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Resource Selection by Indiana Bats During the Maternity Season

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ABSTRACT Little information exists on resource selection by foraging Indiana bats (*Myotis sodalis*) during the maternity season. Existing studies are based on modest sample sizes because of the rarity of this endangered species and the difficulty of radio-tracking bats. Our objectives were to determine resource selection by foraging Indiana bats during the maternity season and to compare resource use between pregnant and lactating individuals. We used an information theoretic approach with discrete choice modeling based on telemetry data to evaluate our hypotheses that land cover, percent canopy cover, distance to water, and prescribed fire affected the relative probability a point was used by a foraging Indiana bat. We fit models for individual bats and a population-level model based on all individuals with a random factor to account for differences in sample size among individuals. We radio-tracked 29 individuals and found variation in resource selection among individuals. However, among individuals with the same supported covariates, the magnitude and direction of the covariates were similar. Eighteen bats selected areas with greater canopy closure and 5 of 6 bats that had areas burned by low-intensity prescribed fire in their home range selected burned areas. Resource selection was related to land cover for 13 individuals; they selected forest and shrubland over agricultural land, which composed >50% of the landscape within 10 km. We found no support for our hypothesis that resource selection was related to individual reproductive condition or Julian date in our population-level model indicating habitat selection was not determined by reproductive status or date within the maternity season. Land use or forest management that greatly reduces canopy cover may have a negative impact on Indiana bat use. Maintaining forest cover in agricultural landscapes is likely critical to persistence of maternity colonies in these landscapes. Sites managed with low severity prescribed fire may be selected by some individuals because of reduced understory vegetation. © 2013 The Wildlife Society.

KEY WORDS discrete choice, foraging, Indiana bat, Missouri, *Myotis sodalis*, resource selection.

Human populations are increasingly modifying landscapes and causing extinctions or decreases in abundance of many wildlife species (Haila 2002, Fischer and Lindenmayer 2007). The Indiana bat (*Myotis sodalis*) has been on the United States Endangered Species List since 1967. Knowledge of how landscape and forest management affect forest wildlife, like the Indiana bat, will allow resource managers to make more informed management decisions that will aid in the recovery of species. Silvicultural practices such as selective harvesting, girdling, and other methods create forest patches with different tree densities and increase snags per hectare for bats and other wildlife (Thomas 1988, Patriquin and Barclay 2003). These management practices may provide roosting and foraging habitat for bats by reducing the structural clutter in the understory (e.g., small trees and shrubs) while keeping the canopy intact, especially during the maternity season (Crampton and Barclay 1998, Patriquin and Barclay 2003). Management techniques that mimic small-scale natural disturbances by wind or fire may be compatible with bat conservation, whereas removal of mature forests likely eliminates bat use since Indiana bats require large trees for roosting (Gardner et al. 1991, Callahan et al. 1997, Britzke et al. 2003, Kurta 2005).

Conservation efforts require better knowledge of foraging resource requirements for female Indiana bats during the maternity season. Most summer studies have focused on roost locations (Gardner et al. 1991, Callahan et al. 1997, Menzel et al. 2001, Britzke et al. 2003, Kurta 2005), whereas few have documented foraging habitats. Indiana bat activity is generally greatest in riparian corridors, upland forests, and bottomland forests (Menzel et al. 2005, Sparks et al. 2005, Carter 2006, Tuttle et al. 2006). Foraging height varies but is typically 2–30 m above the ground and under the forest canopy (Humphrey et al. 1977). Past studies of the summer ecology of Indiana bats did not consider selection at the individual level or by reproductive condition (i.e., pregnancy, lactation, and post-lactation), likely because of the small number of individuals studied (Menzel et al. 2005, Sparks

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et al. 2005). Distances traveled between foraging and diurnal roosting locations are highly variable between reproductive stages (i.e., pregnant or lactating) as well as variable among individuals in the same reproductive status in Indiana (Sparks et al. 2005). However, Sparks et al. (2005) did not investigate differences in resource selection among individuals or reproductive classes. Flight distance and home range size are smaller during lactation than pregnancy in little brown bats (*M. lucifugus*; Henry et al. 2002). Henry et al. (2002) monitored over 50 individuals and demonstrated the importance of studying individual behavior and an adequate sample size. Understanding how bats select resources to meet specific reproductive needs and variation among individuals will aide managers in determining what resources are important for sustaining Indiana bat populations.

Discrete choice models were designed to evaluate customer behavior in the social sciences based on the economic utility theory (Berry 1994) but are also used for wildlife resource selection studies to predict the relative probability of selecting a resource compared to available resources (Cooper and Millspaugh 1999). Our objectives were to determine resource selection by foraging Indiana bats during the maternity season and to compare resource use among pregnant and lactating individuals. We hypothesized Indiana bats would select vegetative conditions that optimize flight and prey capture based on wing morphology and echolocation design (Norberg 1994, Jacobs 1999, Fenton and Bogdanowicz 2002). Indiana bats have low wing loading and aspect ratio, adaptations for slow maneuverable flight around or within clutter. Therefore, we predicted they would prefer managed forest stands with high canopy coverages that were relatively close to water. We used an information theoretic approach with discrete choice modeling to evaluate our hypotheses that land cover, percent canopy cover, distance to water, and prescribed fire affected habitat use by foraging Indiana bats. We fit models for individuals to examine variability in resource selection and a population-level model to evaluate the relationship between resource selection and reproductive status and Julian date. Although we acknowledge that looking at resource selection across sites or landscapes is desirable, we studied individuals intensively at a site to be able to address questions concerning variation among individuals in resources selection—a question not generally addressed for bats.

