees/ha between years 15 and 20. Management resulted in even-aged stands of different successional stages distributed in a mosaic throughout the landscape. A dense hardwood midstory of sweetgum, persimmon (*Diospyros virginiana*), and oaks often were present in stands 20–30 years old. Nonplantation habitats >50 years old, including hardwood-dominated riparian forests (streamside management zones [SMZs]), mature pine–hardwood, and upland hardwood forests were interspersed throughout the site, covering approximately 20% of the forested area.

Methods

Capture and Radiotelemetry

We captured evening bats from late May to early September 2002 and 2003 using 6- to 18-m-wide by 2.4-m-high mist nets set over ponds, small streams, and roadside ditches distributed throughout each study area. We recorded mass (g), forearm length (mm), gender, age (Anthony 1988), and reproductive condition (Racey 1988) of captured bats. We attached 0.43-g, 0.45-g (Micro-Pip; Biotrack, Wareham, Dorset, United Kingdom), or 0.52-g (LB-2, Holohil, Ontario, Canada) radiotransmitters to the fur-clipped inter-scapular region of evening bats using Skin Bond surgical cement (Pfizer, Largo, Florida). We held bats for 20 minutes to allow adhesive to set and released them at point of capture. Transmitter mass was typically <5% of body mass (mean = 4.7%; range 2.5–6.1%) as recommended by

Table 1. Variables measured at evening bat roost sites and random sites in southwestern Georgia, USA, 2002–2003.

Scale	Variable	Definition
Tree	Tree type	Hardwood or pine tree
	dbh[a]	Diameter at breast height (cm) of the tree
	Height	Height (m) of the tree
	Tree condition	Live tree or snag
Plot	Overstory height	Mean height (m) of overstory trees
	Overstory dbh	Mean dbh (cm) of overstory trees
	Overstory distance	Mean distance (m) to overstory trees
	Nearest overstory	Distance (m) to nearest overstory tree
	Percent pine	Percent pine (%) of overstory trees
	Midstory height	Mean height (m) of midstory trees
	Midstory distance	Mean distance (m) to midstory trees
Stand	Open	Distance (m) to open (or clear-cut) stand
	Closed pine	Distance (m) to closed pine stand
	Mature pine	Distance (m) to mature pine stand
	Hardwood	Distance (m) to hardwood stand
	Edge	Distance (m) to nearest edge or road
	Water	Distance (m) to nearest water (pond or stream)
	Stand size	Area (ha) of stand
Landscape	Open	Area (ha) of open habitat within 430 m buffer
	Closed pine	Area (ha) of closed pine within 430 m buffer
	Mature pine	Area (ha) of mature pine within 430 m buffer
	Hardwood	Area (ha) of hardwood within 430 m buffer

[a] Diameter at breast height (1.4 m).

Aldridge and Brigham (1988). We conducted bat capture and handling under University of Georgia Institutional Animal Care and Use Committee guidelines (permit number A2002-10108-0).

We used TRX-2000S (Wildlife Materials, Murphysboro, Illinois), R-1000 (Communications Specialists, Orange, California), and R-2000 (Advanced Telemetry Systems, Isanti, Minnesota) receivers and 4- and 6-element yagi antennas to track bats to day-roosts. Beginning the day after capture, we tracked bats daily, when possible, until the radiotransmitter failed or was recovered. We placed a higher priority on daily tracking of new bats or those with fewer identified roosts. Our approach allowed us to draw inferences based on a larger sample of individual bats (Miller et al. 2003). We conducted dusk emergence counts on a sub-sample of day-roosts to confirm use by bats and to count numbers of exiting bats. We recorded locations of day-roosts using a Pathfinder Pro XR (Trimble Navigation, Sunnyvale, California) Global Positioning System with differential correction and imported locations into ArcGIS© Geographic Information System (GIS; Environmental Systems Research Institute, Redlands, California).

To develop models of day-roost selection by evening bats, we used ArcGIS to generate random points throughout each study area and identified the nearest overstory tree (>9.5-cm dbh) to the random point. Our approach differed from previous studies (Ormsbee and McComb 1998, Menzel et al. 2000, Waldien et al. 2000, Owen et al. 2002) for 2 reasons. First, we chose random structures from throughout each study area because we were interested in roost selection by evening bats at the landscape scale. Second, we considered any overstory tree with or without visible cavities or signs of damage as a candidate random structure. Previous studies and our own data indicated that evening bats select a wide variety of tree types and sizes as roosts, including healthy, live trees with no obvious signs of damage (Menzel et al. 1999, 2001). Random structures were not used by radiotagged bats during our study, but use by untagged bats was unknown (Bernardos et al. 2004).

