

USING OCCUPANCY ESTIMATES TO ASSESS HABITAT USE AND
INTERSPECIFIC INTERACTIONS OF THE INDIANA BAT (*MYOTIS SODALIS*)
AND LITTLE BROWN BAT (*M. LUCIFUGUS*) IN NORTHEAST MISSOURI

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by
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INTERSPECIFIC INTERACTIONS OF THE INDIANA BAT (*MYOTIS SODALIS*)
AND LITTLE BROWN BAT (*M. LUCIFUGUS*) IN NORTHEAST MISSOURI

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ABSTRACT

The Indiana bat (*Myotis sodalis*) has been endangered since 1967 (USFWS 1996) and is the focus of a controversial debate among stakeholders on both public and private lands. Much of this debate is due to a lack of understanding the summer habitat needs of the species. In addition, even less is known about interspecific interactions with other bats and if this could be playing a role in the decline of this species. Our objectives were to estimate the probability of site occupancy for the Indiana bat and the little brown bat (*M. lucifugus*) in three locations in northeastern Missouri from which we could model their summer habitat suitability. We then used our occupancy modeling estimates to determine whether the knowledge of the little brown bat's (*M. lucifugus*) landscape occupancy patterns improved the fit of Indiana bat occupancy models and vice versa.

We used acoustic detection data, collected at 576 sites, in an information theoretic approach to examine *a priori* hypotheses relative to both probability of detection and site occupancy using an objective model selection criterion to rank the candidate models. For the Indiana bat, we found support for the effects of ambient temperature, relative humidity, Julian date, and distance to water on detection probability. The quantity of bottomland hardwood forest in a 7 km landscape was the single most significant factor in determining Indiana bat occupancy. Because bottomland hardwood habitat is scarce

throughout the range of the Indiana bat, this would help explain the species' struggle to rebound. For the little brown bat, we found support for the effects of ambient temperature, relative humidity, and distance to water on detection probability. Site combined with distance to water and canopy cover created the top model determining little brown bat occupancy.

We then combined this information on Indiana and little brown bats to determine whether the little brown bat occupancy improved the probability of Indiana bat occupancy (and vice versa), for which we found it did not. Our findings help managers consider the summer needs of the endangered Indiana bat. We suggest managers ensure adequate bottomland hardwood habitat is available to sustain summer populations of Indiana bats. We also suggest that resource partitioning may exist between Indiana and little brown bats and that managers should use caution in using the little brown bat as a surrogate species when assessing the needs of the Indiana bat.

CHAPTER 1

SUMMER HABITAT OCCUPANCY BY INDIANA BATS (*MYOTIS SODALIS*) IN NORTHEAST MISSOURI

ABSTRACT

Perhaps more than any other North American bat species, the Indiana bat (*Myotis sodalis*) has been at the forefront of scrutiny and controversy among stakeholders on both public and private lands. Understanding habitat selection and subsequent development of summer habitat suitability models for Indiana bats provides a tool to measure the effectiveness of habitat mitigation efforts. Habitat suitability models can also inform forest management decisions on both public and private land; contributing to best management practices for forest management in the presence of summering Indiana bats.

We applied a maximum likelihood approach to estimate probability of site occupancy using acoustic detection data for the Indiana bat in three conservation areas in northeastern Missouri where the species is known to persist. We evaluated *a priori* hypotheses relative to both probability of detection and site occupancy using an objective model selection criterion to rank candidate models. We found support for the effects of ambient temperature, relative humidity, distance to water, and Julian date on detection probability. After inclusion of these detectability metrics in subsequent occupancy models, the quantity of bottomland hardwood forest in a 7 km buffer surrounding each survey point was the single most significant factor in predicting Indiana bat occupancy. Predicted site occupancy increased rapidly (from effectively 0 to effectively 100%) with

just small increases (between 0 and 6%) in the availability of bottomland hardwood forest. We therefore find it important for managers to reestablish and protect bottomland hardwood habitat throughout the Indiana bats' range.

KEY WORDS detectability, occupancy, Program PRESENCE, acoustic monitoring, bottomland forest

INTRODUCTION

Indiana bats (*Myotis sodalis*) have low reproductive rates and roost in colonies during both maternity and hibernation periods, making them susceptible to many threats that typically cause declines in bat populations including disease and human disturbance. The species was listed as endangered by the U.S Department of Interior, Fish and Wildlife Service in 1967 and remains critically imperiled throughout much of its geographic range (USFWS 1996, 2007). The Indiana bat hibernates in relatively few caves, making it extremely vulnerable to human disturbance. Therefore, historic conservation efforts have emphasized protecting known hibernacula (Menzel et al. 2005). Despite these efforts, the species continued to decline rapidly; as much as 58 percent between 1960-1991 (Clawson 2002) and reached a low of approximately 353,000 individuals in 1996 (USFWS 1996). From 1997-2005, Indiana bats steadily increased to an estimated 457,000 individuals (King 2006), but the species has since been impacted by the pathogen *Geomysces destructans*, the causative agent of white-nose syndrome (WNS) which is estimated to have killed more than a third of the Indiana bats in the Northeastern U.S. and greater than 40,000 individuals overall (Szymanski et al. 2009, Thogmartin et al. 2013).

When female Indiana bats emerge from hibernation, usually in April, they typically migrate north, sometimes hundreds of kilometers, and congregate in nursery

colonies comprised of 25 to >100 females and their young (Romme et al. 1995, Menzel et al. 2001). Relatively few of these summer nursery colonies have been discovered and researchers are just beginning to learn about the complex summer habitat requirements of bats in general, and Indiana bats in particular, leaving them highly susceptible to human modification of their landscapes that may be made despite efforts to avoid such negative impacts (Pierson 1998, Menzel et al. 2002, 2005, Tibbels and Kurta 2003). As a result, identifying summer habitat requirements has become increasingly important in the recovery of this species.

While sustainable forest management is considered suitable for maintaining Indiana bat summer habitat, information on the actual effects of forest management on bat populations are limited (USFWS 2007). While the availability of clusters of roost trees is important to summering Indiana bats (Clawson et al. 2006), broader habitat requirements are poorly understood. In an effort to better address this information gap, we initiated a study of summer habitat use in cooperation with the Missouri Department of Conservation (MDC) as a scientific evaluation of management guidelines developed to enhance Indiana bats' summer habitat and to allow managers to more effectively create and maintain Indiana bat habitat. Working at several conservation areas in northern Missouri, our objective was to evaluate patch and landscape factors affecting habitat use and develop models that predict the probability of site occupancy by Indiana bats.

Because Indiana bats are nocturnal, cryptic, largely inaudible, and volant, they are difficult to study without capture or the use of acoustic detectors. We used passive acoustic monitoring in this study which has been used to estimate species presence and relative abundance from counts of calls per time interval (Britzke et al. 1999, Ellison et

al. 1999, Erickson and West 1999, Miller et al. 2001, Broders et al. 2003, Wickramasinghe et al. 2003). We then analyzed this information in an occupancy modeling framework that considers detection probability to better understand the habitat and management features that best predict the distribution of Indiana bats in the study regions. Detection probability (p) is the probability of detecting at least one individual of a species during a specific sampling occasion, given that the species is present (Boulinier et al. 1998, MacKenzie et al. 2002) and reflects variation based on differences in the ability to detect the species when it is actually present at a site. Site occupancy (Ψ) is the probability that a randomly selected site or sampling unit in an area of interest is occupied by a species (MacKenzie et al. 2006) and reflects spatial and temporal variation based on differences in animal behavior and patch or landscape variables. Several studies have used occupancy modeling to link bat species to particular habitat characteristics (Yates and Muzika 2006, Gorresen et al. 2008; Hein et al. 2009, Roberts, et al. 2011). However, only a few studies have estimated species detection probability for bats (Yates and Muzika 2006, Gorresen et al. 2008, Hein et al. 2009). Therefore most studies are indirectly or directly assuming that all species present at a site are detected and are equally likely to be detected (Hayes 1997, Ballantyne and Sherwin 1999, Arnett and Hayes 2000, Hayes 2000). Such assumptions are often invalid. Therefore we used program PRESENCE, which was developed specifically to fit models that simultaneously estimate parameters associated with probability of detection and probability of site occupancy, in an information theoretic approach to evaluate the habitat use of the Indiana bat.

STUDY AREA

We studied Indiana bats on Charlie Heath Memorial Conservation Area (CHMCA), Fox Valley Lake Conservation Area (FVLCA), and Deer Ridge Conservation Area (DRCA) during the summers of 2008-2011. All three sites are part of the Wyaconda River Dissected Till Plains Subsection in extreme northeastern Missouri (Nigh and Schroeder 2002). Postglacial stream erosion has transformed the surface into a series of parallel, low relief ridges and valleys carved from glacial till. These sites are in close proximity (< 64 km) to each other and included both bottomland and upland forest (Table 1, Figure 1). Oak-hickory was the dominate forest type with species including *Carya ovata*, *C. laciniosa*, *C. cordiformis*, *Quercus imbricaria*, *Q. alba*, *Q. rubra*, *Q. macrocarpa*, *Q. velutina*, *Ulmus americana*, *U. rubra*, *Populus deltoides*, *Acer saccharinum*, *Robinia pseudoacacia*, and *Betula nigra*. The study sites are public use areas managed by MDC with a mission of protecting and managing the fish, forest, and wildlife resources of the state while serving the public and facilitating their participation in resource management activities.

