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Habitat Relations

Resource Utilization by Foraging Eastern Red Bats (*Lasiurus borealis*) in the Ozark Region of Missouri

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ABSTRACT Resource selection by animals influences ecological processes such as dispersal, reproduction, foraging, and migration. Little information exists regarding foraging resource selection by bats during the maternity season. We evaluated support for effects of landcover type, landform, and landscape pattern on resource selection by individual foraging female eastern red bats (*Lasiurus borealis*) during the maternity period and compared resource utilization for all individuals pooled (population level), individuals grouped by geographic location, and individuals grouped by stage of lactation (early, mid, and late). We used a resource utilization function (RUF) to relate landcover and landscape attributes to the utilization distributions of individual bats estimated by the fixed-kernel method. We radio-tracked 64 lactating red bats and estimated utilization distributions for 52 individuals. Mean home range size ranged from 1,041 to 1,588 ha from late to mid lactation. The global RUF model was significantly better than the null RUF model for 36 (70%) individuals and the magnitude and direction of coefficients varied among individuals. Resource utilization at the population level was, on average, positively related to ridges and upland drainage landforms, water landcover, and road density; and negatively related to urban and nonforest landcover and distance to edge. Resource use differed between geographic areas by canopy cover, water landcover, and road density. Canopy closure was positively related to RUF in both areas but was greater in the south area. Percent water negatively related to RUF in the north area and positively related in the south area. Road density had a positive relationship in the north and negative relationship in the south with RUF. We did not find a difference in mean RUF coefficients among lactation groups except for canopy cover. On average, canopy cover had a positive effect on use by bats during early and mid-lactation but a negative effect during late lactation. We suggest that management for red bats consider landscape components and provide a range of composition and structural diversity to enhance foraging use by red bats. In highly forested landscapes, gaps or openings may provide forest edges that are important for foraging and commuting. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS eastern red bat, foraging, *Lasiurus borealis*, resource utilization distribution.

Insectivorous bats play key functional roles as predators of insects in temperate ecosystems and declining populations of this diverse mammalian group have been a concern of resource management and conservation agencies worldwide for several decades (Kunz and Racey 1998, Hutson et al. 2001, Racey and Entwistle 2003). Bat numbers are declining because of direct persecution, habitat loss, roost disturbance, environmental contaminants (Hutson et al. 2001), wind turbines (Horn et al. 2008), and climate change (Rebelo et al. 2010). Since 2006, a disease epidemic, white-nose syndrome (WNS) associated with the fungal pathogen *Psuedogymnoascus destructans* (*Geomyces*) (Gargas et al. 2009, Minnis and Lindner 2013), has resulted in large declines in hibernating species in the eastern United States and Canada (Langwig et al. 2012).

Effective management for bat conservation is dependent on our understanding associations between bat populations and their use of resources. Resource selection is a multilevel, hierarchical behavioral process used by a species to obtain, directly or indirectly, elements needed to survive, reproduce, and persist (Johnson 1980, Senft et al. 1987). Studies of resource selection generally assume that high quality resources will be used more than low quality ones, that availability is not uniform, and that use of a resource may change with availability (Manly et al. 2002).

Despite the importance of such information, resource relationships are poorly understood for most bat species. Bats are highly mobile, which allows them access to a wide range of resources. Historically, foraging resource use has been viewed as secondary to roost selection in terms of bat conservation (Kunz 1982). Loss or modification of roosting

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and foraging habitat, or their juxtaposition, may affect critical life-history parameters, such as birth rate or adult survivorship. Recent advances in radio-tracking have allowed for significant progress in our understanding of bat–resource relationships (Barclay and Brigham 1996, Fenton 2003), but there continues to be a lack of information regarding use of foraging habitat by bats (Lacki et al. 2007). Factors potentially influencing the areas used by foraging bats include prey abundance (Barclay 1985), energetic costs associated with flight mechanics (Aldridge and Rautenbach 1987, Brigham et al. 1997), ability to detect and locate prey (Simmons and Stein 1980, Griffin and Thompson 1982, Neuweiler 1989, Fenton and Griffin 1997), risk of predation (Lesiński et al. 2009), proximity of water, and level of human disturbance in the foraging area (Ford et al. 2006).

Resource selection is often determined by comparing used to available resources, but in practice, it is often difficult to assess availability from an animal's point of view (Boyce et al. 2002). Quantification of availability usually consists of a priori or a posteriori measure of the abundance of resources in a defined area using classification-based methods that place animal locations into distinct habitat categories for analysis (Conner et al. 2003, Miller et al. 2003). In contrast, the resource utilization function (RUF) approach (Marzluff et al. 2004, Millspaugh et al. 2006) uses a probability density function (Silverman 1986) that quantifies an individual's or group's use of space in a continuous and probabilistic way (Kernohan et al. 2001). The probability density function is often a kernel-based utilization distribution (UD) and depicts the probability of an animal occurring at each location within its home range as a function of relocation points (White and Garrott 1990:146). The UD has been used to relate relative space use to resource attributes in a spatially explicit way using the RUF approach (Marzluff et al. 2004).

Widespread or abundant bat species, such as eastern red bats (*Lasiurus borealis*), may be the most ecologically and economically important species because of their role in ecosystem health (Pierson 1998). Eastern red bats (subsequently referred to only as red bats) are a migratory, tree dwelling species that roost singly in tree canopies where they hang from leaf petioles or small branches (Perry and Thill 2003, Amelon 2007). Red bats are being killed in high numbers at wind turbines across the continent (Kunz et al. 2007, Winhold et al. 2008). By 2020 an estimated 33,000 to 111,000 migratory bats will be killed annually by wind turbines in the Mid-Atlantic Highlands alone (Kunz et al. 2007). An improved understanding of important site and landscape resources may improve conservation efforts for this species.