Habitat Sampling

To characterize roost structures, we recorded tree species, condition (live or snag), dbh (cm), and height (m) of each roost and random tree (tree metrics; Table 1). We measured variables describing the area surrounding roost and random structures (plot metrics), including distance (m), species, class, dbh, and height of the nearest overstory (>9.5-cm dbh) and midstory (2–9.5-cm) tree, using the point-centered-quarter method (Cottam and Curtis 1956). Because we defined plot metrics as those describing the habitat immediately surrounding the roost and random structures, we assumed overstory trees >30 m and midstory trees >15 m from the roost tree had little impact on bat roost selection at that scale and designated these as maximum distances. We used these maximum distances in calculations when trees were missing from quadrants. We only included an individual tree once in our analysis, regardless of the number of radiotagged bats that utilized the tree. We assumed individual preference for day-roosts did not bias our results and that roost trees were independent observations.

To characterize stand and landscape conditions, we used habitat classification layers in ArcGIS to divide each study area into 4 habitat types (mature pine, closed-canopy pine, open, and hardwood). We simplified habitat classifications describing overstory type to provide consistency between study sites. We defined mature pine as upland stands with a pine-dominated canopy (>70% canopy of pine) and included second-growth longleaf stands (>70 yr old) on the natural site and thinned pine stands (13–30 yr old) on the managed site. Closed-pine stands on both sites were dense, unthinned stands with complete or almost complete canopy closure. Open habitats on the natural site included fields and wildlife openings, and primarily clearcut and regenerating stands <8 years old (pre-canopy closure) on the managed site. Hardwood stands (<25% pine basal area) on both sites were primarily riparian areas and forested wetlands, but a small total area of upland hardwood and mixed pine–hardwood stands was included. All hardwood stands were similar in age and structure. Most riparian and wetland hardwood areas on the managed site were

Table 2. Variables, number of parameters in the model (K), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c value between the model and the model with the lowest AIC_c value (ΔAIC_c), and Akaike weight (w_i) for models with $w_i \geq 0.0001$ (listed in ascending rank by AIC_c value) from the a priori set of 16 candidate models used to predict roost-site selection by evening bats on the natural site in southwestern Georgia, USA, 2002–2003.

Model	K	AIC_c	ΔAIC_c	w_i
Tree Plot Landscape	16	221.8374	0.00	0.4017
Tree Plot Stand Landscape	23	222.0291	0.19	0.3650
Tree Plot Stand	19	223.1428	1.31	0.2091
Tree Plot	12	227.4919	5.65	0.0238
Tree Stand Landscape	16	236.5232	14.69	0.0003
Tree Stand	12	238.2559	16.42	0.0001
Tree Landscape	9	238.9463	17.11	0.0001
Null model	1	304.2123	82.37	0.0000

designated as reserve areas and received limited or no management.

Stand-level metrics included stand size (ha) and distance (m) from the roost structure to water (stream, pond, or wetland), edge (or road), and every other habitat type (Table 1; Elmore et al. 2004). The distance to the habitat in which the roost or random site resided was recorded as zero. We characterized landscape composition by creating a 430-m buffer around each roost and random tree and calculating the area (ha) of each habitat type within each buffer. The buffer size of 430 m was based on the mean maximum distance between roosts used by individual bats. Because total area of the landscape used by each radiotagged bat was unknown, this measure represented a conservative estimate of the landscape that influenced roost-site selection.

Analysis and Model Development

We developed 16 a priori multivariate models to describe day-roost selection by evening bats, pooling data across gender and age classes. Our model set included all possible additive combinations of categories that described tree, plot, stand, and landscape scales (Table 1). Because no data were available to indicate otherwise, we assumed all models had the potential for providing information on the scale at which evening bats select roosts.

We used logistic regression (Allison 2000) to create models and used the second-order Akaike's Information Criteria (AIC_c) to identify the most parsimonious model and predict variable importance (Burnham and Anderson 2002). We considered the model with the lowest AIC_c and all models <2 Δ_i as the best approximating models. We also calculated Akaike weight (w_i) for each model, representing probability of that model as being the best model in the set of candidate models (Burnham and Anderson 2002). We calculated the sum of model weights for each variable using weights of models that contained that variable. We used model-averaged parameter estimates and unconditional standard errors averaged over all models that contained a variable to determine importance of that variable within the set of multivariate models with >0.90 w_i. We calculated odds ratios from averaged parameter estimates that represented the increase in probability of a site being used as a roost by an evening bat for every unit increase in the predictor variable (Allison 2000).