Deer Ridge Conservation Area

Deer Ridge Conservation Area (DRCA) consisted of three tracts totaling 2,856 ha including about 2,185 ha of forested land in Lewis County, Missouri (Figure 2). Old fields, cropland, and wetlands were scattered throughout, along with a 19 ha lake (Deer Ridge Community Lake) and two permanent streams (North Fabius River and Middle Fabius River). There were nearly 32 km of trails throughout DRCA which create potential flight corridors for Indiana bats.

Studies at DRCA in 2001 and 2002 used radio telemetry and ultrasonic detectors to document the largest summer aggregation of Indiana bats known in Missouri (Miller 2003, Timpone 2004). Between 2003 and 2008, 1,093 forested hectares were impacted by timber harvest in an effort to enhance habitat for use by the Indiana bat. Small clear cuts, uneven aged forest harvest, and retention of snag trees were the dominant practices (Figure 3). Other management techniques practiced prior to and during the study included open field cropping, grass management, and wetland management. A limited amount of forest cutting had also occurred on the area prior to 2003 in association with the Riparian Ecosystem Assessment and Management (REAM) project and a private timber sale, resulting in a small clear-cut.

Charlie Heath Memorial Conservation Area

Charlie Heath Memorial Conservation Area (CHMCA) was a 662 ha area located in Clark County, Missouri (Figure 4). The area was 90% forested with the remainder consisting of grasslands and idle fields. An 8 km multi-use trail and over 6 km of the Fox River meandered through the area. The area was characterized by gently rolling forested hills with remnant stands of native grass (*Andropogon gerardii*, *Sorghastrum nutans*), wetlands, streams, shallow ponds, and a cottonwood (*Populus deltoides*) plantation.

No timber management took place within CHMCA during this study, however prescribed fires were conducted on two separate units totaling 33 ha annually in April from 2006-2009.

Fox Valley Lake Conservation Area

Fox Valley Lake Conservation Area (FVLCA) was an 874 ha area located in Clark County, Missouri (Figure 5). The area was about 60% forested with the remaining 40%

consisting of grasslands, row crops, and idle fields. The area included a 44 ha fishing lake and a 5 ha constructed wetland. Over 1 km of the Fox River meandered along the eastern boundary. There were no designated trails in the area.

During the fall and winter of 2008 (after one year of data was collected) commercial uneven aged forest harvest and post-harvest slashing occurred on FVLCA (Figure 6). Harvest design emphasized snag retention and creation of small forest openings.

METHODS

Sample Point Selection

We defined sample point locations by overlaying a 0.1 ha grid on each of the study areas. Grid cells sampled were randomly selected and constrained so that 70% of the points fell within a 30 meter buffer around streams and trails. Bats are known to use these areas, increasing our likelihood of detection and reducing zero inflation. The remaining 30% of the points fell outside the buffer to ensure coverage of the entire area. In the summer of 2008, we sampled 100 points across different types of forest management within each of the three study areas. In subsequent years (2009-2011), we randomly selected 70% of the points used in the previous year so that we could compare between years. We then determined how many of those resampled sites were within the 30 meter buffer, and filled in the new randomly selected 30% accordingly so that we would maximize the number of sites sampled for each area.

Acoustic Monitoring

Bat species emit different patterns of high frequency pulses that can be used to distinguish different species of bats or groups of species. At each sampling site we

passively collected bat echolocation calls using Anabat I and Anabat II detectors coupled with Zero-Crossing Analysis Interface Modules with CF memory card storage (CF ZCAIM; Titley Electronics). An Anabat converts a bat's echolocation pulses into electronic signals by using frequency division without amplitude retention, in which the original frequency of the call is divided by a predetermined factor (Corben 2011). We conducted acoustic sampling from mid-May to early August to coincide with the bats' time spent in nursery colonies. Before each season, we calibrated each Anabat detector to minimize variance in recording distance and to standardize the area sampled (Livengood 2003). We protected Anabat detectors from inclement weather by housing them within waterproof Pelican cases (Figure 7). The microphone was aligned with an opening leading to a polyvinyl chloride (PVC) elbow directed upwards at 45° to minimize noise interference on the ground. A 12-volt battery was also housed within the Pelican case to power the anabat for two consecutive days. The detectors were placed on the ground and oriented towards the area of least canopy cover to maximize call detections. We placed one Anabat detector unit at each point location for two consecutive nights according to a spatial and temporal schedule. We divided each night into two separate sampling visits because bats typically are bimodal in their activity periods with one peak soon after dusk and another pre-dawn: 1800-2400 and 2401-0600. This provided four sampling visits for each point location. If a call was recorded during that time period, we considered the species to occupy the site. In the event of heavy rain or technical failure due to Anabat malfunction, we resurveyed the point.

Data Analysis

Bat echolocation calls were downloaded and analyzed using Analook software (Corben 2011). Species were identified based on qualitative and quantitative parameters derived from local call libraries (S. Amelon, unpubl. data). To minimize error in species identification that could result in false positive or negative detections, we initially used a digital filter to eliminate noise, call sequences with less than five call pulses, and calls of poor quality. Qualitative characteristics were used to further evaluate observable differences in call characteristics including shape, time between calls, consistency of the minimum frequency, presence of >1 bat per file, etc. Species identification and presence determination for each visit was independently determined by at least 2 observers with tested species identification accuracy of >90%. Quantitative call characteristics for call sequences determined to be of high quality including slope (initial and mean), minimum frequency, duration, etc. were calculated using Analook. A species was noted as either detected or not detected by each observer, and if no determination could be made, the site was dropped.

We analyzed the resulting detection history with likelihood-based occupancy modeling using program PRESENCE 4.9 to estimate the proportion of sites occupied (MacKenzie et al. 2002, Royle and Nichols 2003, MacKenzie and Bailey 2004, MacKenzie and Royle 2005). Because our project is designed in part to measure changes associated with forest management over time, we used single-species multiple season occupancy models (MacKenzie et al. 2006). Individual years represented the primary sampling periods while visits nested within each season were secondary sampling periods; this allowed us to evaluate site occupancy on two temporal scales. At the larger

scale, we evaluated occupancy over multiple seasons (e.g., years) allowing the occupancy state of sites to vary between seasons. At the smaller scale (within season) we evaluated occupancy states which were not varied. Essentially, we modeled detection/non-detection as single season models of each primary sampling period and compared between sampling periods by estimating immigration and emigration. This approach considers occupancy of primary periods as a random process in that occupancy status from a different primary sampling period is not relevant (MacKenzie et al. 2006). We used a multi-stage approach by first evaluating the best model for probability of detection and then used this best model to aid in evaluating patch and landscape scale occupancy.

Detection Probability and Site Occupancy Modeling

For detection probability (p) and site occupancy (Ψ) modeling, our general approach was to develop and contrast *a priori* hypotheses (Table 2), which we expressed as models that could be fit to data collected from sample units. We then ranked them in terms of their ability to explain the empirical data relative to Indiana bats using an information-theoretic model selection criterion (Akaike's Information Criteria, AIC_c) (Burnham and Anderson 2002).

Detection models were incorporated to account for variables which we hypothesized to influence detection likelihood due to the influence of the timing or location of sampling events on the likelihood of calls being recorded and identified. We considered single covariate models and all possible additive combinations for a total of 17 models. Because environmental conditions and characteristics of a bat echolocation call influences the range of detection, with low frequency and high intensity calls carrying farthest (Lacki et al. 2007, Weller 2007), we hypothesized that bat detection

would be affected by sound attenuation, time within season, and proximity of water as an attractant.

To model for sound attenuation we used maximum temperature (T), maximum relative humidity (RH), and mean barometric pressure (BP). To model effects on detection probability (p) due to time within season effects we used Julian date (JD), and to model the effects of water as an attractant, we used distance to a water feature (DW). We found little correlation between detection parameters (0.07 to 0.47); however, to reduce the number of models we paired T and RH during modeling. SITE was included as a covariate for psi because we hypothesized that occupancy would vary by Conservation Area(Table 3). Sampling visit (V) was included to evaluate species specific seasonal behavioral patterns (Bailey et al. 2004). Climatic data were derived from the National Oceanic and Atmospheric Administration's (NOAA) Keokuk, Iowa weather station. Distance to a water feature was calculated using the near tool in ArcGIS 9.

Patch-level occupancy (Ψ) models were assessed using patch-scale characteristics along with the most supported p model. We considered single covariate models and all possible additive combinations, while keeping highly correlated tree stocking (TS) and canopy cover (CC) separate, for a total of 46 patch-scale models (Table 4). Habitat structure is an important factor for predicting bat use of a locality (Loeb and O'Keefe 2006, Yates and Muzika 2006). We sampled the vegetation at each point, using a 10 factor prism plot. Within each prism plot, we identified tree species, noting their associated diameter at breast height (DBH), and vertical height. Tree stocking was calculated in program SAS using techniques discussed in Johnson et al. (2009). We

derived area land cover types and CC from the National Land Cover Database (NLCD 2001) verifying with NAIP 2009 aerial photographs of the study area. Greater TS and CC were predicted to increase occupancy as this indicates forest cover. Land cover types at each point location were characterized as upland hardwood (ULHD), bottomland hardwood (BLHD), riparian (RIP), or open crop or pasture (OCP). We hypothesized that Ψ would increase with greater percentages of BLHD and RIP habitat and that we would not see an increase with ULHD or OCP. Bats are known to use both riparian areas (LaVal et al. 1977, Barclay 1991, Waldien and Hayes 2001) as well as trails or roads (Krusic et al. 1996, Zimmerman and Glanz 2000, Menzel et al. 2002) for flyways and foraging. Therefore, we hypothesized that we would see an increase in Ψ with a decrease in the distance a bat had to travel to reach a permanent water source (DW) or a flyway (DF). We calculated DW and DF using the near tool in ArcGIS 9. Individual Conservation Areas were designated by site (SITE).