STUDY AREA

We studied bats during May–July, 2008–2010, at Charles Heath Memorial Conservation Area (CHMCA) in Clark County, Missouri. The 662-ha CHMCA is managed by the Missouri Department of Conservation and is composed of 596 ha of mature upland and bottomland forests and 66 ha of grasslands or idle fields. The uplands are dominated by mature oak-hickory forest typically found in northern Missouri and the mature bottomland forest consists of typical mix species for northern Missouri, including silver maple (*Acer saccharinum*), sycamore (*Platanus occidentalis*), cottonwood (*Populus deltoides*), river birch (*Betula nigra*), and bottomland associated oak species (i.e., pin [*Querus palustris*], swamp [*Querus bicolor*], white [*Querus alba*], bur [*Querus macrocarpa*]). The only recent forest management activities on CHMCA were 2 prescribed fire units (18.2 ha and 14.56 ha) in upland forests managed first in either April 2005 or 2006 and burned annually each April until 2009. The composition of the landscape defined by a 10-km buffer around the center of CHMCA was 56% agricultural (corn, soybeans, and pasture), 27.8% forested (mostly CHMCA), 6.8% shrubland, 3.6% developed, and 4.5% wetland based on the National Land Cover Database 2001 (NLCD; Homer et al. 2004).

METHODS

Capture and Handling

We captured bats with mist nets and harp traps (Tuttle 1974, Kunz and Kurta 1988). We placed each bat in a muslin bag until it was processed. We cleaned bags and equipment and followed the white-nose syndrome decontamination protocol at the time of capture (U.S. Fish and Wildlife Service 2012). We attached radio transmitters weighing 0.43–0.53 g (Holohil Systems Ltd., Carp, ON, Canada) to female Indiana bats that were large enough to carry a transmitter (i.e., transmitter did not exceed 5% of the bat's weight). We trimmed the hair between the shoulder blades of bats with surgical scissors and forceps and glued (Osto-Bond, Montreal Ostomy Inc., Vaudreuil-Dorion, QC, Canada) transmitters to the skin. We placed bats with radio transmitters in a holding bag for 15 minutes to allow the glue to cure. We tried to place transmitters on up to 5 female Indiana bats at a time to maximize field efficiency. Animal procedures were approved under Missouri Department of Conservation permit 14529, Federal permit TE06809A, and University of Missouri Animal Care and Use Committee protocol #4451.

Telemetry

We radio tracked bats by obtaining simultaneous compass bearings from at least 2 locations and triangulated bat locations (Amelon et al. 2009); antennae were either roof-mounted on vehicles (RA-4A model, Teleonics, Mesa, AZ) or on a fixed location 30-foot tower (VHF model, Teleonics). We created a daily monitoring schedule to obtain bearings at intervals of 5–10 minutes, depending on the number of radio tagged animals, and synchronized times of each bearing by using atomic clocks. We tracked all bats from dusk (around 2100 hour) to night roost (0100–0230 hours) and again from about 0300 to dawn (around 0500 hour); monitoring times varied because of variability in individual's night roost time. We monitored all individuals with radio transmitters until the last bat went to night roost for at least 30 minutes. We triangulated locations from bearings and estimated error polygons using the program GTM3 (Sartwell 2000) and excluded locations with error polygons >200 m^2 (mean 42 ± 2.66 m^2) from the analysis.

We selected 3 random points as the choice set for comparison to each bat location. We calculated the maximum distance that an individual bat traveled each night as the greatest distance between all pair wise combinations of locations from a night. We then created a buffer around each

location for each bat for that night using the maximum distance (mean: 2,089 m; range: 289–7,826 m) as the diameter. We selected 3 random points within each bat's buffer area using Hawths tools (ArcGIS; ESRI, Redlands, CA).

Model Covariates

We derived land cover classes and percent canopy cover from the National Land Cover Database from 2001 (NLCD; Homer et al. 2004). We verified the dependability of these coverages by comparing them to National Agriculture Imagery Program 2009 (NAIP) aerial photographs of the study area. Water features in the study area were underrepresented in the NLCD so we digitized all water features from NAIP 2009 photographs and United States Geological Survey quad maps using ArcGIS (ESRI, ver. 9.1). We grouped land use and land cover types from the NLCD into the following land cover categories: shrub-grassland, agriculture, bottomland forest, and upland hardwood forest and assigned each bat location and random point to one of these land cover categories. Since agriculture was the dominant land cover, we used agriculture as the reference category and excluded it from models to avoid linearly dependent covariates. Developed land and wetlands occurred within the 10-km buffer of our study area but no used or random points fell within either category so we did not include them in the analysis. We created an additional land cover category for upland hardwood forest managed with prescribe fire (mULHW) based on boundaries delineated in a polygon shape file provided by Missouri Department of Conservation. We calculated the distance from water (DisW) for each bat location and random point using the near tool in ArcGIS.

Data Analysis

We used an information theoretic approach to evaluate a priori hypotheses using Akaike's Information Criterion (AIC) to rank candidate models in terms of their ability to explain the empirical data for each individual bat and at the population level (Burnham and Anderson 2002). For resource selection by individuals, we compared bat locations to random points in the choice set using conditional logit discrete choice models (Proc MDC, SAS/ETS 9.2; SAS Institute, Cary, NC; SAS, 2010). Conditional logit discrete choice models consider the effects of the choice set attributes on each choice probability (Bonnot et al. 2009). The candidate models consisted of single covariate models with percent canopy cover, distance to water, and our land cover variables; all additive combinations of these covariates; and a null (intercept only model).

To examine resource selection at the population level, we pooled observations from all individuals and used mixed logit discrete choice models, which allow for random effects. We included a random effect for individuals to acknowledge heterogeneity among individuals and to account for varying sample sizes among individuals by treating individuals as subjects in the model. We evaluated support for reproductive condition (pregnant or lactating) and Julian date by comparing support for models with and without interactions between reproductive condition and Julian date with land cover, percent canopy cover, and distance to water and with percent canopy cover and distance to water; we also considered a null model with only an intercept parameter.