Results

We radiotracked 99 evening bats to 168 individual roost trees. On the natural site, we tracked 32 females to 55 trees, 19 males to 34 trees, and 9 juveniles to 22 trees ($n = 60$ bats to 111 trees). On the managed site, we tracked 18 females to 28 trees, 15 males to 21 trees, and 6 juveniles to 8 trees ($n =$ 39 bats to 57 trees). The mean number of roost trees observed per radiotagged individual was 2.0 ± 0.14 on the natural site and 1.6 ± 0.15 on the managed site. Mean distance from capture location to roost was 1,217 ± 145 m on the managed site and 853 ± 58 m on the natural site. Fourteen trees (natural = 9, managed = 5) were used by >1 radiotagged bat. Adult males always roosted alone, while females and juveniles roosted in groups or alone. We identified 11 maternity colonies with 30–100 bats and 8 with >100 bats (max. = 490) on the natural site, and 2 colonies with 7 bats on the managed site.

Evening bats roosted in a variety of trees, but live conifers, including pine and bald cypress (*Taxodium distichum*), were the most common tree type used on both study areas. On the natural site, 58% ($n = 64$) of roosts were in live pines (94% longleaf, 6% loblolly), 17% ($n = 19$) were in live hardwoods (primarily oaks), and 25% ($n = 28$) were in snags (68% pine, 32% hardwood). On the managed site, 32% ($n = 18$) of roosts were in loblolly pine, 30% ($n = 17$) were in bald cypress, 12% ($n = 7$) were in hardwoods, and 26% ($n = 15$) were in snags (33% pine, 54% hardwood, 13% bald cypress). Of the live loblolly pines used on the managed site, 78% ($n = 14$) were fork-topped (bifurcated-topped) trees that had a cavity at the base of the main fork. Because bald cypress roosts occurred in streamside management zones and forested wetlands (hardwood habitat type), we classified them as hardwoods for our analyses. Mature pine was the most common habitat type used by roosting evening bats on the natural site (78%), while hardwood (48%) and mature pine (31%) types were used most often on the managed site.

Roost-Site Modeling

We obtained the model with the lowest AIC_c on the natural site using tree, plot, and landscape characteristics (Nagelkerke's $R^2 = 0.547$; Table 2). Two models that contained tree, plot, and stand characteristics (Nagelkerke's $R^2 =$ 0.568) and tree, plot, stand, and landscape characteristics (Nagelkerke's $R^2 = 0.605$) were <2 Δ_i and were considered strongly competing. The w_i for the top model ($w_i = 0.402$) was only slightly greater than the next 2 closest models ($w_i =$ 0.365 and 0.209). The sum w_i of the top 3 models exceeded 0.90, indicating that there was a >90% chance that one of these models was the best approximating model of the 16 considered. The sum of Akaike weights (Σw_i) for all variables was nontrivial (>0.50), but only 9 variables had model-averaged confidence intervals that did not contain zero, indicating that they provided the most information about roost-site selection (Table 3). These included 2 tree

Table 3. Model-averaged parameter estimates, unconditional standard errors, odds ratios, and sum of Akaike weights (Σw_i) of predictor variables found in logistic regression models of evening bat roost-site selection on the natural site in southwestern Georgia, USA, 2002–2003.

Scale	Variable	Estimate	SE	Odds ratio	Σw_i
Tree	Tree type	−0.2510	0.353	0.77800	1.0000
	dbh[a]	0.0480[b]	0.018	1.04914	1.0000
	Height	0.0650	0.068	1.06711	1.0000
	Tree condition	−2.4817[b]	0.684	0.08360	1.0000
Plot	Overstory height	−0.1708[b]	0.080	0.84302	0.9996
	Overstory dbh	0.0247	0.022	1.02497	0.9996
	Overstory distance	−0.2720[b]	0.078	0.76184	0.9996
	Nearest overstory	0.0234	0.077	1.02363	0.9996
	Percent pine	0.8700	0.934	2.38694	0.9996
	Midstory height	−0.0257	0.074	0.97466	0.9996
	Midstory distance	0.1044	0.075	1.11001	0.9996
Stand	Open	0.0041	0.003	1.00410	0.5745
	Closed pine	−0.0005	0.000	0.99950	0.5745
	Mature pine	−0.0224[b]	0.009	0.97783	0.5745
	Hardwood	−1.20E-05	0.003	0.99999	0.5745
	Edge	−0.0025	0.007	0.99747	0.5745
	Water	−0.0018[b]	0.001	0.99823	0.5745
	Stand size	−3.46E-07	8.76E-07	1.00000	0.5745
Landscape	Open	1.63E-05[b]	5.88E-06	1.00002	0.7670
	Closed pine	5.39E-06	1.36E-05	1.00001	0.7670
	Mature pine	1.23E-05[b]	5.74E-06	1.00001	0.7670
	Hardwood	1.32E-05[b]	4.88E-06	1.00001	0.7670