We then assessed landscape-scale characteristics along with the most supported p model. We chose 7 km as the landscape scale to evaluate effects because Womack et al. (2012) found 7 km as the maximum foraging distance traveled by female Indiana bats at CHMCA. Thus, vegetative composition was measured within a 7 km buffer around each sampling site. We considered a total of 8 landscape-scale models (Table 5). We first evaluated landscape composition, determined which parameters fell within the top 90% AIC weight, and ran those in all possible combinations with edge density (ED) and forest connectivity (FC). We used percent upland hardwood (perULHD), percent bottomland hardwood (perBLHD), percent open crop and pasture (perOCP), percent riparian (perRIP) and percent water (perW) to describe landscape composition surrounding each

point. We calculated these covariates in ArcGIS 9 and using NLCD 2001 projections.

We calculated FC as an index ranging from 0-100, with 100 representing a single contiguous block of forest and 0 representing the maximum possible number of small unconnected forest patches and ED in m/ha between forest and open land in FRAGSTATS 3.3 (MacGarigal et al. 2002).

In our final step, we combined top models from both the patch and landscape scale occupancy models with the most supported p model (see results) to estimate best approximating models across scales on probability of occupancy. We determined our top model covariates at the patch and landscape levels using an approach adopted from Arnold (2010) to eliminate uninformative parameters. We considered all possible model combinations resulting in 3 models (Table 6). The models were ranked according to AIC_c outputs. The top model covariates were model averaged (Burnham and Anderson 2002, Wintle et al. 2003). We then calculated odds ratios and 95% odds ratio confidence intervals for parameter estimates to assess which of our top parameters influenced Ψ and p and plotted variables whose 95% odds ratio confidence interval differed from 1. Because program PRESENCE does not determine goodness-of-fit for multi-season models, we determined goodness-of-fit for our models by running a single season analysis of the global model from our combined patch and landscape effects using the 2008 data for each of our study areas.

RESULTS

We obtained acoustic data from 576 sites across the three conservation areas (CHCMA = 202; DRCA = 171; FVLCA = 203) during the summers of 2008-2011. All surveys were conducted between 13 May- 21 August (Julian date 133- 234). The range of maximum

temperature, maximum relative humidity, and mean barometric pressure documented during our surveys were as follows: 11 - 34 degrees C, 59 - 97%, and 28.95- 29.68 in. Hg. Across all survey points, tree stocking ranged from 0 – 306% (mean = 55%) and canopy cover from 0 – 100% (mean = 48%). Distance to water ranged from 1.02 – 680.76 m (mean = 211.57 m) and distance to flyway from 0.08 – 1239.24 m (mean = 183.77 m).

We detected all 10 bat species known to have ranges within the region (*Myotis sodalis*, *M. lucifugus*, *M. septentrionalis*, *M. grisescens*, *Eptesicus fuscus*, *Lasiurus borealis*, *L. cinereus*, *Lasionycteris noctivagans*, *Nycticeius humeralis*, *Pipistrellus subflavus*). Overall, we detected an Indiana bat during one or more surveys at 316 (55%) of the sites. Within each area we detected Indiana bats at 78% of sites within CHMCA, 79% of sites within DRCA, and 11% of sites within FVLCA.

Indiana Bat Probability of Detection

The best supported model for probability of detection included all possible parameters except BP, and carried 71% of the Akaike weight (Table 3). Temperature was positively related to p and JD, RH and DW were negatively related to p . Charlie Heath Memorial Conservation Area was positively related, and FVLCA was negative related to p compared to DRCA, the reference site.

Indiana Bat Patch-level Effects

Site was the most supported patch-level model with 23% of the Akaike weight and the only parameter accounted for in the best model set (Table 4). Site, which indicated differences in occupancy by conservation area, showed CHMCA to be positively and FVLCA to be negatively associated relative to DRCA.

Indiana Bat Landscape-level Effects

At the landscape-level, perBLHD was the most supported covariate, positively affecting Ψ . It alone represented our top model, carried 53% of the Akaike weight, and was the only variable considered to be included in the best model set (Table 5).

Indiana Bat Combined Patch and Landscape-level Effects

Model averaged parameter estimates and odds ratios indicate that perBLHD positively influenced Ψ , showing significant support and carrying 82% of the Akaike weight (Table 6, 7). Predicted occupancy based on exact means for each conservation area are plotted (Figure 8). The additional models of per BLHD+SITE and SITE did not overcome the AIC point penalty and had odds ratio confidence intervals which overlapped 1 indicating no significance. Percent bottomland hardwood combined with SITE carried 13%, and SITE alone carried the remaining 5%. A goodness-of-fit test using the 2008 data suggests unexplained variability with differing results among sites (CHMCA: $P = 0.002$, $c\text{-hat} = 3.112$ and DRCA: $P = 0.001$, $c\text{-hat} = 2.7994$). We were unable to assess a $c\text{-hat}$ score for FVLCA due to the low detection of Indiana bats at this area creating zero inflation to high to allow convergence of models, however $P = 0.9980$.

DISCUSSION

We found strong support for a positive relationship of the amount of bottomland hardwood with site occupancy by summering Indiana bats. In all three of our study areas, bottomland hardwood was the least represented vegetative type, yet the top predictor for Indiana bat occupancy. No other factor or combination of factors had significant and strong effects on occupancy. Our study indicated very little detection (11%) of Indiana bats at FVLCA compared to that of CHMCA (78%) and DRCA (79%).

Vegetative composition was relatively similar between all three areas with the exception of the amount of bottomland hardwood. Even so, this is only representing the difference between 1.6% bottomland hardwood within our buffered landscape at FVLCA, 2.8% at DRCA, and 3.4% at CHMCA. Even small increases of percent bottomland hardwood in the landscape shows a large increase in predicted Indiana bat occupancy. Other studies have similarly found support for the importance of bottomland forest, indicating Indiana bats forage preferentially in riparian and floodplain forest, even though they will also use upland forest, edges, old fields, and ponds (Humphrey et al. 1977, Clawson et al. 2006). A bottomland forest provides more diverse prey opportunities as both aquatic and terrestrial prey are available. Because these areas are subject to periodic flooding, the understory is usually free of dense clutter, and the mature canopy remains intact which in turn may open flyways for foraging (Womack, 2012). This periodic flooding also tends to create snags typical of Indiana bat roosts.

Carter (2006) assessed three broad reasons for why Indiana bats seem to prefer “hydric” habitats: 1) anthropogenic forces, 2) roosting resources, and 3) foraging resources. He determined that anthropogenic changes in land use did not pressure bats into using hydric habitats, as large expanses of upland forest are not selected for over smaller, more manipulated hydric habitats (Ulrey et al. 2005). The literature supports Carter’s hypothesis that foraging resources do influence the preference of hydric habitats by Indiana bats as evident in a number of studies. Humphrey et al. (1977) indicated that Indiana bats restricted their foraging to riparian areas. For example, Murray and Kurta (2002) showed a correlation of foraging with the presence of hydric habitats through a diet of aquatic insects. Menzel et al. (2005) showed that Indiana bats foraged

preferentially closer to forests, roads, and riparian habitats versus grasslands and agricultural land. Sparks et al. (2005) found that Indiana bats chose wooded corridors associates with local streams to forage in even though the majority of the habitat within their range consisted of agriculture. Thus collectively this work emphasizes the importance of hydric habitat such as bottomland forest for Indiana bats.

However, Indiana bats also require adequate roost trees in addition to their preference of hydric habitats which continues to be impacted by stream channelization, conversion of forests to agriculture, and urbanization (Conlin 1976, Garner and Gardner 1992). Carter (2006) determined that roosting resources did not influence Indiana bats' use of hydric habitat. This was evident at CHMCA where roost trees were documented in both upland and bottomland habitats (Womack, 2012). Womack (2012) also attributed her finding of canopy cover as a significant factor for Indiana bats to its association to roost trees. Our study found no association to canopy cover, thus we hypothesize that although a high percentage canopy cover may be indicative of good roost habitat, it is not a principal driver of Indiana bat occupancy.

We incorporated detectability models into our analysis methodology due to the nature of using acoustic detection to determine presence/absence of the Indiana bat. Detection distances vary with amplitude of the echolocation calls, atmospheric attenuation, structural clutter, directional characteristics and sensitivity of the detector used. All but one parameter (BP) combined for the most support for our detectability of Indiana bats. Our models included very high K values in part due to the large number of parameters derived from these detectability models, and in particular because our study included such a large number of sampling visits (16) over four seasons. Because a high

number of parameters were a concern, we conducted exploratory analyses with simplified models and found no indication of a high K value to be problematic. We also had poor resolution of our models at the patch occupancy level, but good resolution at the landscape-level, indicating that the broader landscape composition is more important for predicting the distribution of Indiana bats and perhaps should be considered when designing management plans for this species.