Red bats consume diverse prey species that include Lepidopterans, Coleopterans, Ephemeropterans, and Hymenopterans (Whitaker 1972, Carter et al. 1998, Clare et al. 2009). Red bats have been reported to use open habitats along the edge of forested areas, agricultural fields, roadways (Salcedo et al. 1995, Saugey et al. 1998), above the tree canopy (Barclay et al. 1999), upland and bottomland hardwoods, pine forest, clearcuts, and nonforest areas (Hickey 1987, Carter 1998, Hutchinson and Lacki 1999, Mager and Nelson 2001). Because red bats seem to use a variety of habitats for foraging, the landscape context and/or foraging resources used at different life-history stages may be important to meet the diet requirements or other fitness characteristics.

Our objectives were 1) to evaluate support for effects of landcover type, landform, and landscape pattern on resource use by individual foraging female red bats during the maternity period and at a population level when individual bat RUFs are averaged (Marzluff et al. 2004, Millspaugh et al. 2006) and 2) to compare resource use among individuals grouped by geographic area (north or south), and stage of lactation (early, mid, and late). We hypothesized that female red bats would forage in locations that optimize conditions for fast flight, including ridgetops and drainages, and along edges (nonforest next to forest) and/or in locations conducive to obtaining water or commuting, including along linear features (such as rivers or roads; Salcedo et al. 1995, Saugey et al. 1998, Hutchinson and Lacki 1999). We hypothesized that diverse landcover types may increase use by either creating additional edge or providing a wider variety of resource options (Hutchinson and Lacki 1999, Elmore et al. 2005). We also hypothesized foraging area would increase through lactation or at least might change from early to late lactation because foraging patterns of females would potentially reflect changing needs of pup development. Specifically, that as females are able to leave pups for longer periods between nursing bouts, they would use resources farther from roosting sites (Barclay 1989).

STUDY AREA

We studied red bats in 2 geographic areas within the Salem Plateau physiographic region within the Ozark Highlands aquatic sub-region of Missouri (Sowa et al. 2005; Fig. 1). These areas were primarily within the administrative boundaries of the Houston-Rolla and the Eleven Point Ranger Districts of the Mark Twain National Forest and represent a range of management practices that result in savanna, woodland, and forest communities. The southern

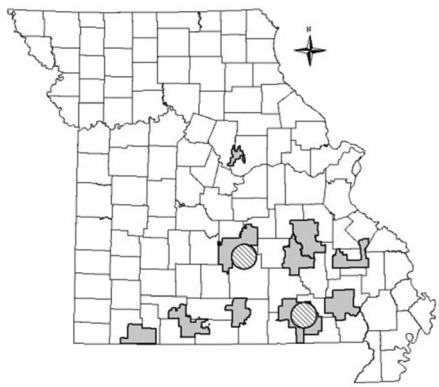

Figure 1. Location of 2 study areas for trapping and radiotracking foraging female red bats in the Ozark Region of Missouri 2001–2003. Circles with cross hatch indicate location of telemetry study, gray shaded units represent Mark Twain National Forest Administrative boundaries.

area focused on a 4,100-ha pine-savanna restoration area. The landscape within a 10-km buffer of the area was 8% nonforest and 92% forest. Land cover within the uplands was primarily shortleaf pine (*Pinus echinata* Mill.) and mixed shortleaf pine with black oak (*Quercus velutina*), scarlet oak (*Q. coccinea* Muench), and white oak (*Q. alba*) and an open understory of grasses such as big and little bluestem (*Andropogon gerardii* Vitman., *Schizachyrium scoparium* Michx.). Occasional prairie and savanna openings were also common in areas along river bluffs. The northern area focused on a 1,500-ha oak-savanna restoration area. The landscape within a 10-km buffer was 41% nonforest and 59% forest. Land cover within the uplands consisted of open woodlands and savannas comprised of post oak (*Quercus stellata* Wang.), black oak, and white oak and an understory of grasses such as big and little bluestem. The predominant forest management on both areas was thinning, even- and uneven-aged regeneration, and landscape-scale prescribed fire.

METHODS

Capture and Telemetry

We captured and tracked bats over 3 maternity seasons (1 Jun–15 Aug 2001–2003). We identified available trapping locations throughout each area (suitable ponds and streams) where mist nets could be used to catch bats and randomly selected a subset of these. We captured bats in mist nets and assessed reproductive condition of females by palpation and visual examination. We classified females as pregnant if a fetus was present, lactating if milk was expressed from mammary glands, or post-lactating if hair was absent around nipples and we saw no evidence of active milk production. We later classified each radio-tracked bat into 1 of 3 lactation periods based on the observations of the bat and its pups. Parturition in red bats in Missouri typically occurs between 28 May and 14 June. Because actual dates are difficult to determine and varied by year, we estimated a mean parturition date in each year as the mean date of pregnant bat captures. Mean parturition date estimates were 2 June, 6 June, and 9 June for years 2001, 2002, and 2003, respectively. Early lactation was from parturition to approximately 26 days post-parturition and when the pups were non-volant. Mid lactation was approximately 27–52 days post-parturition and when pups were mostly non-volant but beginning to fly short distances. Late lactation (and post-lactation) was from approximately 52 days post-parturition to the end of the monitoring period when pups were volant and weaned.