Traditional goodness-of-fit methods are not appropriate because discrete choice models use unique choice sets for each known location; therefore, we validated the top ranking model for each individual and the population using a modified *k*-fold approach (Boyce et al. 2002). We randomly removed 20% of the cases, fit the model with the remaining data, and tested the ability of the fit model to identify used points versus random points for the 20% of cases withheld, and repeated this 5 times. We report the mean percent concordance averaged over the 5 data subsets as the percentage of the time the used points had a greater predicted probability of use than the 3 random points in the choice set; values >25% indicate the model performed better than randomly selecting the used point (Bonnot et al. 2009).

We examined occurrence of covariates in the most supported models across individuals to assess variation among individuals. We evaluated the magnitude and 95% confidence intervals of model averaged coefficients for a confidence set of models ($w_i \geq 0.95$; Burnham and Anderson 2002); except where specifically noted, we only interpret covariates with 95% confidence intervals that did not overlap zero. We used the most supported population-level model to predict relative probability of use (±95% CI) over the observed range of supported covariates, while holding other covariates at their mean; we rescaled plots of continuous covariates so the maximum probability was 1 to facilitate comparison among covariates (McDonald et al. 2006).

RESULTS

We obtained 3,124 foraging locations for 29 female Indiana bats during summer 2008–2010. We monitored 14 pregnant, 12 lactating, 1 non-reproductive, and 2 post-lactating individuals but excluded non-reproductive and post-lactating individuals from population analysis (Table 1). We monitored individuals on average 5 nights (range: 2–9) and did not use individuals in analyses with <30 triangulated locations (range: 32–208). Bats moved on average 810 m (range: 25–1,025 m) in a 5- to 10-minute period so we concluded selection of use points by bats were sufficiently independent for discrete choice analysis.

We removed the land cover category, managed upland hardwood forest, from the models for 9 individuals (Bats 151238, 151400, 151440, 151481, 151538, 151759, 151799, 51839, 151859) because no used and <2% of random points were in the managed units and the coefficient could not be estimated (Supplementary Table S1, available online at www.onlinelibrary.wiley.com). The null model was not the most supported model for any bat. Percent concordance was 27–97% and exceeded that expected by chance (Table 1). We found variation in resources selected among individuals. Canopy cover, distance to water, and land cover classes appeared in the top model for 15, 14, and 13 bats; respectively (Table 1). For all but 2 individuals, model selection uncertainty existed so we model averaged parameter estimates and predictions (Supplementary Tables S1, S2; available online at www.onlinelibrary.wiley.com). The relative

Table 1. Reproductive condition and top supported discrete choice models for 29 individual Indiana bats study in northeast Missouri, 2008–2010. Akaike weight (w_i) is the weight of evidence for the top model relative to other candidate models, percent concordance is a measure of model fit, and n is the number of use and random points in the discrete choice model.

Bat ID	Reproductive condition	n	Model[a]	w_i	% Concordance
150181	Lactating	136	CAN	0.616	39
151078	Lactating	316	CAN + DisW	0.283	31
151538	Lactating	276	CAN	0.266	30
151759	Lactating	512	CAN	0.268	61
151177	Lactating	460	$LAND^1$ + DisW	0.500	47
151440	Lactating	664	$LAND^2$ + DisW	0.705	45
151839	Lactating	315	CAN + DisW	0.306	35
151481	Lactating	104	DisW	0.285	44
151578	Lactating	480	DisW	0.349	27
150000	Lactating	296	$LAND^1$	0.329	52
151718	Lactating	240	$LAND^1$	0.410	27
151900	Lactating	416	$LAND^1$ + DisW	0.559	43
151118	Pregnant	160	CAN	0.631	27
151859	Pregnant	100	CAN	0.258	42
151929	Pregnant	368	CAN	0.263	36
151238	Pregnant	368	$LAND^2$	0.361	56
151799	Pregnant	876	$LAND^1$ + DisW	0.734	55
151970	Pregnant	320	CAN + DisW	0.558	42
151018	Pregnant	376	$LAND^1$ + DisW	0.685	97
151539	Pregnant	616	$LAND^1$ + CAN + DisW	0.449	54
151878	Pregnant	272	DisW	0.654	43
151400	Pregnant	136	DisW	0.473	38
151098	Pregnant	260	$LAND^1$	0.294	54
151428	Pregnant	240	$LAND^1$ + CAN	0.546	53
151898	Pregnant	140	CAN	0.299	40
151913	Pregnant	384	CAN	0.247	40
151638	Non Reproductive	400	$LAND^1$ + CAN	0.238	41
151677	Post-lactating	420	CAN	0.506	36
151618	Post-lactating	300	$LAND^1$ + DisW	0.512	54

[a] CAN = percent canopy coverage; DisW = distance to water (m); $LAND^1$ = 4 dummy variables representing upland hardwood forest, upland hardwood forest managed with prescribed fire, bottomland hardwood forest, and shrubland-grassland; $LAND^2$ = excludes upland hardwood forest managed with prescribed fire, all other variables are included from previous LAND model; agricultural land use was the reference category.

probability a point was selected increased 1.2–5.3% for a 10% increase in canopy cover for the 4 individuals that the confidence interval did include 0 (Fig. 1). The relative probability a point was selected increased 2.2–7.1% for a 10-m increase in distance to water for the 8 individuals that the confidence interval did include 0 (Fig. 1). We found a positive relationships of shrubland, bottomland hardwood, upland hardwood, and managed upland hardwood forest with resource selection for 6, 9, 7, and 4 individuals, respectively, for which confidence intervals did not overlap 0 (Figs. 1 and 2; Supplementary Table S2). The increase in the relative probability a point was selected ranged across individuals, 84–227% if it was shrubland, 76–256% if it was bottomland hardwoods, 86–288% if it was upland hardwoods, and 46–629% if it was managed upland hardwoods versus agriculture (Figs. 1 and 2; Supplementary Table S2). Confidence intervals for model averaged coefficients did not include zero for 20–30% of individuals, and in all these cases the relationships with selection were positive.