MANAGEMENT IMPLICATIONS

Bottomland hardwood forests once covered approximately twelve million ha across the southeastern United States. Because of its rich soils, the economic benefits of agricultural production make it a target for conversion from its natural state and currently only about 40% of the historic amount of this forest type remains with the majority found in Gulf States and south of the Indiana bat range (EPA 2012). However, approximately 30% of the endangered species, including the Indiana bat, within the southeastern United States depend on bottomland hardwoods during some portion of the year (Ernst and Brown 1989). Particular care should be taken to protect and manage remaining bottomland hardwood forests as even small tracts may be useful. This may be helped by targeting private landowners to donate existing bottomland hardwood habitat on their property as a conservation easement to a land trust. We further recommend that managers target reestablishment of bottomland hardwood forest as an important goal for restoring Indiana bats.

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Table1. Landscape Composition of Charlie Heath Memorial Conservation Area, Deer Ridge Conservation Area, and Fox Valley Lake Conservation Area including a 7 km buffer around each area. OCP is open crop and pasture, ULHD is upland hardwood, BLHD is bottomland hardwood, RIP is riparian.

Study Area Landscape Composition			
Fox Valley CA	Sq. meters	Hectares	Percent
OCP	226436400	22644	69.7
ULHD	68304600	6830	21.0
BLHD	5073300	507	1.6
WATER	1367100	137	0.4
RIP	23862600	2386	7.3
TOTAL	325044000	32504	100.0
Charlie Heath CA	Sq. meters	Hectares	Percent
OCP	167515200	16752	62.4
ULHD	68323500	6832	25.4
BLHD	9063000	906	3.4
WATER	2683800	268	1.0
RIP	21022200	2102	7.8
TOTAL	268607700	26861	100.0
Deer Ridge CA	Sq. meters	Hectares	Percent
OCP	292872600	29287	71.4
ULHD	78169500	7817	19.0
BLHD	11419200	1142	2.8
WATER	2448900	245	0.6
RIP	25555500	2556	6.2
TOTAL	410465700	41047	100.0

Table 2. Covariate hypotheses for Indiana bat occupancy.

Affect	Covariate	Measurement	Hypotheses	Model
Detection Probability (p)				
Sound	Temperature (T)	Maximum each night during sampling interval	> T = > attenuation of sound = < detectability of high frequency calls	$p(T)$
	Relative Humidity (RH)	Maximum each night during sampling interval	> RH = > attenuation of sound = < detectability of high frequency calls	$p(RH)$
	Barometric Pressure (BP)	Mean for each night during sampling interval	> BP = > attenuation of sound = < detectability of high frequency calls	$p(BP)$
Temporal	Julian Date (JD)		seasonal affects = > insect noise levels = < detectability of calls	$p(JD)$
Attractant	Distance to Water (DW)	Km	< DW = > bat abundance = > detection	$p(DW)$
Occupancy (ψ)				
Patch	Vegetation Type (VT)	Mixed hardwoods + upland topographic position (ULHD)	< ULHD = > bat occupancy	$\psi(ULHD)$
		Mixed hardwoods + lowland topographic position (BLHD)	> BLHD = > bat occupancy	$\psi(BLHD)$
		Riparian landscape within 30m of permanent streams (RIP)	> RIP = > bat occupancy	$\psi(RIP)$
		Open crop and pasture (OCP)	< OCP = > bat occupancy	$\psi(OCP)$
	Tree Stocking (TS)	Stems per hectare (measured greater than 2.5 cm)	> TS = > bat occupancy	$\psi(TS)$
	Distance to Nearest Permanent Water Source (DW)	Km	< DW = > bat occupancy	$\psi(DW)$
	Distance to Flyways (DF)	km to roads and trails	< DF = > bat occupancy	$\psi(DF)$
	Canopy Closure (CC)	Measured with densitometer	> CC = > bat occupancy	$\psi(CC)$
Landscape (7km)	Vegetative/Water Composition	% Forest (ULHD+ BLHD) (%F)	> %F = > bat occupancy	$\psi(%F)$
		% Open crop and pasture (%OCP)	< %OCP = > bat occupancy	$\psi(%OCP)$
		% Water (%W)	> %W = > bat occupancy	$\psi(%W)$
		% Riparian (%RIP)		
	Forest Connectivity (FC)	Connectivity (FRAGSTATS)	> FC = > bat occupancy	$\psi(FC)$
	Edge Density (ED)	Edge Density (FRAGSTATS)	> ED= < bat occupancy	$\psi(ED)$

Table 3. Ranking of detection probability models assessing temporal and environmental variables for Indiana bats in Charlie Heath Memorial Conservation Area, Deer Ridge Conservation Area, and Fox Valley Lake Conservation Area during summer 2008- 2011 surveys. K is the number of parameters in the model, -2*LL is -2*log- likelihood, AICc is Akaike's Information Criterion, Δ AIC_c is the difference in AIC_c value from the top model, w_i is the Akaike weight, and ML is the model likelihood.

Detection Probability (p) Model	K	-2*LL	AICc	Δ AICc	w_i	ML
psi(SITE),gamma(),eps(),p(V+JD+T+RH+DW)	25	3311.75	3361.75	0	0.71	1
psi(SITE),gamma(),eps(),p(V+JD+T+RH+BP+DW)	26	3311.57	3363.57	1.82	0.29	0.4
psi(SITE),gamma(),eps(),p(V+JD+T+RH)	24	3324.03	3372.03	10.28	0	0
psi(SITE),gamma(),eps(),p(V+JD+T+RH+BP)	25	3323.79	3373.79	12.04	0	0
psi(SITE),gamma(),eps(),p(V+T+RH+DW)	24	3329.26	3377.26	15.51	0	0
psi(SITE),gamma(),eps(),p(V+T+RH+BP+DW)	25	3328.86	3378.86	17.11	0	0
psi(SITE),gamma(),eps(),p(V+JD+BP+DW)	24	3330.97	3378.97	17.22	0	0
psi(SITE),gamma(),eps(),p(V+JD+DW)	23	3338.04	3384.04	22.29	0	0
psi(SITE),gamma(),eps(),p(V+BP+DW)	23	3338.31	3384.31	22.56	0	0
psi(SITE),gamma(),eps(),p(V+JD+BP)	23	3340.77	3386.77	25.02	0	0
psi(SITE),gamma(),eps(),p(V+DW)	22	3342.91	3386.91	25.16	0	0
psi(SITE),gamma(),eps(),p(V+T+RH)	23	3341.5	3387.5	25.75	0	0
psi(SITE),gamma(),eps(),p(V+T+RH+BP)	24	3341.04	3389.04	27.29	0	0
psi(SITE),gamma(),eps(),p(V+JD)	22	3347.2	3391.2	29.45	0	0
psi(SITE),gamma(),eps(),p(V+BP)	22	3349.07	3393.07	31.32	0	0
psi(SITE),gamma(),eps(),p(V)	21	3352.97	3394.97	33.22	0	0
psi(SITE),gamma(),eps(),p(.)	6	3464.7	3476.7	114.95	0	0

Table 4. Ranking of occupancy models assessing vegetative and spatial variables, while incorporating the most supported detection (p) model, for Indiana bats in Charlie Heath Memorial Conservation Area, Deer Ridge Conservation Area, and Fox Valley Lake Conservation Area during summer 2008- 2011 surveys. K is the number of parameters in the model, -2*LL is -2*log- likelihood, AICc is Akaike's Information Criterion, Δ AIC_c is the difference in AIC_c value from the top model, w_i is the Akaike weight, and ML is the model likelihood.

Patch-scale Occupancy (Ψ) Model	K	-2*LL	AICc	Δ AICc	w_i	ML
psi(SITE),gamma(),eps(),p(V+JD+T+RH+DW)	25	3311.75	3361.75	0	0.23	1
psi(SITE+DF),gamma(),eps(),p(V+JD+T+RH+DW)	26	3311.44	3363.44	1.69	0.10	0.43
psi(SITE+DW),gamma(),eps(),p(V+JD+T+RH+DW)	26	3311.51	3363.51	1.76	0.10	0.41
psi(SITE+CC),gamma(),eps(),p(V+JD+T+RH+DW)	26	3311.59	3363.59	1.84	0.09	0.40
psi(SITE+TS),gamma(),eps(),p(V+JD+T+RH+DW)	26	3311.6	3363.6	1.85	0.09	0.40
psi(SITE+DF+TS),gamma(),eps(),p(V+JD+T+RH+DW)	27	3311.23	3365.23	3.48	0.04	0.18
psi(SITE+DF+CC),gamma(),eps(),p(V+JD+T+RH+DW)	27	3311.28	3365.28	3.53	0.04	0.17
psi(SITE+DF+DW),gamma(),eps(),p(V+JD+T+RH+DW)	27	3311.29	3365.29	3.54	0.04	0.17
psi(SITE+TS+DW),gamma(),eps(),p(V+JD+T+RH+DW)	27	3311.29	3365.29	3.54	0.04	0.17
psi(SITE+DW+CC),gamma(),eps(),p(V+JD+T+RH+DW)	27	3311.32	3365.32	3.57	0.04	0.17
psi(SITE+VT),gamma(),eps(),p(V+JD+T+RH+DW)	28	3309.79	3365.79	4.04	0.03	0.13
psi(SITE+VT+DW),gamma(),eps(),p(V+JD+T+RH+DW)	29	3307.92	3365.92	4.17	0.03	0.12
psi(SITE+DF+DW+TS),gamma(),eps(),p(V+JD+T+RH+DW)	28	3311.03	3367.03	5.28	0.02	0.07
psi(SITE+DF+DW+CC),gamma(),eps(),p(V+JD+T+RH+DW)	28	3311.11	3367.11	5.36	0.02	0.07
psi(SITE+DF+VT),gamma(),eps(),p(V+JD+T+RH+DW)	29	3309.12	3367.12	5.37	0.02	0.07
psi(SITE+DF+VT+DW),gamma(),eps(),p(V+JD+T+RH+DW)	30	3307.5	3367.5	5.75	0.01	0.06
psi(SITE+CC+VT),gamma(),eps(),p(V+JD+T+RH+DW)	29	3309.74	3367.74	5.99	0.01	0.05
psi(SITE+TS+VT),gamma(),eps(),p(V+JD+T+RH+DW)	29	3309.77	3367.77	6.02	0.01	0.05
psi(SITE+VT+DW+TS),gamma(),eps(),p(V+JD+T+RH+DW)	30	3307.87	3367.87	6.12	0.01	0.05
psi(SITE+VT+DW+CC),gamma(),eps(),p(V+JD+T+RH+DW)	30	3307.88	3367.88	6.13	0.01	0.05
psi(SITE+VT+DF+TS),gamma(),eps(),p(V+JD+T+RH+DW)	30	3309.09	3369.09	7.34	0.01	0.03
psi(SITE+VT+DF+CC),gamma(),eps(),p(V+JD+T+RH+DW)	30	3309.11	3369.11	7.36	0.01	0.03
psi(SITE+VT+DW+DF+TS),gamma(),eps(),p(V+JD+T+RH+DW)	31	3307.44	3369.44	7.69	0.01	0.02
psi(SITE+VT+DW+DF+CC),gamma(),eps(),p(V+JD+T+RH+DW)	31	3307.48	3369.48	7.73	0	0.02