We attached either a 0.6-g (±0.02; Blackburn, Nacogdoches, TX) or a 0.52-g (±0.02; model LB-2, Holohil Systems, Inc., Ontario, Canada) radio transmitter to bats by clipping hair between the scapulae and using non-toxic surgical glue (Skin-Bond, Smith and Nephew United, Largo, FL). We selected the transmitter type such that the transmitter package was <5% of body weight (4.4 ± 0.5%; Sikes and Gannon 2011). We released bats at the point of capture and monitored initial movements on the night of release to determine approximate direction of flight from the release site, but we did not use locations from the night of release in analyses. We alternated between which area (North or South) was trapped first annually to reduce seasonal bias between areas. We captured and fit transmitters on bats until 10–15 individuals were tagged within a study area (active area) and began capture and tagging in the alternate area when the number of tagged bats in the active area was <5. We continued monitoring the remaining bats in the active area while beginning capture and tagging activities in the alternate area. All activities were conducted according to University of Missouri animal care and use protocol #4451.

We radio-tracked bats using receivers (Model R2000/2100; Advanced Telemetry Systems, Isanti, MN) and 5-element antennas mounted on vehicles (RA-4A VHF; Telonics, Mesa, AZ) or 14-element antennas (RA-4C VHF; Telonics) mounted 9 m above the ground on a receiver tower (Woeck et al. 2002, Amelon et al. 2003). We determined geographic coordinates of tower locations with a global positioning system (GPS) with 1–3-m accuracy (Trimble, Sunnyvale, CA) and of mobile positions with a GPS with 5–7-m accuracy (Garmin^{TM}12XL; Garmin International, Olathe, KS). We measured compass azimuths with an electronic compass and digital readout (C100^{TM} Compass Engine, accuracy ± 0.5°; KVH Industries, Inc., Middletown, RI) calibrated to eliminate interference from mounting materials.

We radio-tracked all bats every night for the life of the transmitter (10–21 days) or until the transmitter fell off the bat. Two observers at towers and 2–4 observers in vehicles obtained simultaneous azimuths for triangulation. We obtained simultaneous azimuths each night at pre-specified times and by an atomic clock to synchronize time. We offset scheduled location times each night by rotating the order of bats so that locations represented the range of times each bat foraged (2015 to 0600 hours). We attempted to determine each bat's location at least once per hour during the night. We estimated azimuths as the center of the bisected angle between the nulls (Fuller et al. 2005, Amelon et al. 2009). Observers at towers and vehicles were usually <1,500 m and <700 m, respectively, from bats being tracked because of the relatively short range of the transmitters. We communicated by radios or cellular telephones to confirm azimuths and to determine if observers needed to relocate to a better location for taking azimuths.

We determined standard deviations of directional azimuths and azimuth error for each observer based on 6 receiver locations with stationary transmitters placed in multiple locations throughout the study area and with transmitters attached to a fiberglass pole mounted to a vehicle and driven at 5 mph within the study area. Locations of these transmitters were logged by time with a GPS (White and Garrott 1990). Azimuth standard deviation averaged ± 4.1° and ranged from 1.7° to 7.7° for individual observers. We estimated bat locations from azimuths with the computer program GTM (Sartwell 2003) using the Length maximum likelihood estimator (MLE) with estimated azimuth standard deviation for each observer (White and Garrott 1990). We did not use locations with error polygons greater

than 15 ha. Error polygons of relocations used in the analysis had a mean size of 4.1 ± 0.11 ha.

Estimating the Utilization Distribution (UD)

We entered bat locations determined by triangulation or visual observations onto a georeferenced base map using ArcInfo GRID® and Arc-View 3.2 (Environmental Systems Research Institute, Inc., Redlands, CA). We considered only bats with >30 locations for analysis because 30–50 locations are sufficient to accurately estimate a home range using kernel-based methods (Seaman et al. 1999). We estimated UDs using fixed-kernel estimation and the KDE folder (Beardah and Baxter 1995) in MATLAB (version 5.3 (R11); MathWorks, Inc., Natick, MA). We used the plug-in method (Gitzen et al. 2006) and smoothed the x and y coordinates independently. We used 99% kernel isopleths to delineate foraging areas (Millspaugh et al. 2006). We excluded the outer 1% of the UD (by volume) to reduce potential bias from lowest use areas of the UD (Millspaugh et al. 2006). Foraging areas only include roost locations if the bat was actively foraging near the roost location at a scheduled reading.

Patch and Landscape Covariates

We measured landcover, landform, distance to edge and canopy cover at each grid point in each bat's UD by intersecting individual bat UDs with georeferenced landscape data using ArcInfo® GRID functions. We derived landscape data from 30-m × 30-m resolution Landsat Thematic Mapper satellite imagery classified into 16 vegetative land cover classes (Missouri Resource Assessment Partnership 2002). We condensed 16 land cover classes to 6 landcovers: 1) deciduous forest and woodland composed of oak, hickory, and mixed hardwood forest types; 2) pine and oak-pine forest and woodland composed of shortleaf pine and oak-pine types; 3) bottomland hardwoods composed of sycamore (*Platanus occidentalis*), cottonwood (*Populus deltoides*), elm (*Ulmus americana, U. rubra*), ash (*Fraxinus pennsylvanica*), and mixed hardwood types; 4) nonforest consisting of cool or warm season grassland with forbs and shrubs; 5) urban representing non-vegetated areas; and 6) water including swamp, marsh, wet herbaceous, and open water habitats.