[a] Diameter at breast height (1.4 m).
[b] 95% confidence intervals do not include zero.

variables (dbh, condition), 2 plot variables (mean overstory height, mean overstory distance), 2 stand variables (distance to mature pine, distance to water), and 3 landscape variables (area in open, hardwood, and mature pine).

On the managed site, the model with the lowest AIC_c was obtained using only tree and plot characteristics (Nagelkerke's $R^2 = 0.615$; Table 4). The best model had a $w_i = 0.959$ indicating that there was >95% chance that this was the best approximating model of the 16 considered. No other models were within 7.5 AIC_c units of the top model. Only variables describing the tree and plot had $\Sigma w_i > 0.1$ (tree and plot $\Sigma w_i > 0.99$), indicating that these were the most important variables. Five of these variables (tree condition, mean overstory distance, distance to nearest overstory tree, mean midstory height, mean midstory distance) provided the most information about evening bat roost-site selection on the managed site, as indicated by confidence intervals that did not contain zero (Table 5).

Table 4. Variables, number of parameters in the model (K), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c value between the model and the model with the lowest AIC_c value (ΔAIC_c), and Akaike weight (w_i) for models with $w_i \geq 0.0001$ (listed in ascending rank by AIC_c value) from the a priori set of 16 candidate models used to predict roost-site selection by evening bats on the managed site in southwestern Georgia, USA, 2002–2003.

Model	K	AIC_c	ΔAIC_c	w_i
Tree Plot	12	109.2854	0.00	0.9589
Tree Plot Stand	19	116.7411	7.46	0.0231
Tree Plot Landscape	16	117.6277	8.34	0.0148
Tree	5	121.8171	12.53	0.0018
Plot	8	123.1823	13.90	0.0009
Tree Landscape	9	125.6453	16.36	0.0003
Tree Plot Stand Landscape	23	127.3036	18.02	0.0001
Plot Stand	15	128.4323	19.15	0.0001
Null model	1	150.1379	40.85	0.0000

Discussion

Evening bats roosted under bark or in cavities of live and dead trees of a variety of species and sizes. They exhibited greater plasticity in roost structure selection than reported for most cavity-roosting bat species (Betts 1998, Ormsbee and McComb 1998, Weller and Zabel 2001). Waldien et al. (2000) suggested that use of multiple roost types by western long-eared myotis allowed individuals to adjust to availability of different types of roosts throughout the landscape. The evening bats in our study appeared to have a similar plasticity, allowing them to exploit a diversity of forest conditions.

Although we cannot identify causal mechanisms regarding the observed differences in evening bat roost selection between the natural longleaf and intensively managed loblolly pine landscapes because our study lacked replication at the landscape scale, the differences likely can be attributed to differences in availability of roost structures between the landscapes. The older stand structure of the natural site (i.e., most stands 70–90 yr old) provided numerous snags and large, live trees, suitable as roost sites, throughout the landscape. Conversely, the managed site consisted of a high proportion of young stands that contained no large trees and few snags. Large trees and most snags were found in SMZs, which covered a small proportion of the total area. Fork-topped loblolly pines were the most frequent type of live pine used as day-roosts on the managed landscape. Forked-tops may be genetically controlled or created when the terminal bud of a growing tree is damaged during early growth stages (H. Duzan, Weyerhaeuser Company, person-

Table 5. Model-averaged parameter estimates, unconditional standard errors, odds ratios, and sum of Akaike weights (Σw_i) of predictor variables found in logistic regression models of evening bat roost-site selection on the managed site in southwestern Georgia, USA, 2002–2003.