JD+T+RH+DW)						
psi(DF+VT),gamma(),eps(),p(V+JD+T+RH+DW)	27	3417.79	3471.79	110.04	0	0
psi(DF+DW+VT),gamma(),eps(),p(V+JD+T+RH+DW)	28	3417.74	3473.74	111.99	0	0
psi(DF+DW+CC+VT),gamma(),eps(),p(V+JD+T+RH+DW)	29	3415.94	3473.94	112.19	0	0
psi(DF+DW+TS+VT),gamma(),eps(),p(V+JD+T+RH+DW)	29	3417.68	3475.68	113.93	0	0
psi(DF+CC),gamma(),eps(),p(V+JD+T+RH+DW)	25	3429.01	3479.01	117.26	0	0
psi(DF+DW+CC),gamma(),eps(),p(V+JD+T+RH+DW)	26	3427.03	3479.03	117.28	0	0
psi(DF+DW+TS),gamma(),eps(),p(V+JD+T+RH+DW)	26	3435.06	3487.06	125.31	0	0
psi(DF+TS),gamma(),eps(),p(V+JD+T+RH+DW)	25	3437.88	3487.88	126.13	0	0
psi(DF+DW),gamma(),eps(),p(V+JD+T+RH+DW)	25	3441.15	3491.15	129.4	0	0
psi(DF),gamma(),eps(),p(V+JD+T+RH+DW)	24	3445.59	3493.59	131.84	0	0
psi(CC+VT),gamma(),eps(),p(V+JD+T+RH+DW)	27	3439.9	3493.9	132.15	0	0
psi(VT),gamma(),eps(),p(V+JD+T+RH+DW)	26	3442.56	3494.56	132.81	0	0
psi(DW+CC+VT),gamma(),eps(),p(V+JD+T+RH+DW)	28	3438.71	3494.71	132.96	0	0
psi(VT+DW),gamma(),eps(),p(V+JD+T+RH+DW)	27	3441.54	3495.54	133.79	0	0
psi(TS+VT),gamma(),eps(),p(V+JD+T+RH+DW)	27	3442.56	3496.56	134.81	0	0
psi(CC),gamma(),eps(),p(V+JD+T+RH+DW)	24	3448.78	3496.78	135.03	0	0
psi(DW+TS+VT),gamma(),eps(),p(V+JD+T+RH+DW)	28	3441.53	3497.53	135.78	0	0
psi(CC+DW),gamma(),eps(),p(V+JD+T+RH+DW)	25	3448.55	3498.55	136.8	0	0
psi(TS),gamma(),eps(),p(V+JD+T+RH+DW)	24	3458.35	3506.35	144.6	0	0
psi(TS+DW),gamma(),eps(),p(V+JD+T+RH+DW)	25	3457.73	3507.73	145.98	0	0
psi(.),gamma(),eps(),p(V+JD+T+RH+DW)	23	3463.71	3509.71	147.96	0	0
psi(DW),gamma(),eps(),p(V+JD+T+RH+DW)	24	3462.24	3510.24	148.49	0	0

Table 5. Modeling landscape-scale factors for Indiana bats in Charlie Heath Memorial Conservation Area, Deer Ridge Conservation Area, and Fox Valley Lake Conservation Area during summer 2008- 2011 surveys. K is the number of parameters in the model, -2*LL is -2*log- likelihood, AICc is Akaike's Information Criterion, ΔAIC_c is the difference in AIC_c value from the top model, w_i is the Akaike weight, and ML is the model likelihood.

Landscape-scale Occupancy (Ψ) Model	K	-2*LL	AICc	ΔAIC_c	w_i	ML
psi(perBLHD),gamma(),eps(),p(V+JD+T+RH+DW)	24	3307.93	3355.93	0	0.53	1
psi(perBLHD+ED),gamma(),eps(),p(V+JD+T+RH+DW)	25	3307.89	3357.89	1.96	0.20	0.38
psi(perBLHD+FC),gamma(),eps(),p(V+JD+T+RH+DW)	25	3307.93	3357.93	2	0.20	0.37
psi(perBLHD+FC+ED),gamma(),eps(),p(V+JD+T+RH+DW)	26	3307.89	3359.89	3.96	0.07	0.14
psi(perED),gamma(),eps(),p(V+JD+T+RH+DW)	24	3461.14	3509.14	153.21	0	0
psi(),gamma(),eps(),p(V+JD+T+RH+DW)	23	3463.71	3509.71	153.78	0	0
psi(perED+FC),gamma(),eps(),p(V+JD+T+RH+DW)	25	3460.9	3510.9	154.97	0	0
psi(FC),gamma(),eps(),p(V+JD+T+RH+DW)	24	3463.47	3511.47	155.54	0	0

Table 6. Final modeling output for Indiana bats in Charlie Heath Memorial Conservation Area, Deer Ridge Conservation Area, and Fox Valley Lake Conservation Area during summer 2008- 2011 surveys. K is the number of parameters in the model, -2*LL is -2*log- likelihood, AICc is Akaike's Information Criterion, Δ AIC_c is the difference in AIC_c value from the top model, w_i is the Akaike weight, and ML is the model likelihood.

Final Model Output	K	-2*LL	AICc	Δ AICc	w_i	ML
psi(perBLHD),gamma(),eps(),p(V+JD+T+RH+DW)	24	3307.93	3355.93	0	0.82	1
psi(SITE+perBLHD),gamma(),eps(),p(V+JD+T+RH+DW)	26	3307.62	3359.62	3.69	0.13	0.16
psi(SITE),gamma(),eps(),p(V+JD+T+RH+DW)	25	3311.75	3361.75	5.82	0.04	0.05

Table 7. Model averaged parameter estimates of the top model set for Indiana bats in Charlie Heath Memorial Conservation Area, Deer Ridge Conservation Area, and Fox Valley Lake Conservation Area during summer 2008- 2011 surveys. LCL is lower confidence level, UCL is upper confidence level, perBLHD is percent bottomland hardwood within the 7 km landscape and SITE is conservation area relative to Deer Ridge Conservation Area: s1= Charlie Heath Conservation Area, s2 = Fox Valley Lake Conservation Area.

	Parameter Coefficient	Odds Ratio	LCL	UCL
perBLHD	1.720969657	5.58994617	1.91996902	16.27500125
SITE (s1)	-0.112623349	0.893487129	0.536118486	1.489072419
SITE (s2)	0.711651817	2.037353817	0.167707998	24.75022432