For the population-level analysis, the percent canopy cover + distance to water + land cover model received overwhelming support (w_i = 0.998; % concordance = 0.38) with virtually no support for the model with the interactive terms for reproductive condition or Julian date (Table 2). The relative probability a point was selected increased 6% for a 10% increase in canopy cover and 3% for a 10-m increase in distance to water (Table 3). The relative probability a point was selected increased 545%, 940%, 527%, and 347% if it was bottomland forest, managed upland forest, shrubland, or upland forest, respectively, compared to agricultural land cover (Table 3). The predicted relative probability a point was selected increased across the range of distance to water and canopy cover, and was greatest for managed upland forest followed by bottomland forest, shrubland, and upland forest compared to agricultural land cover (Fig. 3).

DISCUSSION

We evaluated resource selection by individuals to identify variation in habitat use by Indiana bats that may have been unapparent or averaged out in the population-level model and to understand how individuals select resources (Cooper and Millspaugh 1999, Bolnick et al. 2002, Svanback and Bolnick 2007). We studied females during the maternity season because of the importance of reproduction and proximate high quality foraging sites to the conservation of the species. We found strong support for relationships between selection and canopy cover, distance to water, and land cover for only 20–30% of individuals and, overall, these relationships were supported at the population level. We think that some covariates were not supported at the individual level because of true variation among individuals, whereas for others large confidence intervals resulting from smaller

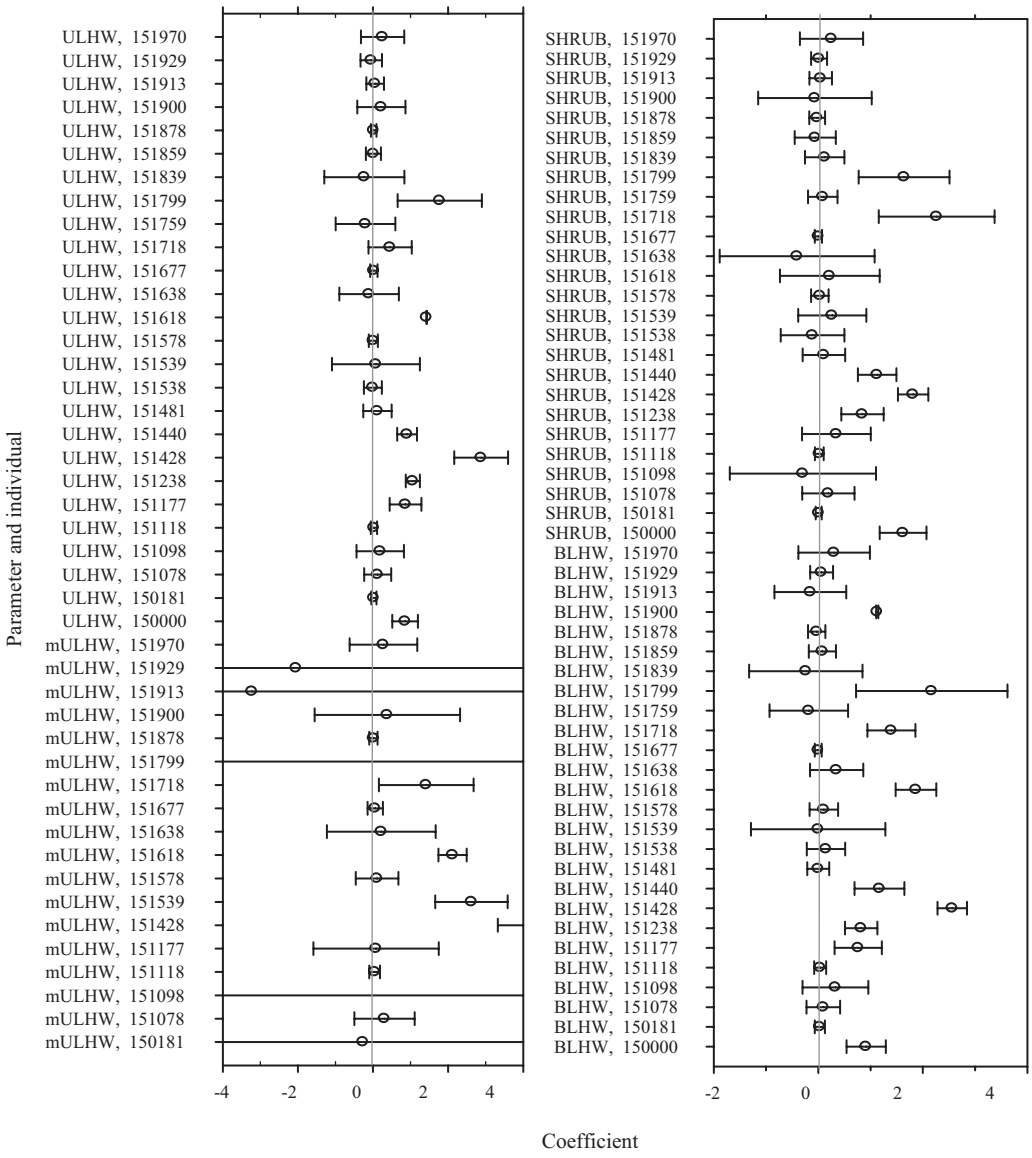

Figure 1. Model averaged coefficients (open circles) and 95% confidence intervals (bars) for discrete choice models for 29 individual Indiana bats in northeast Missouri, 2008–2010. Coefficients are for binary variables representing use of upland hardwood forest managed with prescribed fire (mULHW), upland forest (ULHW), open shrubland-grassland (SHRUB), or bottomland hardwoods (BLHW) versus agricultural land use.

sample sizes could have contributed to a lack of support. The magnitude of coefficients in the population model were in the lower range of coefficients in individual models, likely because any particular covariate was only supported for about half the individuals. However, population models do not necessarily represent what all individuals select, but rather an average across potentially substantial individual variability.