Scale	Variable	Estimate	SE	Odds ratio	Σw_i
Tree	Tree type	0.3547	0.704	1.42573	0.9990
	dbh[a]	0.0707	0.056	1.07326	0.9990
	Height	0.1694	0.110	1.18454	0.9990
	Tree condition	−2.0735[b]	0.707	0.12574	0.9990
Plot	Overstory height	0.0283	0.141	1.02874	0.9979
	Overstory dbh	−0.0330	0.081	0.96756	0.9979
	Overstory distance	−0.4125[b]	0.155	0.66201	0.9979
	Nearest overstory	0.3529[b]	0.145	1.42320	0.9979
	Percent pine	−1.5938	1.485	0.20315	0.9979
	Midstory height	−0.3536[b]	0.155	0.70217	0.9979
	Midstory distance	0.2258[b]	0.081	1.25338	0.9979
Stand	Open	0.0006	0.001	1.00064	0.0233
	Closed pine	−0.0002	0.002	0.99980	0.0233
	Mature pine	−0.0011	0.002	0.99889	0.0233
	Hardwood	−1.20E-05	0.004	1.00473	0.0233
	Edge	0.0066	0.009	1.00660	0.0233
	Water	0.0042	0.003	1.00420	0.0233
	Stand size	−4.84E-06	1.99E-06	1.00000	0.0233
Landscape	Open	−1.04E-05	8.50E-06	0.99999	0.0152
	Closed pine	−5.29E-06	5.38E-06	0.99999	0.0152
	Mature pine	−8.58E-06	6.63E-06	0.99999	0.0152
	Hardwood	−5.56E-06	5.56E-06	0.99999	0.0152

[a] Diameter at breast height (1.4 m).
[b] 95% confidence intervals do not include zero.

al communication). Some fork-topped trees develop a cavity between the 2 main forks of the tree, providing a suitable roosting location for single bats or maternity colonies. Evening bat colonies in fork-topped loblolly pines also have been documented in intensively managed pine stands in Mississippi (D. A. Miller, Weyerhaeuser Company, unpublished data) and South Carolina (Menzel et al. 2001, C. D. Hein, University of Georgia, unpublished data).

The best multivariate models on each site contained tree and plot variables (Tables 2 and 4). The importance of characteristics of the roost structure and area immediately around the structure (plot) in roost selection by evening and other bat species is well-documented (Vonhof and Barclay 1996, Ormsbee and McComb 1998, Rabe et al. 1998, Menzel et al. 1999, 2001, Owen 2000). However, evening bats on the natural site selected roosts based not only on tree and plot characteristics, but also on stand and landscape characteristics. Specifically, roost trees on the natural site were closer to mature pine habitat and open water sources, and they were surrounded by more open, hardwood, and mature pine habitat than randomly selected trees (Table 6). Mature pine, open, and hardwood habitat types are preferred foraging locations for evening bats (Clem 1993, Carter 1998, Carter et al. 2004). We contend that greater availability of roosting structures (large trees and snags) throughout the landscape allowed evening bats to select roost sites that had more favorable landscape characteristics (i.e., closer to water and foraging sites) and, therefore, may have provided benefits from reduced commuting costs. Conversely, evening bats on the managed site selected roost sites based only on tree and plot characteristics. Roost-sites were more limited throughout the landscape on the managed site and evening bats did not have the advantage of selecting roosts with favorable landscape characteristics, possibly increasing energetic costs of commuting from roosting to foraging and drinking sites. However, water availability was greater on the managed site, based on distances of random structures to water on the 2 sites, suggesting distance to water may not have been important in roost-site selection, providing a plausible alternative explanation for lack of selection at the stand scale. Selection at the landscape scale on the managed site was not supported by our data.

Our results suggest that snags were important roost sites to evening bats on both sites. Large, lightning-strike-created snags with thick sloughing bark in mature pine stands were important as maternity sites on the natural site. Snags in mature pine stands on the managed site generally were small and rarely used as roosts. Small snags have fewer cavities and thinner bark, and likely do not provide adequate thermal conditions for roosting bats (Kurta 1985, Menzel et al. 2000). Pine and hardwood snags in SMZs and other hardwood habitats were used more commonly on the managed site.