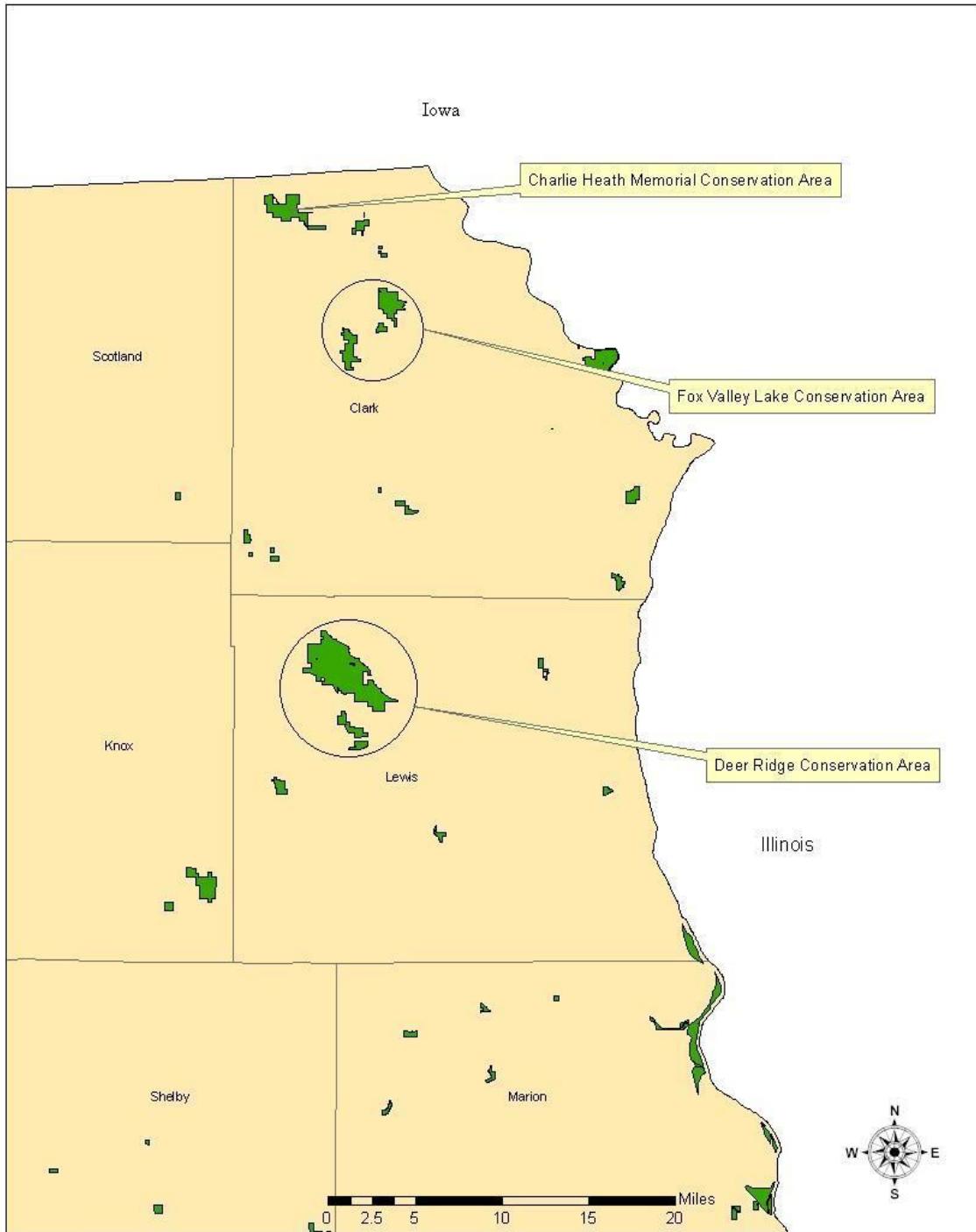


Figure 1. Northeast corner of Missouri showing Missouri Department of Conservation owned land including the 3 study sites (figure by T. Elliot, Missouri Department of Conservation).

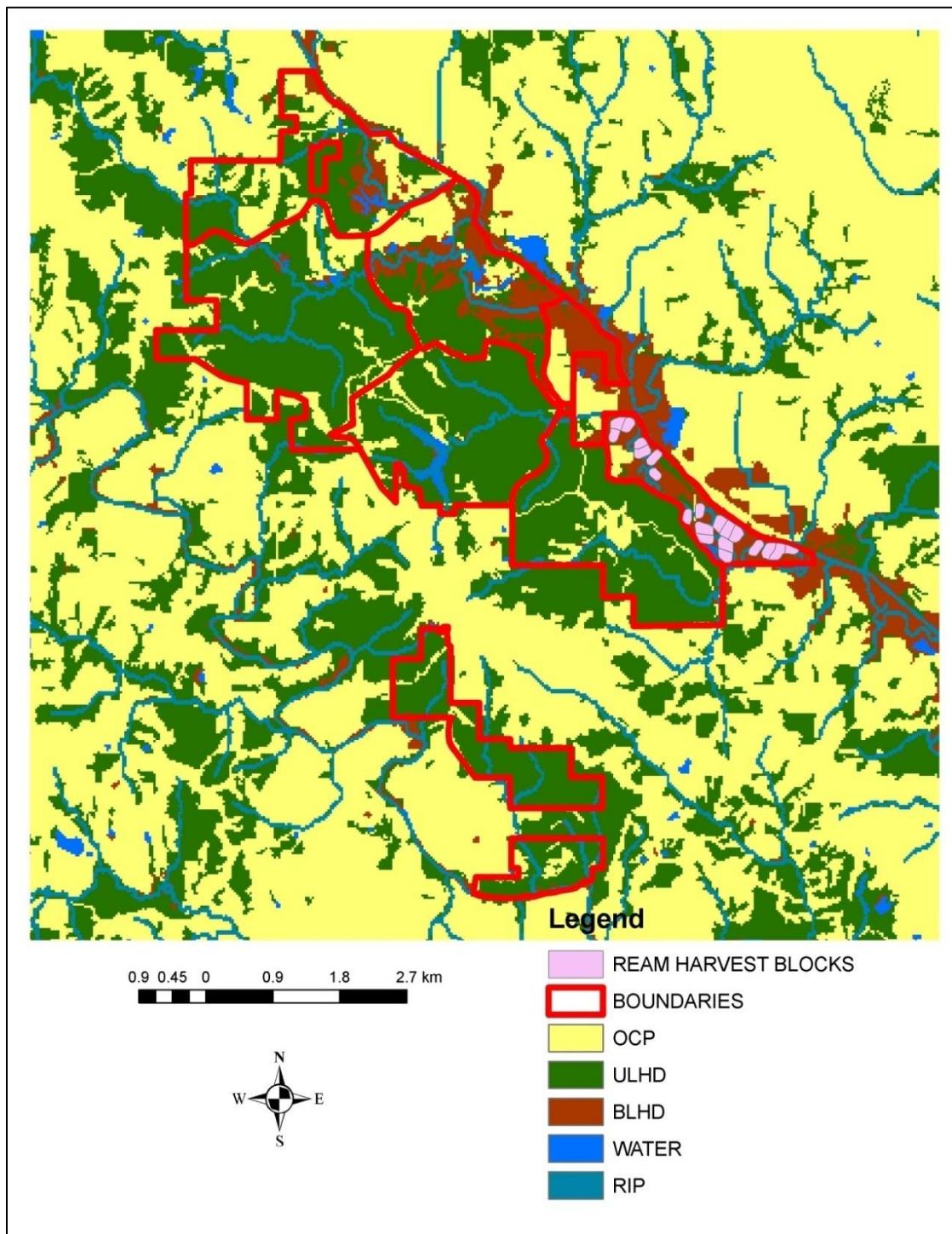
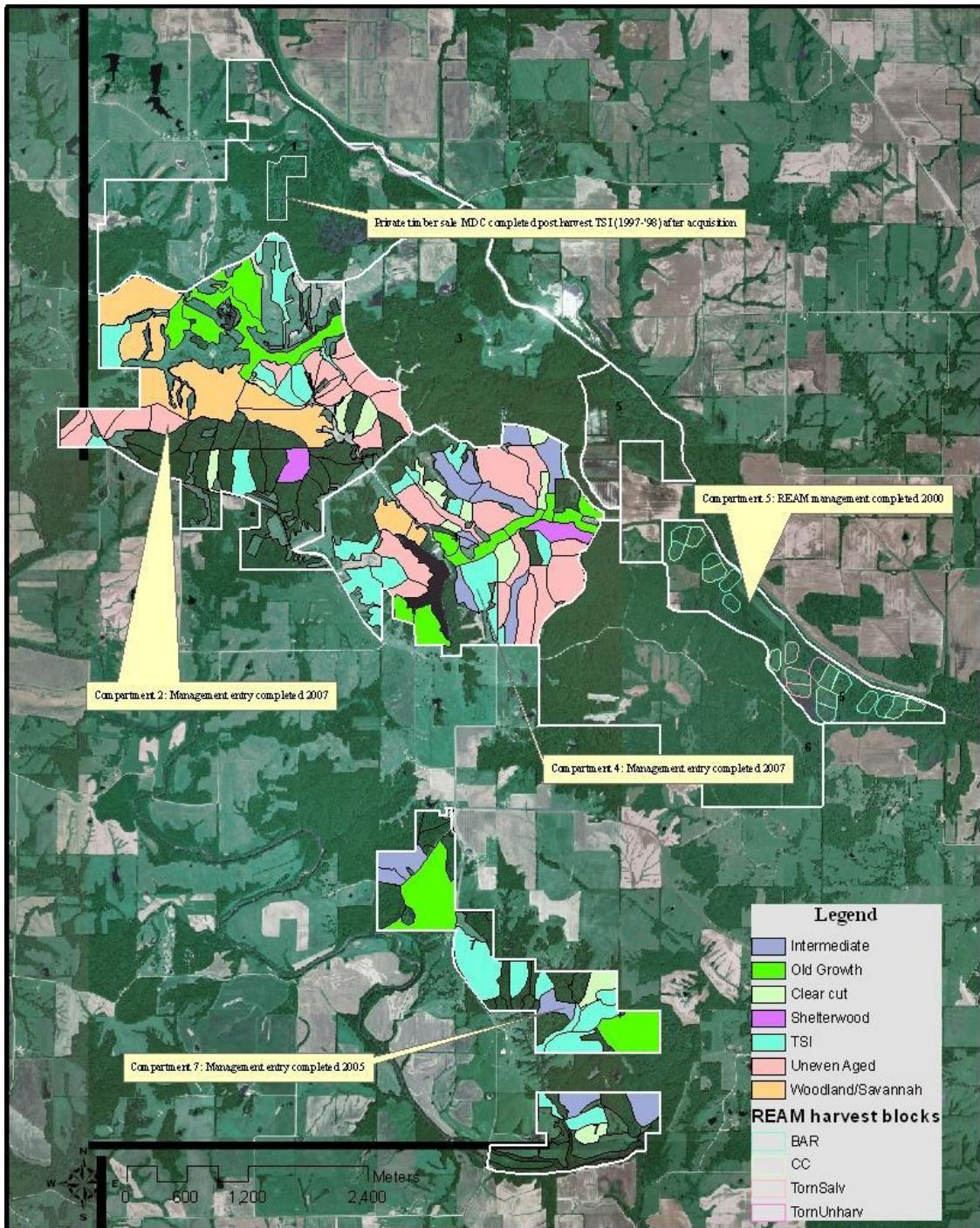


Figure 2. Deer Ridge Conservation Area, Lewis County, Missouri. REAM = Riparian Ecosystem Assessment and Management Project, OCP = Open Crop and Pasture, ULHD = Upland Hardwood Forest, BLHD = Bottomland Hardwood Forest, Water = water, RIP = Riparian Habitat.