Intra-specific variation in resource selection, foraging behavior, and diet is known or suspected in a wide variety of species including insects (Howard 1993, Cronin et al. 1999), reptiles (Daltry et al. 1998), birds (Giraldeau and Lefebvre 1985, Annett and Pierotti 1999), ungulates (Clutton-Brock et al. 1982), bats (Fleming and Heithaus 1986), and mammalian carnivores (Kruuk and Moorhouse 1990, Ragg 1998). Foraging resources and diet breadth at the population level could be affected by differences in population size or strong intraspecific competition for limiting resources. The concept of variation in foraging behavior in Indiana bats is not especially surprising for a species living in a diverse environment with a large number of potential prey species and high temporal or spatial variability in prey populations. Individual foraging variation may have ramifications to population ecology. Reproductive success often depends upon the ability to compete for limiting resources. Although individual variation in diet remains largely unexplored from the standpoints of both theory and empirical detail, an individual may succeed or fail through their ability to obtain enough to eat.

A positive relationship of canopy cover with selection was the most frequently supported covariate for individuals and was supported in the population model. Increased use of areas with high canopy cover is consistent with others studies showing Indiana bats are found in areas with high canopy coverage (Humphrey et al. 1977, Menzel et al. 2005).

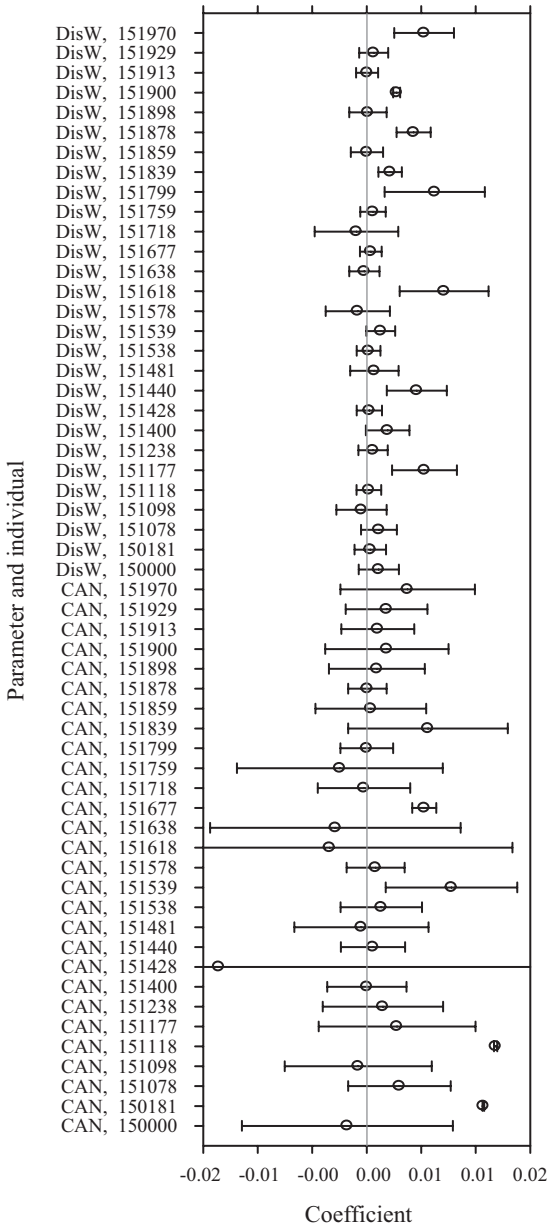

Figure 2. Model averaged coefficients (open circles) and 95% confidence intervals (bars) for discrete choice models for 29 individual Indiana bats in northeast Missouri, 2008–2010. Coefficients represent relationships of percent canopy cover (CAN) and distance to water (DisW) measured in meters with the probability of use.

Indiana bats' small body size, low wing loading, and high echolocation frequency allow them to navigate well in high clutter environments such as closed canopy forest (Owen et al. 2004). The distribution of canopy cover values for use and random points was skewed toward 0% and 100% with approximately 25% of points with 0% canopy cover and 25% with >90% canopy cover; nevertheless, we recorded values throughout the range. This distribution of canopy cover reflected the distribution of use and random points among land cover types; 68% and 59% of use and random points, respectively, were in forested land covers and the balance in shrub or agricultural land. Therefore, the positive relationship with canopy cover was largely driven by the contrast between forest and non-forest, although bats did make frequent use of non-forested or open areas 25% of the time. In addition to being adapted to foraging in closed canopy forest, Indiana bats may be associated with high canopy cover forest for roosting habitat. Out of 48 Indiana bat roost trees in Missouri, 32 were in closed-canopy forest, 12 in intermediate canopy cover, and 4 in open-canopy areas (Gardner et al. 1991).

We found a greater relative probability of use of areas managed with fire for 5 of 20 individuals that we were able to evaluate. We did not observe negative relationships with forest managed with prescribed fire for any individual, and a positive relationship was also supported in the population model. Other studies have also shown increased use by foraging Indiana bats of forests treated by prescribed fire that opened up the understory while keeping the mature forest canopy intact (Owen et al. 2004). Besides lower understory density, increased use of forests managed with prescribed fire could also be related to prey density. Lacki et al. (2009) found greater prey densities and northern long-eared bat (*Myotis septentrionalis*) activity in Kentucky forests managed with prescribed fire; however, insect prey densities were not greater in the stands with fire that we studied (Womack 2011). We think that Indiana bats likely selected sites treated with prescribed fire because of more open understories.

We found no support for temporal changes in resource use by females associated with reproductive condition or day of year in our population model. Brigham et al. (1992) also found no differences in habitat use between 4 reproductive classes (pregnant, lactating, post-lactating, and juveniles) of Yuma bats (*Myotis Yumanensis*) and attributed this finding to

Table 2. Support for population-level discrete choice models based on 29 female Indiana bats in a resource selection study in northeast Missouri, 2008–2010 (n = 8,831). Model support is indicated by Akaike's Information Criterion (AIC), the difference in AIC between the top model and indicated model (ΔAIC), Akaike weights (w_i), log likelihood value (log(L)), and number of estimated parameters in the model (K).