Although evening bats selected roosts based on tree and plot characteristics on both sites, the specific variables important in roost selection at those scales, as indicated by confidence intervals that did not contain zero (Tables 3 and 5), differed between sites. Similar to the findings of Menzel et al. (2000), evening bats on the natural site selected roost structures that were larger and surrounded by a shorter overstory canopy than random structures (Table 6). The relatively old age structure of the pine stands on the natural site provided a range of live tree and snag sizes, allowing bats

Table 6. Mean and standard error of variables measured at evening bat roost and random sites on natural and managed landscapes in southwestern Georgia, USA, 2002–2003.

	Natural ($n = 111$)				Managed ($n = 57$)			
	Roost		Random		Roost		Random	
Scale/variable	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Tree								
dbh (cm)	50.0	1.8	42.1	2.5	26.3	1.3	19.9	1.0
Height (m)	22.2	0.5	19.5	0.6	15.4	0.9	13.6	0.5
Plot								
Overstory height (m)	19.7	0.4	18.2	0.6	15.4	0.7	13.4	0.4
Overstory dbh (cm)	37.4	1.1	37.1	1.9	23.6	1.1	19.6	0.9
Overstory distance (m)	9.8	0.4	13.0	0.7	5.1	0.6	6.2	0.5
Nearest overstory (m)	5.2	0.3	6.4	0.6	3.0	0.6	2.6	0.2
Percent pine (%)	70.0	0.0	60.0	0.0	40.0	10.0	63.0	5.6
Midstory height (m)	3.0	0.3	3.5	0.3	4.1	0.4	5.2	0.2
Midstory distance (m)	13.0	0.3	11.3	0.4	8.2	0.7	5.1	0.5
Stand								
Open (m)	100.0	9.4	87.7	10.0	392.9	40.7	306.0	49.5
Closed pine (m)	659.3	39.7	719.5	53.0	176.3	17.9	181.9	26.4
Mature pine (m)	7.8	2.6	43.7	9.9	98.8	19.1	109.7	25.6
Hardwood (m)	91.0	8.8	78.3	9.4	60.2	13.8	78.6	13.7
Edge (m)	28.0	2.8	27.3	3.0	60.3	8.3	35.9	6.0
Water (m)	333.3	23.4	428.6	29.6	163.5	18.4	191.9	19.3
Stand size (ha)	18.0	2.4	16.0	2.1	29.8	3.3	34.6	5.4
Landscape								
Open (ha)	10.8	0.7	10.9	0.9	2.0	0.5	4.8	1.1
Closed pine (ha)	0.7	0.2	1.2	0.2	10.9	1.5	15.0	1.8
Mature pine (ha)	33.4	1.0	28.2	1.3	21.2	1.8	20.3	1.8
Hardwood (ha)	10.3	0.7	11.7	0.8	17.8	2.0	12.2	1.1

to select larger roost structures. The younger, more homogeneous structure of the pine stands on the managed site reduced opportunities to choose larger roosts. Large trees and snags may be preferred as roosts because they provide more permanent bark and cavities, may be easier to locate and access, and provide more favorable thermoregulatory properties than smaller or less exposed structures (Vonhof and Barclay 1996, Menzel et al. 2000). Evening bats on the managed site selected roosts that were farther from the nearest overstory tree and had a shorter, more open midstory than random trees. Greater distance from the nearest overstory tree on the managed site reflects that roosts were most commonly located in hardwood forest types, which were less dense than pine stands. An open midstory results in lower clutter around the roost site, which may reduce energy expenditure of flight and reduce amount of time bats are exposed to aerial predators (Vonhof and Barclay 1996, Betts 1998). We did not observe midstory differences between roost and random structures on the natural site because the 2-year fire rotation employed throughout this site created open stands with an almost absent midstory.

Our study suggests that evening bats select roost sites in the context of the habitat conditions of the site (Rabe et al. 1998, Waldien et al. 2000). However, because we lack replication at the landscape level, additional replicated studies are needed to quantify landscape differences and identify causal mechanisms. We hypothesize that differences in evening bat roosting ecology between our sites were due to differences in availability of preferred roosting structures across the landscape. Our study suggests that roost selection by evening bats differs depending on landscape context and further emphasizes the need for multi-scale, replicated landscape studies.

Management Implications

Our study suggests that availability of roost structures across the landscape is an important factor influencing roost-site selection by evening bats. The 2-year prescribed fire cycle, retention of snags, and mature nature of most pine stands on the natural site provided abundant roost structures and favorable stand conditions (i.e., open midstory) across the landscape. Similar stand conditions and land management practices exist on nonindustrial, privately owned forest lands of the southeastern Coastal Plain. For example, management for northern bobwhite (*Colinus virginianus*) on hunting plantations (Stoddard 1931), habitat management for the endangered red-cockaded woodpecker (*Picoides borealis*; U.S. Fish and Wildlife Service 2003), and restoration of longleaf forests (Barnett 1999) warrant similar management practices, providing concurrent benefits to bats.