We derived 4 landforms from a digital elevation model (DEM) using a Topographic Position Index, which is the elevation of a particular cell minus the mean elevation of cells in a moving window neighborhood divided by the standard deviation of the mean cell elevation (Jenness 2006). We evaluated a cell's elevation compared to the large scale variation and small scale variation in elevation to define 4 landform classes: lowlands, upland drainage, slopes (>5% slope), and ridges (<5% slope; Tirpak et al. 2007). We calculated distance (m) to the nearest edge between nonforest and forest cover types. We obtained percent canopy cover from Moderate Resolution Imaging Spectroradiometer (MODIS) data which is measured from the National Aeronautics and Space Administration's Terra spacecraft and represents the amount of skylight obstructed by tree canopies equal to or greater than 5 m in height on a 500-m pixel (Hansen et al. 2003). We combined the water class from the landcover classification with the county-level perennial stream coverage (Missouri Spatial Data and Information System [MSDIS] 2004) to identify water sources. We used a county-wide road and trails layer (MSDIS 2004) to calculate road density (m/ha). We calculated landscape diversity as the Shannon–Weaver diversity index based on the amount of each landcover.

Resource Utilization Functions

We evaluated support for our hypotheses that resource use was related to landform, landcover, distance to edge, and landscape diversity. We treated slopes and deciduous forest as the reference categories for landform and landcover, respectively, which resulted in the following global model: RUF = β (intercept) + [β(ridge) + β(lowlands) + β(upland drainage)] + [β(nonforest) + β(percent water) + β(mixed forest) + β (urban)] + [β(dist forest edge) + β(road density)] + [β(diversity index) + β(percent forest canopy)]. We also fit a null model: (RUF = β(intercept)).

We fit RUF for each individual bat (Type III design of Manly et al. 2002) in PROC MIXED (SAS, version 9.1, SAS Institute, Cary, NC). We estimated resource use at each grid cell in the UD as the average height of the kernel density estimate and related this continuous measure of use to the covariates using multiple linear regression (Marzluff et al. 2004). We examined the covariates in the model for multicollinearity and it was low (tolerance values 0.74–0.91; PROC REG, SAS, version 9.1). The kernel analysis induced correlation among adjacent cells in the UD and this spatial autocorrelation can result in underestimation of variance estimates if not considered in the model (Marzluff et al. 2004) but does not affect the parameter estimates (McCullagh and Nelder 1983). We compared our global model to the null model using an objective model selection criterion (Akaike's Information Criterion [AIC]; Burnham and Anderson 2002) and a likelihood ratio test.

We calculated average RUFs based on all individuals (the population) and individuals in geographic areas and lactation groups. We calculated parameter estimates for the averaged RUFs as the arithmetic means of the unstandardized coefficients across animals and the variance of each coefficient as per Equation 2 in Millspaugh et al. (2006). We tested the hypothesis that each coefficient in the population (or group) RUF was 0 with a t-test (alpha = 0.95); coefficient values significantly greater than 0 indicated use of a resource was greater than expected and coefficients significantly less than 0 indicated use of a resource less than expected. We tested the hypothesis that resource utilization was different among lactation groups or between geographic areas for each covariate using analysis of variance (PROC ANOVA, version 9.1, SAS Institute).

RESULTS

We radio-tracked 64 lactating red bats for 3–21 days. We estimated UDs for 52 individuals with >30 foraging locations ($\bar{x} = 79$, range 31–163) that represented 43 bats in the north area and 9 in the south area and 18, 20, and 14

Figure 2. Examples of utilization distributions of foraging red bats in the Ozark Region of Missouri 2001–2003, (a) bat 150944 and (b) bat 151600. Colors indicate intensity of use: black highest use to white lowest use.

bats in early, mid, and late lactation, respectively. Most bats had an area of high use near their roosts and multiple areas of lower use (Fig. 2). Mean home range size was 1,357 ha and ranged from 202–3,727 ha (See Table S1, available online at www.onlinelibrary.wiley.com). Mean home range sizes were 1,329, 1,587, and 1,041 ha for early, mid, and late lactation, respectively, and 1,323 and 1,516 ha for the north and south geographic areas, respectively (Table 1). A regression analysis indicated no relationship between the number of locations or days tracked and home range size across all individuals ($r^2 = 0.086$, $P = 0.50$ and $r^2 = 0.076$, $P = 0.55$, respectively). The maximum foraging distance observed during this study was 20 km.

We found differences in resources in the north and south geographic areas, which were reflected in the landscape and habitat attributes within 99% isopleths of UDs of bats in those respective areas. Utilization distributions from bats in the north area included less canopy cover, distance to water, and deciduous forest; and greater road density and nonforest area than bats in the south area (Table 2).

The global RUF model was better ($P < 0.05$) than the null RUF model for 36 (70%) individuals (Table S2, available online at www.onlinelibrary.wiley.com). Across the sample of individuals, resource utilization was positively related to ridge and upland drainage landforms, water landcover, and road density; negatively related to urban landcover and distance to edge for 70% of individuals; and negatively related to nonforest landcover for 58% of individuals (Table S2, available online at www.onlinelibrary.wiley.com). We found variation among individuals in magnitude and direction of coefficients for each variable; this is particularly evident in box plots that show the percentile distribution of coefficients for individual bats grouped by geographic area and lactation groups (Fig. 3).

We found significant effects of landscape and habitat covariates when we pooled all individuals and averaged coefficients at the population level (Table 3, Figs. 4 and 5). On average, use was positively related to ridges and upland drainage landforms relative to slopes, the reference category (Table 3). Probability of use decreased with urban and nonforest and increased with water relative to deciduous forest (Table 3); urban landcover had the lowest probability of use (Fig. 4). The probability of use decreased with distance to edge, but increased with road density (Table 3, Fig. 5).