Model[a]	K	log(L)	AIC	ΔAIC	w_i
LAND + CAN + DisW	7	−2,861	5,736		0.998
LAND × jul + CAN × jul + DisW × jul	7	−2,867	5,748	12	0.002
CAN + DisW	3	−2,887	5,780	43	0.000
LAND × rc + CAN × rc + DisW × rc	7	−2,883	5,780	45	0.000
CAN × jul + DisW × jul	3	−2,894	5,794	58	0.000
CAN × rc + DisW × rc	3	−2,900	5,806	69	0.000
NULL	1	−3,061	6,124	389	0.000

[a] CAN = percent canopy coverage; DisW = distance to water (m); LAND represents 4 dummy variables for bottomland hardwood forest, shrubland-grassland, upland hardwood forest, upland hardwood forest managed with prescribed fire; jul = Julian date; rc = reproductive condition (pregnant or lactating); NULL = intercept only model.

Table 3. Model coefficients, standard errors, confidence intervals, and selection ratios for the most supported population-level discrete choice model based on 29 female Indiana bats in a resource selection study in northeast Missouri, 2008–2010.

Variable	Estimate	SE	95% CI	Selection ratio
Canopy cover (%)	0.006	0.0011	0.0039–0.0138	1.006
Distance to water (m)	0.003	0.0002	0.0028–0.0087	1.003
Bottomland forest[a]	0.545	0.120	0.31–1.152	1.725
Managed upland forest[a]	0.940	0.212	0.524–1.968	2.560
Shrubland[a]	0.527	0.099	0.333–1.180	1.694
Upland forest[a]	0.347	0.119	0.114–0.57	1.415

[a] Dummy variables coded as 1 if the point fell in the defined land cover type; agricultural land was the reference category.

the rarity of foraging areas (i.e., forests) in the system, which is similar to the landscapes we studied. In red bats (*Lasiurus borealis*), differences were noted between reproductive stages relative to selection for percent canopy cover and landscape percent water (Amelon 2007). Indiana bats have a different behavioral structure than red bats; Indiana bats roost in colonies under tree bark, whereas red bats are a solitary foliage roosting species. Henry et al. (2002) determined home range size differs between pregnant and lactating little brown bats, but they did not investigate resource selection by reproductive stage. Bat ecology studies in the future need to consider the individuals within populations to more fully understand what resources are selected by the species.

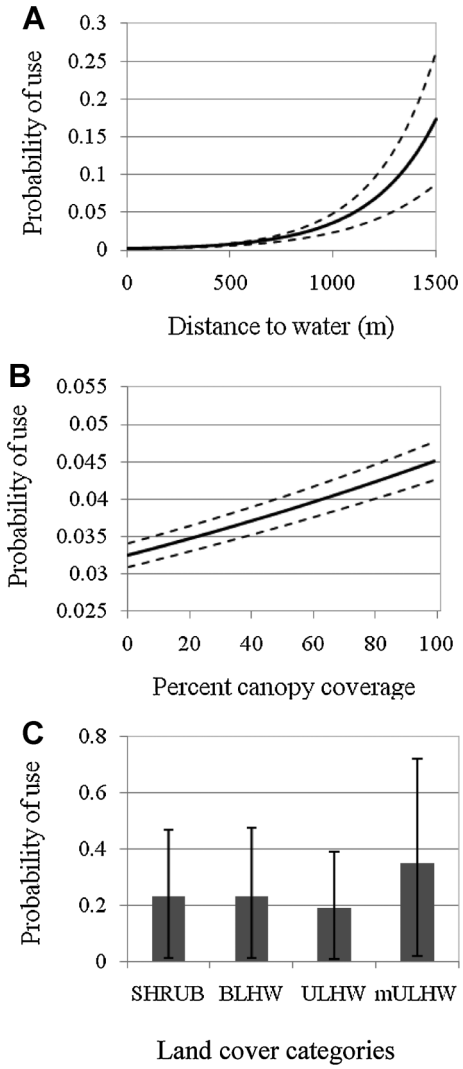

Figure 3. Predicted relative probability of site use for a population of female Indiana bats ($n = 29$) as a function of (A) distance to water in meters; (B) percent canopy cover; and (C) Land cover categories: shrub-grassland (SHRUB), bottomland forest (BLHW), upland forest (ULHW), and managed upland forest (mULHW).

Our resource selection results for land cover types are generally consistent with previous foraging studies for Indiana bats. Sparks et al. (2005) reported Indiana bats preferred closed-canopy forest over agricultural land and Murray and Kurta (2004) found most individuals foraged in forest in a landscape dominated by agriculture. Indiana bat maternity colonies generally occur in forest and in landscapes with 10–80% forest, 55–67% agriculture, 0–19% wetland, and 0–6% urban (Gardner et al. 1991, Kurta et al. 2002). Our landscape was 28% forest, which is at the lower end of percent forest composition for Indiana bats. In regions with very limited forest cover, Indiana bats may be constrained to landscapes with enough suitable forest cover. Differences in spatial foraging dynamics exhibited between forest-dominated versus agriculture-dominated landscapes have been described for this species as well as other *Myotis* species (Britzke et al. 2003, Sparks et al. 2005, Henderson and Broders 2008).

Our finding that relative probability of use increased with distance to water may not seem consistent with previous studies reporting high use of riparian corridors by foraging Indiana bats (Menzel et al. 2005, Carter 2006, Yates and Muzika 2006). However, water was abundant on our study area and all bat locations were within 1.5 km of water, well within the area of use for each individual. Therefore, no individuals were ever truly distant from water (i.e., >1,500 m).

Our use of discrete choice modeling differs from previous approaches used to determine resource selection by foraging Indiana bats, such as compositional analysis (Sparks et al. 2005). Compositional analysis is usually used to compare habitat use and availability within an individual's home range. Bats are capable of moving large distances compared to other mammals similar in size. Therefore, limiting the available area for potential use to home range is likely an underestimation of the potential foraging habitat available to individuals (Kurta 2001). To address this issue of availability, we used the maximum distance an individual flew each night to define an area from which we sampled points to be in our choice set. The use of discrete choice modeling also let us consider relationships with continuous covariates, unlike compositional analysis, which considers use of vegetation or land cover types.