Management objectives on industrial timberlands often dictate silvicultural practices that are not conducive to establishment or maintenance of large snags or older trees across these landscapes. We recommend maintaining a mature forest component via reserve areas and SMZs, as appropriate and practical, in managed landscapes to provide additional roost sites for bats. Allowing maturation and senescence of trees in these areas to promote snag and cavity formation would increase potential roosting habitat across the landscape. Although snags often are present in intensively managed pine stands, especially after silvicultural thinning (Paxton et al. 2004), snags in pine stands were rarely used as roosts in our study. Fork-topped loblolly pines, the most frequently used type of live pine on the managed landscape, and documented to be used by bats on other intensively managed landscapes in the Southeast, may provide an alternative to old trees and snags. Leaving fork-topped trees until final harvest of the stand, when practical, would potentially increase roosting habitat in upland pine stands throughout the rotation.

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Literature Cited

Aldridge, H. D. J. N., and R. M. Brigham. 1988. Load carrying and maneuverability in an insectivorous bat: a test of the 5% "rule" of radio-telemetry. Journal of Mammalogy 69:379–382.

Allison, P. D. 2000. Logistic regression using the SAS system: theory and application. SAS Institute, Cary, North Carolina, USA.

Anthony, E. L. P. 1988. Age determination in bats. Pages 47–55 *in* T. H. Kunz, editor. Ecology and behavioral methods for the study of bats. Smithsonian Institution, Washington, D.C., USA.

Barnett, J. P. 1999. Longleaf pine ecosystem restoration: the role of fire. Journal of Sustainable Forestry 9:89–96.

Bernardos, D. A., C. L. Chambers, and M. J. Rabe. 2004. Selection of gambel oak roosts by southwestern myotis in ponderosa pine-dominated forests, Northern Arizona. Journal of Wildlife Management 68:595–601.

Betts, B. J. 1998. Roosts used by maternity colonies of silver-haired bats in northeastern Oregon. Journal of Mammalogy 79:643–650.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Carter, T. C. 1998. The foraging ecology of three species of bats at the Savannah River Site, South Carolina. Thesis, University of Georgia, Athens, USA.

Carter, T. C., M. A. Menzel, B. R. Chapman, and K. V. Miller. 2004. Partitioning of food resources by synoptic eastern red (*Lasiurus borealis*), Seminole (*L. seminolus*) and evening (*Nycticeius humeralis*) bats. American Midland Naturalist 151:186–191.

Chapman, S. S., and B. R. Chapman. 1990. Bats from the coastal region of southern Texas. Texas Journal of Science 42:13–22.

Clem, P. D. 1993. Foraging patterns and the use of temporary roosts in female evening bat, *Nycticeius humeralis*, at an Indiana Maternity Colony. Proceedings of the Indiana Academy of Science 102:201–206.

Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451–460.

Elmore, L. W., D. A. Miller, and F. J. Vilella. 2004. Selection of diurnal roosts by red bats (*Lasiurus borealis*) in an intensively managed pine forest in Mississippi. Forest Ecology and Management 199:11–20.

Goebel, P. C., B. J. Palik, and L. K. Kirkman. 1997. Landscape ecosystem types of Ichauway. Joseph W. Jones Ecological Research Center, Technical Report 97-1, Newton, Georgia, USA.

Humphrey, S. R. 1975. Nursery roosts and community diversity of nearctic bats. Journal of Mammalogy 56:321–346.

Jennings, W. L. 1958. The ecological distribution of bats in Florida. Dissertation, University of Florida, Gainesville, USA.

Kalcounis-Rüppell, M. C., J. M. Psyllakis, and R. M. Brigham. 2005. Tree roost selection by bats: an empirical synthesis using meta-analysis. Wildlife Society Bulletin 33:1123–1132.

Kunz, T. H. 1982. Roosting ecology of bats. Pages 1–55 *in* T. H. Kunz, editor. Ecology of bats. Plenum, New York, New York, USA.

Kurta, A. 1985. External insulation available to a non-nesting mammal, the little brown bat, *Myotis lucifugus*. Comparative Biochemistry and Physiology 82:413–420.