Patterns in resource use were similar to the population level for individuals pooled by geographic area or lactation group, but some effects did vary between groups (Fig. 3). On average, canopy cover was positively related to resource use in both the north and south geographic areas but greater in the south area (ANOVA, $F_{1,\ 50} = 16.3$, $P < 0.001$). Percent water was negatively related to resource use in the north and positively related in the south (ANOVA, $F_{1,\ 50} = 9.1$, $P = 0.004$). Road density was positively related to resource use in the north but not the south (ANOVA, $F_{1,\ 50} = 6.0$, $P = 0.018$). All other coefficients did not differ between geographic areas (ANOVA, $F_{1,\ 50} < 5.3$, $P > 0.05$; Fig. 3). We did not find a difference among lactation groups in mean RUF coefficients (ANOVA, $F_{2,\ 49} < 4.0$, $P > 0.05$; Fig. 3) except for canopy cover (ANOVA, $F_{2,\ 49} = 5.6$, $P = 0.007$). On average, increasing canopy cover had a positive effect on use by bats during early and mid-lactation but a negative effect during late lactation (Fig. 3).

DISCUSSION

We evaluated 99% UDs to estimate use area and developed RUFs to investigate factors affecting foraging habitat utilization by female red bats during the maternity period. Home range size and resource use varied among individuals

Table 1. Home-range size based on 99% fixed-kernel isopleths of foraging red bats in the Ozark Region of Missouri 2001–2003 by full group of individuals, lactation groups (early, mid, late), and geographic location groups (south, north).

Lactation group	*n*	Mean (ha)	SE	Min. (ha)	Max. (ha)
All bats	52	1,357.12	122.21	201.57	3,727.63
Early	18	1,329.30	182.63	206.59	3,505.95
Mid	20	1,587.68	194.29	523.58	3,608.21
Late	14	1,040.94	267.46	201.57	3,727.63
South	9	1,515.84	333.17	206.59	3,505.95
North	43	1,323.11	131.59	201.57	3,727.63

Table 2. Landscape and habitat attributes within 99% isopleths of utilization distributions for red bats in 2 landscapes (north, south) in the Ozark region of Missouri, 2001–2003.

	North ($n = 43$)		South ($n = 9$)	
Variable	**Mean**	**SE**	**Mean**	**SE**
Landscape diversity	1.6	0.02	1.3	0.03
Percent canopy	52.2	0.98	69.6	1.39
Percent water	3.1	0.18	1.2	0.20
Distance to edge (m)	125.1	7.14	335.2	36.32
Road density (m^2/ha)	70.2	3.72	23.4	1.19
Percent bottom	21.6	0.93	27.0	1.48
Percent ridge	40.5	0.85	37.4	1.70
Percent upland drainage	7.4	0.26	6.6	0.22
Percent slope	30.5	1.18	29.0	2.66
Percent mixed forest	8.9	0.31	5.1	1.36
Percent nonforest	22.3	2.08	5.3	1.96
Percent urban	5.9	0.63	0.3	0.21
Percent water	3.1	0.20	1.2	0.22
Percent deciduous forest	60.0	2.12	88.2	2.37