Deer Ridge CA forest management prescriptions and timing.

Figure 3. Deer Ridge Conservation Area forest management prescriptions and timing (T. Elliot, Missouri Department of Conservation).

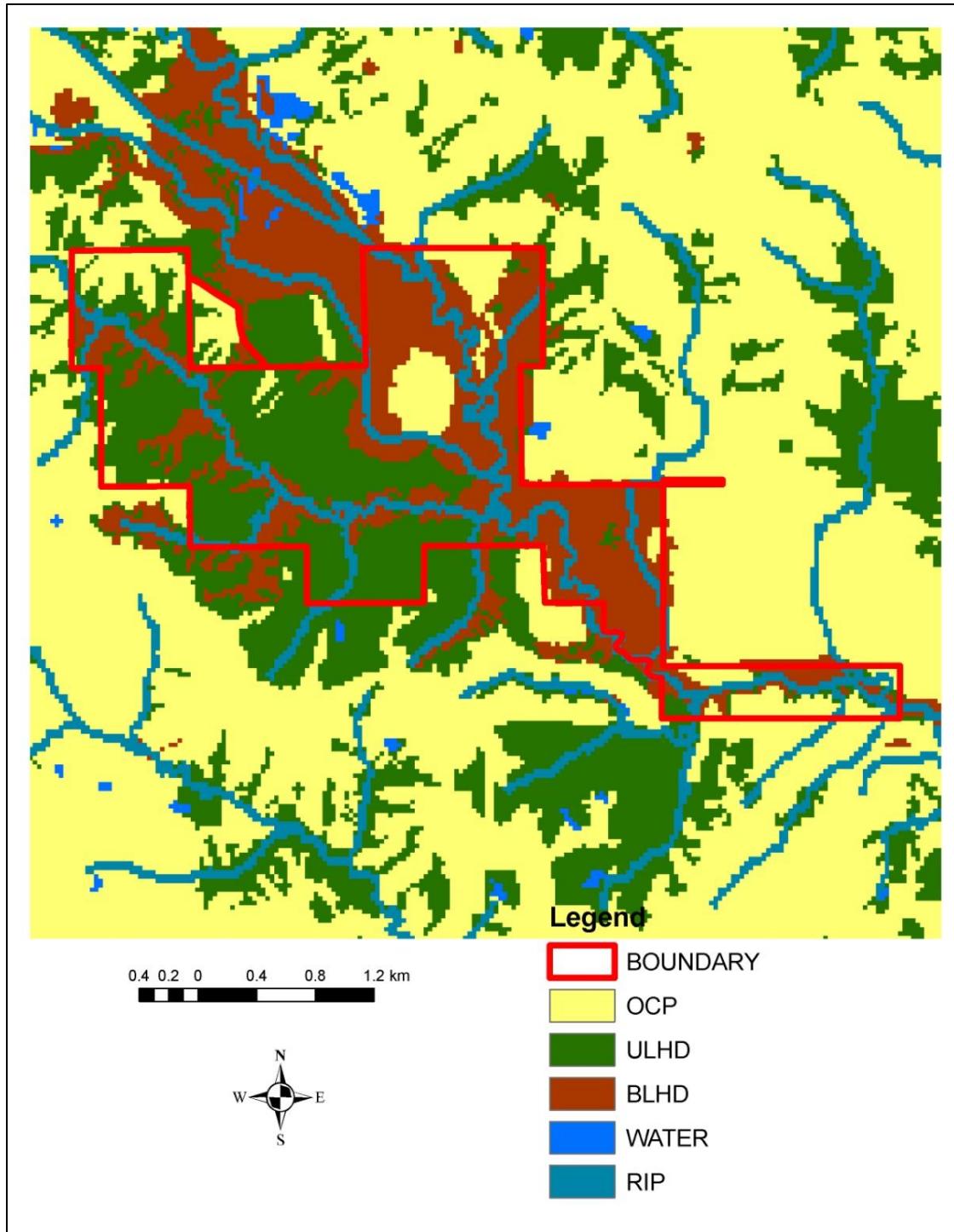


Figure 4. Charlie Heath Memorial Conservation Area, Clark County, Missouri. OCP = Open Crop and Pasture, ULHD = Upland Hardwood Forest, BLHD = Bottomland Hardwood Forest, Water = water, RIP = Riparian Habitat.

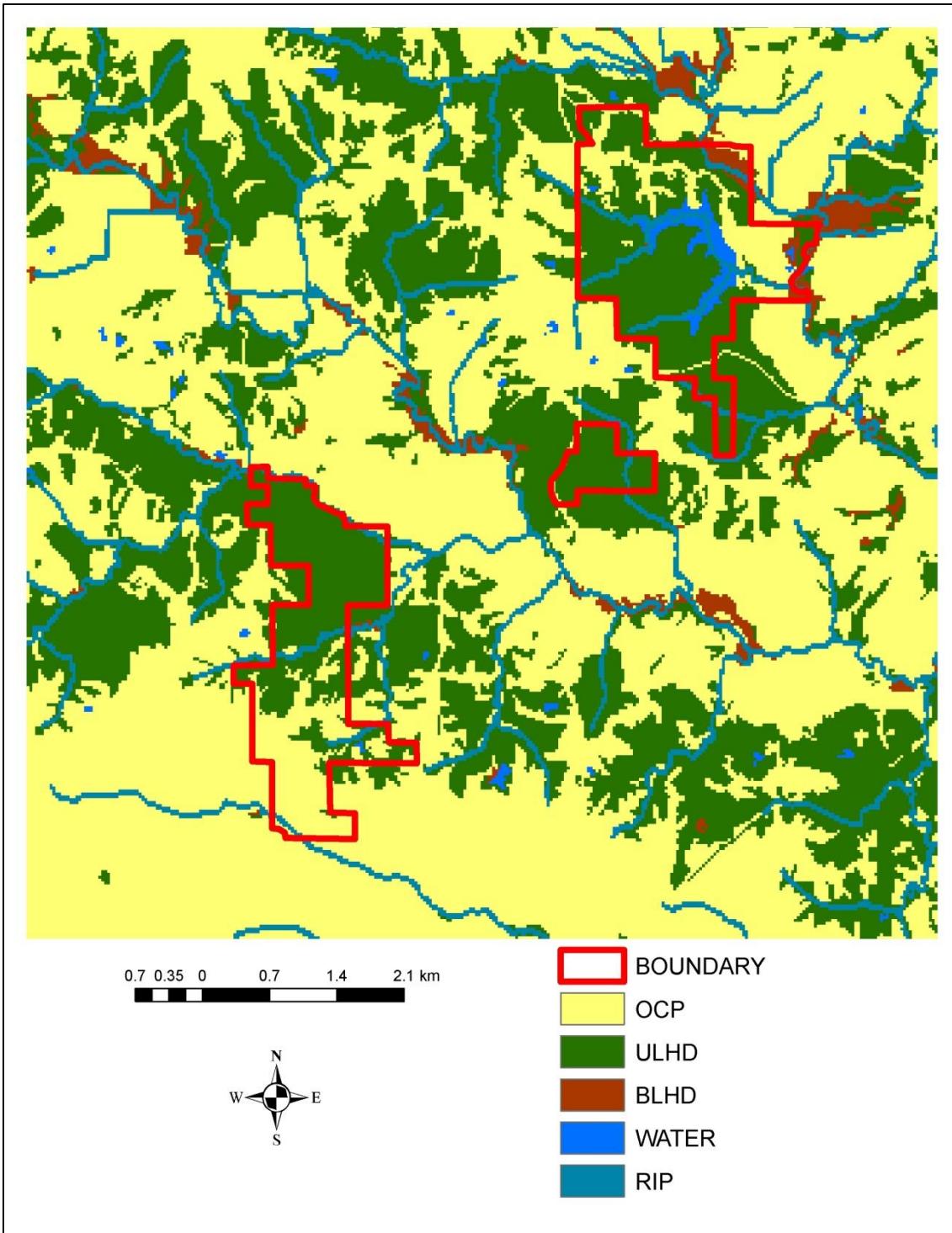


Figure 5. Fox Valley Lake Conservation Area, Clark County, Missouri. OCP = Open Crop and Pasture, ULHD = Upland Hardwood Forest, BLHD = Bottomland Hardwood Forest, Water = water, RIP = Riparian Habitat.