Landers, J. L., D. H. Van Lear, and W. D. Boyer. 1995. The longleaf pine forests of the Southeast: requiem or renaissance. Journal of Forestry 93:39–44.

Menzel, M. A., T. C. Carter, W. M. Ford, and B. R. Chapman. 2001. Tree roost characteristics of subadult and female adult evening bats (*Nycticeius humeralis*) in the upper Coastal Plain of South Carolina. American Midland Naturalist 145:112–119.

Menzel, M. A., T. C. Carter, W. M. Ford, B. R. Chapman, and J. Ozier. 2000. Summer roost tree selection by eastern red, Seminole, and evening bats in the upper Coastal Plain of South Carolina. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 54:304–313.

Menzel, M. A., D. M. Krishon, T. C. Carter, and J. Laerm. 1999. Notes on tree roost characteristics of the northern yellow bat (*Lasiurus intermedius*), the Seminole bat (*L. seminolus*), the evening bat (*Nycticeius humeralis*), and the eastern pipistrelle (*Pipistrellus subflavus*). Florida Scientist 62:185–193.

Miller, D. A., E. B. Arnett, and M. J. Lacki. 2003. Habitat management for forest bats of North America: a critical review of habitat studies. Wildlife Society Bulletin 31:30–44.

National Commission on Science for Sustainable Forestry. 2005. Summary report of the National Commission on Science for Sustainable Forestry (NCSSF). NCSSF Project 9C, Washington, D.C., USA.

Ormsbee, P. C., and W. C. McComb. 1998. Selection of day roosts by female long-legged myotis in the central Oregon Cascade Range. Journal of Wildlife Management 62:596–603.

Owen, S. F. 2000. Impacts of timber harvest in the central Appalachians hardwood region on bat foraging and roosting behavior. Thesis, University of Georgia, Athens, USA.

Owen, S. F., M. A. Menzel, W. M. Ford, J. W. Edwards, B. R. Chapman, K. V. Miller, and P. B. Wood. 2002. Roost tree selection by maternal colonies of northern long-eared myotis in an intensively managed forest. U.S. Department of Agriculture Forest Service General Technical Report NE-292, Newtown Square, Pennsylvania, USA.

Paxton, B. J., M. D. Wilson, and B. D. Watts. 2004. Relationships between standing dead wood dynamics and bird communities within North Carolina pine plantations. College of William and Mary, Center for Conservation Biology, Technical Report Series CCBTR-04-08, Williamsburg, Virginia, USA.

Rabe, M. J., T. E. Morrell, H. Green, J. C. DeVos, Jr., and C. R. Miller. 1998. Characteristics of ponderosa pine snag roosts used by reproductive bats in northern Arizona. Journal of Wildlife Management 62:612–621.

Racey, P. A. 1988. Reproductive assessment in bats. Pages 31–43 *in* T. H. Kunz, editor. Ecology and behavioral methods for the study of bats. Smithsonian Institution, Washington, D.C., USA.

Stoddard, H. L. 1931. The bobwhite quail: its habits, preservation and increase. Charles Scribner and Sons, New York, New York, USA.

United States Fish and Wildlife Service. 2003. Recovery plan for the red-cockaded woodpecker (*Picoides borealis*): second revision. U.S. Fish and Wildlife Service, Atlanta, Georgia, USA.

Vonhof, M. J., and R. M. R. Barclay. 1996. Roost-site selection and roosting ecology of forest-dwelling bats in southern British Columbia. Canadian Journal of Zoology 74:1797–1805.

Waldien, D. L., J. P. Hayes, and E. B. Arnett. 2000. Day-roosts of female long-eared myotis in western Oregon. Journal of Wildlife Management 63:785–796.

Wear, D. N., and J. G. Greis. 2002. The southern forest resource assessment: summer, report. U.S. Department of Agriculture Forest Service General Technical Report SRS-54, Asheville, North Carolina, USA.

Weller, T. J., and C. J. Zabel. 2001. Characteristics of fringed myotis day roosts in northern California. Journal of Wildlife Management 65: 489–497.

Wigley, T. B., D. A. Miller, and G. K. Yarrow. In press. Planning for bats on forest industry lands in North America. *In* M. J. Lacki, J. P. Hayes, and A. Kurta, editors. Bats in forests: conservation and management. Johns Hopkins, Baltimore, Maryland, USA.

Wilkinson, G. S. 1992. Information transfer at evening bat colonies. Animal Behavior 44:501–518.

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