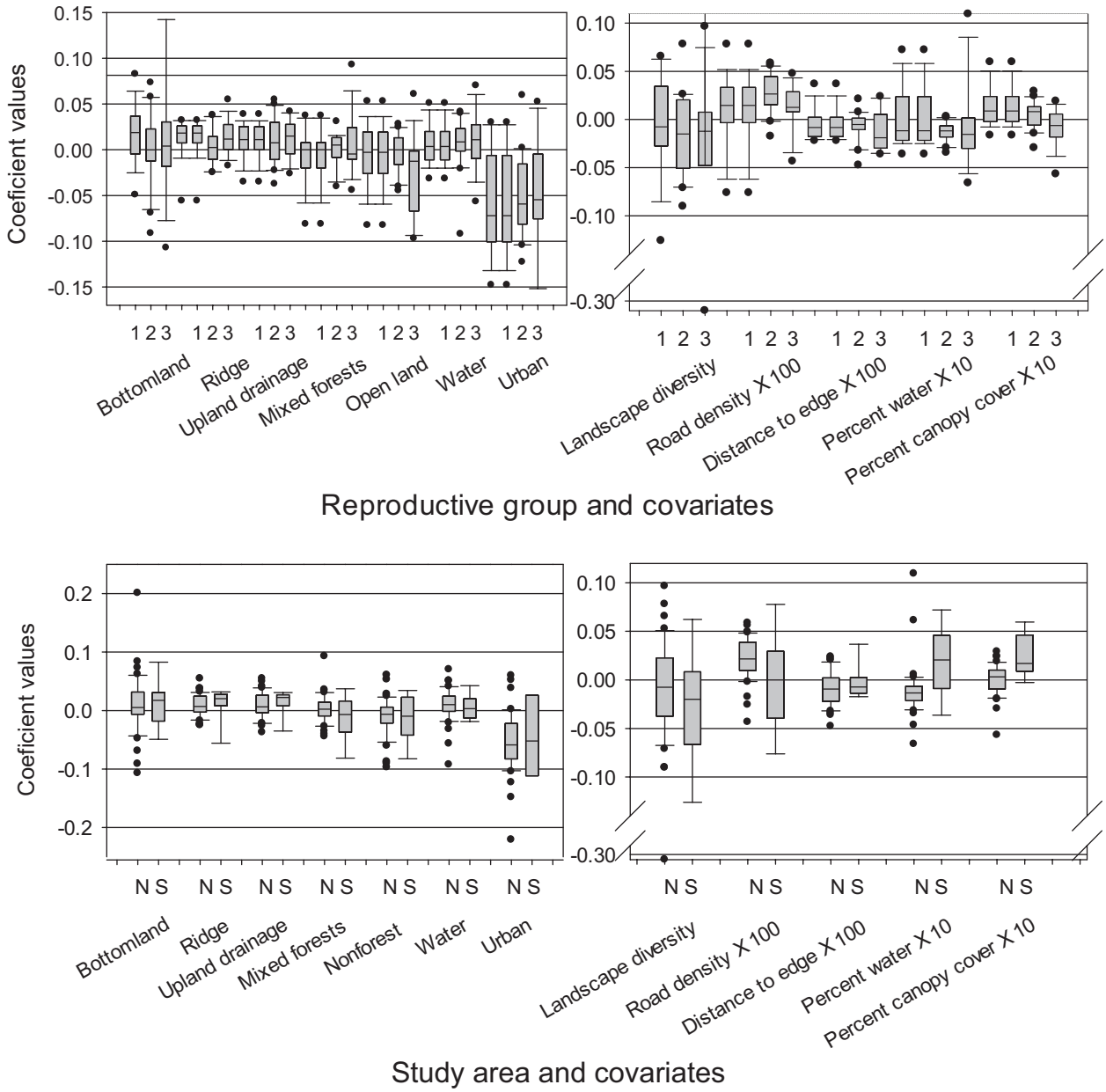

Figure 3. Mean (line), 25th and 50th percentiles (shaded box), 5th and 95th percentiles (error bars) and outlying values of regression coefficients (circles) for groups of foraging female red bats in (a) early (1; $n = 18$), mid (2; $n = 20$), and late (3; $n = 14$) lactation and (b) north (N; $n = 43$) or south (S; $n = 9$) geographic areas in the Ozark Region of Missouri 2001–2003.

Table 3. Mean unstandardized resource utilization function coefficients for 52 red bats in the Ozark Region of Missouri 2001–2003.

Variable	Coefficient	SE	*P*-value	Number coefficients	
				+	−
Intercept	0.0898	0.02479	<0.001		
Bottom	0.0105	0.00653	0.114	30	22
Ridge*	0.0096	0.00269	<0.001	38	14
Upland drainage*	0.0106	0.00298	<0.001	37	15
Slopes					
Mixed forest	0.0001	0.00372	0.982	26	25
Nonforest*	−0.0092	0.0046	0.050	22	30
Urban*	−0.0538	0.00719	<0.001	7	43
Water*	0.0078	0.00369	0.039	37	15
Deciduous forest					
Distance to edge (m)*	−0.0001	0.00002	0.002	15	37
Landscape diversity	−0.0155	0.00858	0.076	20	32
Percent canopy cover	0.0005	0.00026	0.094	33	19
Percent water	−0.0006	0.00041	0.161	13	39
Road density (m^2/ha)*	0.0002	0.00004	<0.001	43	9

Significant effects are indicated with an asterisk (*). Last columns refer to number of individual bats with positive (+) or negative (−) coefficient values.

but, nevertheless, the RUFs at the population level still maintained strong relationships with some resource factors. Foraging use was, on average, greatest for deciduous forest patches on ridges and upland drainages in areas close to nonforest edge, with relatively high road density, and away from urban areas. Our analysis of RUFs for individual bats resulted in several important considerations for resource use studies of bats. Use at a landscape or geographic scale may be an important component for bat studies because of red bats' ability to cover large areas very quickly. The high variation in resource use among individuals in this study may simply indicate lactating red bats are capable of behavioral plasticity when faced with the demands of foraging versus the need to provide energy for the growth and development of young or it may indicate use is influenced by the interaction of site and landscape components (vegetative composition and distribution patterns) within a larger geographic region.

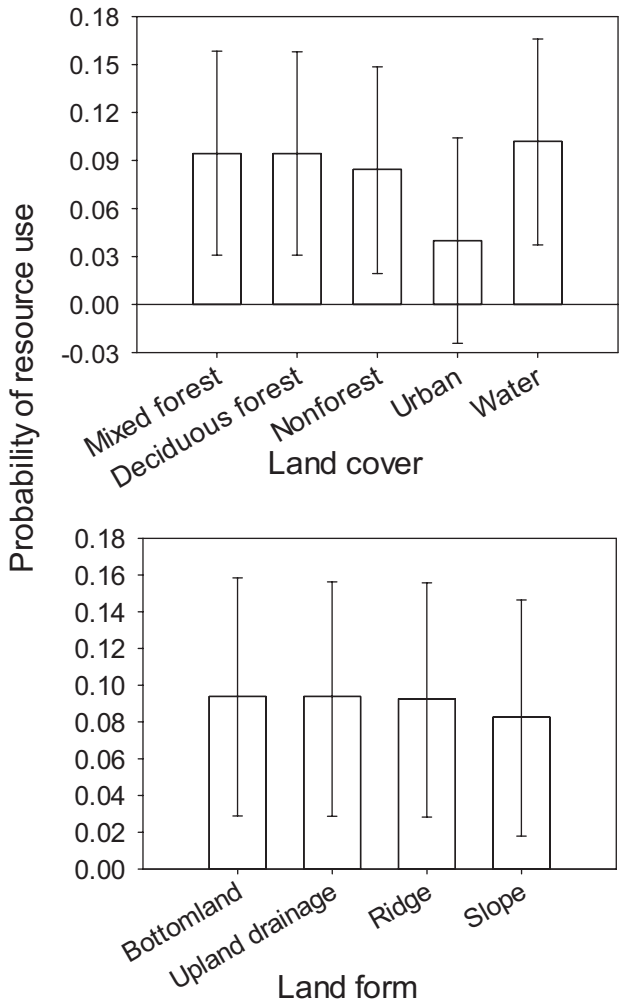

Figure 4. The relationship between land form and land cover with resource use by red bats in the Ozark Region of Missouri 2001–2003 (+95% CI).