MANAGEMENT IMPLICATIONS

Discrete choice models were a valuable tool for determining resource selection of individual foraging bats and provided insight into variability in resource selection by individuals not possible from population models. The probability a bat selected a point was greater for shrubland and forest habitats

than agricultural habitat and increased with canopy cover. Therefore, practices that eliminate forest or greatly reduce canopy cover over large areas may have negative impacts on Indiana bats. Our study supports the premise that bats will use a broad array of vegetation types for foraging. Maintaining forest cover within landscapes dominated by agriculture is likely critical to persistence of Indiana bat maternity colonies in these landscapes. A positive relationship of selection with prescribed fire in upland forest was supported for 25% of the individuals that had managed stands available to them and no individuals had a negative relationship with fire; therefore, prescribed fire may improve habitat for Indiana bats and its use for this purpose warrants further research. Although our results suggest Indiana bats were selecting mature forests with relatively high canopy closure for foraging locations, we recommend further examination of the relationship between these forest structures, bat foraging, and bat fitness. We recommend that management activities proceed under an adaptive management framework to monitor bat population response to management such as partial tree harvest and prescribed fire.

LITERATURE CITED

Amelon, S. K. 2007. Multi-scale factors influencing detection, site occupancy and resource use by foraging bats in the Ozark Highlands of Missouri. Dissertation, University of Missouri, Columbia, USA.

Amelon, S. K., D. C. Dalton, J. J. Millspaugh, and S. A. Wolf, 2009. Radiotelemetry; techniques and analysis. Pages 57–77 *in* T. H. Kunz and S. Parsons, editors. Ecological and behavioral methods for the study of bats. John Hopkins University Press, Baltimore, Maryland, USA.

Annett, C. A., and R. Pierotti. 1999. Long-term reproductive output in Western gulls: consequences of alternative diet choice. Ecology 80:288–297.

Berry, S. T. 1994. Estimating discrete-choice models of product differentiation. Rand Journal of Economics 25:242–262.

Bolnick, D. I., L. H. Yang, J. A. Fordyce, J. M. Davis, and R. Svanback. 2002. Measuring individual-level resource specialization. Ecology 83: 2939–2941.

Bonnot, T. W., J. J. Millspaugh, and M. A. Rumble. 2009. Multi-scale nest-site selection by black-backed woodpeckers in outbreaks of mountain pine beetles. Forest Ecology and Management 259:220–228.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modeling 157: 281–300.

Brigham, R. M., H. D. J. N. Aldridge, and R. L. Mackey. 1992. Variation in habitat use and prey selection by yuma bats, *Myotis yumanensis*. Journal of Mammalogy 73:640–645.

Britzke, E. R., M. J. Harvey, and S. C. Loeb. 2003. Indiana bat, *Myotis sodalis*, maternity roosts in the Southern United States. Southeastern Naturalist 2:235–242.

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

Callahan, E. V., R. D. Drobney, and R. L. Clawson. 1997. Selection of summer roosting sites by Indiana bats (*Myotis sodalis*) in Missouri. Journal of Mammalogy 78:818–825.

Carter, T. C. 2006. Indiana bats in the Midwest: the importance of hydric habitats. Journal of Wildlife Management 70:1185–1190.

Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer: behavior and ecology of two sexes. University of Chicago Press, Chicago, Illinois, USA.

Cooper, A. B., and J. J. Millspaugh. 1999. The application of discrete choice model to wildlife resource selection studies. Ecology 80:566–575.

Crampton, L. H., and R. M. R. Barclay. 1998. Selection of roosting and foraging bats in different-aged aspen mixed hardwood stands. Conservation Biology 12:1347–1358.

Cronin, G., T. Schlacher, D. M. Lodge, and E. L. Siska. 1999. Intraspecific variation in feeding preference and performance of *Galerucella nymphaeae* (Chrysomelidae: Coleoptera) on aquatic macrophytes. Journal of the North American Benthological Society 18:391–405.

Daltry, J. C., W. Wüster, and R. S. Thorpe. 1998. Intraspecific variation in the feeding ecology of the Crotaline snake *Calloselasma rhodostoma* in Southeast Asia. Journal of Herpetology 32:198–205.

Fenton, M. B., and W. Bogdanowicz. 2002. Relationships between external morphology and foraging behaviour: bats in the genus Myotis. Canadian Journal of Zoology 80:1004–1013.

Fischer, J., and D. B. Lindenmayer. 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16:265–280.

Fleming, T. H., and E. R. Heithaus. 1986. Seasonal foraging behavior of the frugivorous bat *Carollia perspicillata*. Journal of Mammalogy 67: 660–671.

Gardner, J. E., J. D. Garner, and J. E. Hofmann. 1991. Summer roost selection and roosting behavior of *Myotis sodalis* (Indiana bat) in Illinois. Final report. Illinois Natural History Survey and Illinois Department of Conservation, Champaign, USA.

Giraldeau, L.-A., and L. Lefebvre. 1985. Individual feeding preferences in feral groups of rock doves. Canadian Journal of Zoology 63:189–191.

Haila, Y. 2002. A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. Ecological Applications 12:321–334.

Henderson, L. E., and H. G. Broders. 2008. Movements and resource selection of the northern long-eared Myotis (*Myotis septentrionalis*) in a forest-agriculture landscape. Journal of Mammalogy 89:952–963.

Henry, M., D. W. Thomas, R. Vaudry, and M. Carrier. 2002. Foraging distances and home range of pregnant and lactating little brown bats (*Myotis lucifugus*). Journal of Mammalogy 83:767–774.

Homer, C., C. Huang, L. Yang, B. Wylie, and M. Coan. 2004. Development of a 2001 National Landcover Database for the United States. Photogrammetric Engineering and Remote Sensing 70:829–840.