Home ranges were among the largest reported for temperate insectivorous bats. Previously reported mean home ranges for red bats were 176 and 444 ha for reproductive and non-reproductive females, respectively, in upland hardwoods in Kentucky (Hutchinson and Lacki 1999), 453 ha in bottomland forest and hardwoods in South Carolina (Carter 1998), 82 ha for adult females in Mississippi (Elmore et al. 2005), and 69 ha for females near Indianapolis airport (Walters et al. 2007). Only 9 of 52 individual home ranges in our study were smaller than 500 ha; the mean (1,357 ha) was nearly 3 times that of other studies reported. Several factors may influence home-range size including study methods, foraging strategy and availability or distribution of food in space and time. The large home ranges in our study may be due to use of the 99% kernel to describe the area, differences in equipment used, or larger scale geographical differences in red bat foraging behavior. Similar numbers of relocations were reported in the previous studies as was use of a kernel-based estimator. The difference in our study between the 95% and 99% kernel would only account for a maximum 60-ha decrease in estimated foraging area; which would not account for the large difference in home range estimates between this and other studies.

The use of radiotelemetry to investigate resource use by small bats is a relatively new technique and most studies have evaluated <10 individuals by demographic group (Miller et al. 2003). Intra-species variation could cause results to be

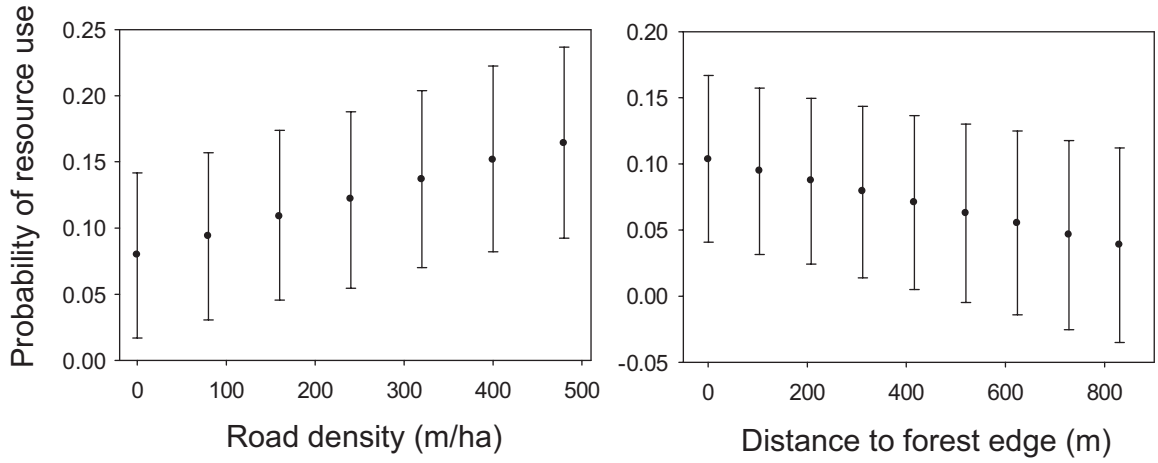

Figure 5. The relationship between distance to forest edge and road density within 1 km with resource use by red bats in the Ozark Region of Missouri 2001–2003 (+95% CI).

skewed, in studies with small sample sizes (Table S1, available online at www.onlinelibrary.wiley.com). Transmitter signals can be detected at greater distances with higher gain receiving antennas. Greater reception range and more precise directionality can be obtained by using larger antennas and elevating receiving antennas (Anderka 1987). Methods used in each of the previous studies used 3-element Yagi hand-held antennas, whereas our study used 5- and 14-element elevated antennas, which allow signals to be heard at greater distances. Our use of an elevated tower system enhanced the reception distance of bat transmitters (Amelon et al. 2003). We also had a mobile crew that allowed us to locate bats even when they moved to more distant locations, in some of the previous studies, bats were noted as leaving the study area but locations were not determined.

Home ranges in our geographic area may differ from those in previous studies. Pine plantations, urban development, and mesophytic deciduous forests may result in different foraging behavior in red bats than in a more xeric deciduous forest because of distribution of watering sites, roosting sites, or availability of insect prey. Additional studies in similar landscapes to previously reported studies using equipment designed to detect signals at greater distances would be needed to determine if red bats do vary in behavior in different forest types or different geographical regions.

Red bats are morphologically adapted for fast, open air flight (Norberg and Raynor 1987, Jung et al. 1999) and migrate over long distances (Cryan 2003). Other species of bats commute over distances of 1–50 km from their roosts to foraging areas; distances that would be easily attainable by red bats (Sahley et al. 1993, Fenton 1997, O'Donnell 2001). As use of distant areas from roost sites increase, larger home ranges would be expected. Use of large areas may indicate bat species have detailed knowledge of habitat patches in their range with high prey availability (Wai-Ping and Fenton 1989, Entwistle et al. 1996), allowing them to maximize food intake by preferentially feeding in such sites (Entwistle et al. 1996). We observed highly predictable foraging behavior on a nightly basis in the majority of our individual bats. Specifically, they had routine routes to specific foraging locations, and often would use the same foraging sites at the same time on a night to night basis. We believe the large areas used by red bats reflect their great mobility (access to more distant areas), adaptable foraging strategy, and dispersion of food resources.

We predicted that size of area used would increase from early to late lactation as juveniles were weaned and became volant based on the hypothesis that lactating females would not have to return as frequently to the roost to nurse pups. However, we found largest areas were used during early and mid-lactation. Red bats may be able to use large areas during early lactation because they are adapted for very fast flight, which may allow them to forage at greater distances from the roost even when nursing young. Additionally, juvenile red bats begin to thermoregulate at a younger age than non-migratory species, which may allow females to be gone for longer periods of time. An alternative hypothesis would be that during early to mid-lactation, energetic demands of the female would be highest and she would need to use areas providing high quality food resources, which could require her to move larger distances to reach these resources. Use of smaller areas in late lactation could potentially be the result of some type of social interaction between mothers and pups when the pups first begin to forage but before they can fly long distances (Masters et al. 1995, Page and Ryan 2006).

At the population level, ridges and upland drainages had a positive influence on use compared to slopes (Table 3), as predicted. Use of these sites may suggest red bats commute to foraging areas by topographic features (Elmore et al. 2005). Water had a positive influence on use, whereas nonforest and urban had a negative effect on use compared to deciduous forest landcover. The probability of use of nonforest was not much less than forest landcovers and 42% of individuals were positively affected (Table 3). Red bats have generally been described as adapted for openland foraging or as an edge associated species (Salcedo et al. 1995, Carter 1998, Saugey et al. 1998, Hutchinson and Lacki 1999, Mager and Nelson 2001). Thirteen female red bats in Indiana selected

new tree fields, pasture, and parks (Walters et al. 2007). In Mississippi, habitat use by 16 red bats of mixed age and sex was random in an intensively managed pine landscape, but this study did not include a nonforest type (Elmore et al. 2005). In our north area, 25 of 43 individuals (58%) had negative coefficients for nonforest landcover and in the south area, 5 of 9 (55%) demonstrated the same negative relationship. This suggests that although red bats use edge habitats, they use forested components more often and there may be an optimum percentage or spatial arrangement of nonforest components. Based on acoustic data from the same area, Amelon (2007) found an upper limit of nonforested component in the landscapes used by red bats. Additionally, roosting studies have consistently found red bats roosting in deciduous uplands (Hutchinson and Lacki 2000, Perry et al. 2007, O'Keefe et al. 2009).

We expected urban landcover to have a positive influence on at least some individual bats. One of 9 bats (11%) in the south area and 15 of 43 (35%) in the north area were visually observed foraging at lights either at rural residences or in rural towns; however, only 7 of the 52 (13%) bats had a positive coefficient for urban landcover. Several individuals had predictable flight paths that began at 1 side of a small town and moved systematically between lights at businesses or residences. McCracken et al. (1997) and Hickey and Fenton (1996) similarly reported red bats concentrating foraging activity around street lights. A close examination of the landcover maps we used indicated that urban was only designated for sites with no vegetative cover. Many individual residences and housing areas where bats were frequently seen had relatively high vegetative cover and were not classified as urban. Our urban landcover was more similar to the industrial land type reported by Limpert et al. (2007) and the commercial type reported by Walters et al. (2007), which were similarly less represented in the 1,000-m buffer surrounding red bat roost sites or less used for foraging, respectively.

As predicted, we found strong associations between red bat resource use and measures of edge. Use decreased with distance to edge and increased with road density (Fig. 5), both indicators of selection of edges created between forest and nonforest areas. Roads provided additional edge and corridors for commuting within the forested landscape. Hart et al. (1993) and Furlonger et al. (1987) similarly found a positive association of red bats with edge components.

On average, percent of water in our landscapes was low (<1%). The southern unit had very low percent surface water; most streams were losing streams (discharging water into subsurface outlets) and very few manmade ponds were present, this low availability of watering sites supports the use of water resources by bats in the southern area. Lactating females roosting in deciduous trees are subject to high water losses during the day and need to drink when foraging (Neuweiler 2000). Red bats use stream corridors for feeding, drinking or commuting (Elmore et al. 2005), wetlands for feeding and drinking (Carter 1998, Hutchinson and Lacki 1999), and bottomland hardwoods for foraging or drinking (Menzel et al. 2003); we predicted the high use of water areas (37 of 52 individuals had a positive parameter coefficient). Although insect abundance is often high close to water features (Nakano and Murakami 2001), we were not able to assess insect abundance.

MANAGEMENT IMPLICATIONS

We saw a strong positive relationship with forested landcover, water, ridges, upland drainages, and edge factors in resource use by red bats. We suggest there may be an upper limit to amount of nonforest in a landscape that red bats will use and that may vary by geographic location. In increasingly human-dominated landscapes, maintaining forested areas over large portions of the landscape may be critical to conservation of red bat populations. Although forest type did not appear to be an important factor determining foraging habitat use, it likely influences roosting ecology (Perry et al. 2007). We suggest management strategies that provide a range of composition and structural diversity will favor foraging use by red bats. As suggested by this and other studies of red bats, landscape context may be an important component in considering management strategy (Elmore et al. 2005, Perry et al. 2007). For example, in highly fragmented landscapes managers may need to enhance the extent of deciduous forest. Whereas, in highly forested landscapes, managers may want to consider creating gaps or openings that offer additional edge resource or linkages between nonforest and watering sites to provide additional foraging or commuting options. However, creation of edge habitats in association with wind facilities along forested ridge tops may contribute to the high fatalities of red bat (Kunz et al. 2007). Future studies should be evaluated at a relatively large landscape level, especially in light of the ever increasing percentage of urban and wind energy development within the range of red bats.

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