Howard, R. W. 1993. Cuticular hydrocarbons and chemical communication. Pages 179–226 *in* D. Stanley-Samuelson and D. Nelson, editors. Insect lipids: chemistry, biochemistry and biology. Lincoln University Press, Lincoln, Nebraska, USA.

Humphrey, S. R., A. R. Richter, and J. B. Cope. 1977. Summer habitat and ecology of the endangered Indiana bat, *Myotis sodalis*. Journal of Mammalogy 58:334–346.

Jacobs, D. S. 1999. The diet of the insectivorous Hawaiian hoary bat (*Lasiurus cinereus semotus*) in an open and a cluttered habitat. Canadian Journal of Zoology-Revue Canadienne De Zoologie 77:1603–1608.

Kruuk, H., and A. Moorhouse. 1990. Seasonal and spatial differences in food selection by otters (*Lutra lutra*) in Shetland. Journal of Zoology 221:621–637.

Kunz, T. H., and A. Kurta. 1988. Capture methods and holding devices. Pages 1–29 *in* T. H. Kunz, editor. Ecological and behavioral methods for the study of bats. Smithsonian Institution Press, Washington, DC, USA.

Kurta, A. 2001. Bats on the surface: the need for shelter, food, and water. Pages 197–204 *in* K. C. Vories and D. Throgmorton, editors. Proceeding of Bat conservation and mining. Office of Surface Mining, U.S. Department of Interior, Alton, Illinois, USA.

Kurta, A. 2005. Roosting ecology and behavior of Indiana bats (*Myotis sodalis*) in summer. Pages 29–38 *in* K. C. Vories and A. Harrington, editors. Proceedings of the Indiana bat and coal mining: a technical interactive forum. Office of Surface Mining, U.S. Department of the Interior, Alton, Illinois, USA.

Kurta, A., S. W. Murray, and D. Miller. 2002. Roost selection and movements across the summer landscape. Pages 118–129 *in* A. Kurta and J. Kennedy, editors. The Indiana bat: biology and management of an endangered species. Bat Conservation International, Austin, Texas, USA.

Lacki, M. J., D. R. Cox, L. E. Dodd, and M. B. Dickinson. 2009. Response of northern bats (*Myotis septentrionalis*) to prescribed fires in eastern Kentucky forests. Journal of Mammalogy 90:1165–1175.

McDonald, T. L., B. F. J. Manly, R. M. Nielson, and L. V. Diller. 2006. Discrete-choice modeling in wildlife studies exemplified by northern spotted owl nighttime habitat selection. Journal of Wildlife Management 70:375–383.

Menzel, J. M., W. M. Ford, M. A. Menzel, T. C. Carter, J. E. Gardner, J. D. Garner, and J. E. Hofmann. 2005. Summer habitat use and home-range

analysis of the endangered Indiana bat. Journal of Wildlife Management 69:430–436.

Menzel, M. A., J. M. Menzel, T. C. Carter, W. M. Ford, and J. W. Edwards. 2001. Review of the forest habitat relationships of the Indiana bat (*Myotis sodalis*). General Technical Report NE-284. United States Department of Agriculture Forest Service, Newtown Square, Pennsylvania, USA.

Murray, S. W., and A. Kurta. 2004. Nocturnal activity of the endangered Indiana bat (*Myotis sodalis*). Journal of Zoology 262:197–206.

Norberg, U. 1994. Wing design, flight performance and habitat use in bats. Pages 205–239 *in* P. C. Wainwright and S. M. Reilly, editors. Ecological morphology: integrative organismal biology. University of Chicago Press, Chicago, Illinois, USA.

Owen, S. F., M. A. Menzel, J. W. Edwards, W. M. Ford, J. M. Menzel, B. R. Chapman, P. B. Wood, and K. V. Miller. 2004. Bat activity in harvested and intact forest stands in the Allegheny mountains. Northern Journal of Applied Forestry 21:154–159.

Patriquin, K. J., and R. M. R. Barclay. 2003. Foraging by bats in cleared, thinned and unharvested boreal forests. Journal of Applied Ecology 40:646–657.

Ragg, J. R. 1998. Intraspecific and seasonal differences in the diet of feral ferrets (*Mustela furo*) in a pastoral habitat, East Otago, New Zealand. New Zealand Journal of Ecology 22:113–119.

Sartwell, J. 2000. Geographic telemetry model (GTM) v. 2.3.5. Missouri Department of Conservation, Columbia, Missouri, USA.

SAS. 2010. Overview: MDC Procedure. SAS/ETS(R) 9.2 User's Guide. SAS Institute, Cary, North Carolina, USA.

Sparks, D. W., C. R. Ritzi, J. E. Duchamp, and J. O. Whitaker, Jr., 2005. Foraging habitat of the Indiana bat (*Myotis sodalis*) at an urban-rural interface. Journal of Mammalogy 86:713–718.

Svanback, R., and D. I. Bolnick. 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proceedings of the Royal Society 274:839–844.

Thomas, D. W. 1988. The distribution of bats in different ages of douglas-fir forests. Journal of Wildlife Management 52:619–626.

Tuttle, M. D. 1974. An improved trap for bats. Journal of Mammalogy 55:475–477.

Tuttle, N. M., D. P. Benson, and D. W. Sparks. 2006. Diet of the *Myotis sodalis* (Indiana bat) at an urban/rural interface. Northeastern Naturalist 13:435–442.

U.S. Fish and Wildlife Service. 2012. White-nose syndrome decontamination protocol—version 03.15.2012. <http://www.fws.gov/WhiteNoseSyndrome/pdf/National_WNS_Decontamination_Protocol_v03.15.2012.pdf> Accessed 6 Jul 2012.

Womack, K. M. 2011. Habitat and management effects of foraging activity of Indiana bats (*Myotis sodalis*) in northern Missouri. Thesis, University of Missouri, Columbia, USA.

Yates, M. D., and R. M. Muzika. 2006. Effect of forest structure and fragmentation on site occupancy of bat species in Missouri Ozark forests. Journal of Wildlife Management 70:1238–1248.

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