FOX VALLEY COMPARTMENT 1

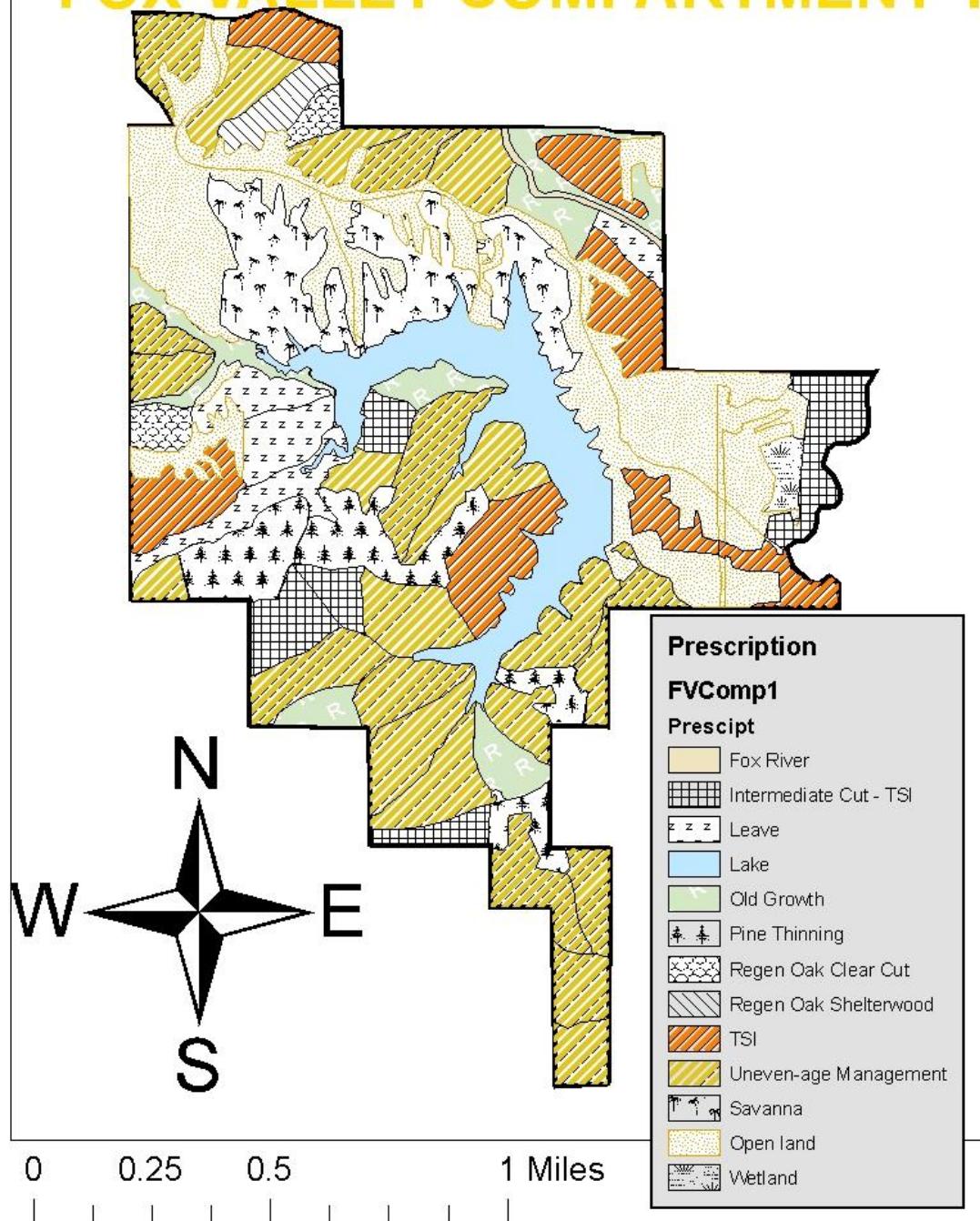


Figure 6. Forest management prescription for Fox Valley Lake Conservation Area (T. Elliot, Missouri Department of Conservation).



Figure 7. Anabat detector housed within a Pelican case for protection from inclement weather. The microphone is aligned with an opening leading to a polyvinyl chloride (PVC) elbow directed upwards at 45 degrees to minimize noise interference on the ground. A 12-volt battery is used to power the anabat for two consecutive days (Design by Joe Amelon).

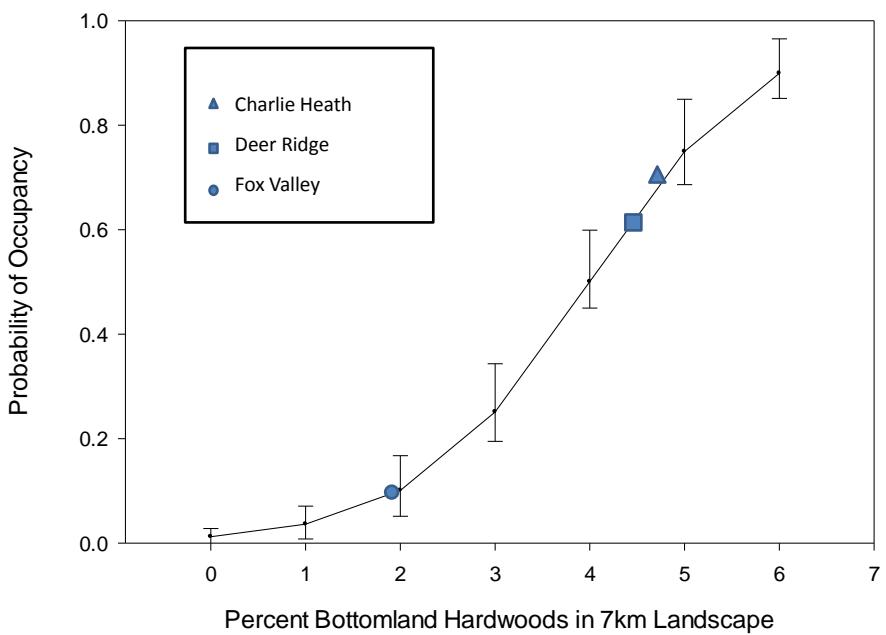


Figure 8. Predicted mean (+/- 95% CI) probability of site occupancy based on effect of percent bottomland hardwoods for Indiana bats in northeast Missouri 2008-2011. Predicted effects are model averaged over the best model set for site occupancy at 7 kilometer spatial scale. Calculated mean for each conservation area was as follows for Indiana bats: CHMCA = 0.677, DRCA = 0.612, FVLCA = 0.082.

CHAPTER 2

DIFFERENCES IN HABITAT USE BY INDIANA (*MYOTIS SODALIS*) AND LITTLE BROWN (*M. LUCIFUGUS*) BATS: INSIGHTS FROM OCCUPANCY MODELING

ABSTRACT

The Indiana bat (*M. sodalis*) has been listed as endangered since 1967 and remains critically imperiled throughout its range. Past conservation efforts have emphasized protecting known hibernacula, with a current trend towards addressing summer habitat needs, so far with little success towards recovering the species. Little is known about interspecific interactions such as competition, and its potential role in directly or indirectly predicting habitat use. In a previous study we constructed landscape occupancy models for the Indiana bat, finding that bottomland hardwood habitat was the best predictor of Indiana bat occupancy. We applied a similar maximum likelihood approach to estimate probability of site occupancy using acoustic detection data for the little brown bat (*M. lucifugus*) in three locations in northeastern Missouri. We evaluated *a priori* hypotheses relative to both probability of detection and site occupancy using an objective model selection criterion to rank the candidate models. Top models predicting little brown bat occupancy were principally based on patch-scale measures of distance to water and canopy cover. We then used this information to determine whether knowledge of the little brown bat's landscape occupancy patterns improved the fit of Indiana bat occupancy models and vice versa. We found they did not. The Indiana bat shows a

strong preference for bottomland hardwood habitat, while the little brown bat appears to be more of a generalist. The little brown bat has been suggested as an ecological surrogate for the endangered Indiana bat. Their differential habitat use indicates such treatment should proceed with caution.

KEY WORDS acoustic monitoring, Program PRESENCE, interspecific competition, resource partitioning, landscape occupancy

INTRODUCTION

A major goal of community ecology is to understand mechanisms of species coexistence. Many bat species are morphologically similar and appear to be opportunistic foragers, leading to predictions that competitive niche arrangements would play a minor role in bat community organization (Arlettaz 1999), or that bat communities are under the control of non-deterministic processes and that species co-occur simply by chance (Willig and Moulton 1989, Arita 1997). Alternatively, while little is known regarding interactions such as interspecific competition among bat species, it has been shown to occur. Kunz (1973) and LaVal et al. (1977) both showed multiple species (including the Indiana bat, *Myotis sodalis* and little brown bat, *M. lucifugus*, the subjects of this paper) establishing differences in temporal and spatial foraging patterns putatively to lower direct competition. Varying degrees of differential insect selection has been shown among bat species in southwestern New Mexico, presumably as a result of competition (Black 1974). Husar (1976) showed that two largely allopatric species of *Myotis* changed their food preferences to avoid competition in areas of sympatry. Arlettaz et al. (2000) suggest that competition for food by expanding pipistrelle bat populations (*Pipistrellus pipistrellus*) might be contributing to the decline of lesser horseshoe bats (*Rhinolophus*

hipposideros). And more recently, Bumrungsri et al. (2007) found a clear example of resource partitioning by means of diet and habitat partitioning between two closely related fruit bats in Thailand.

We used occupancy modeling to provide insight into the distribution of two closely related, sympatric, and potentially competing species, the endangered Indiana bat and the common little brown bat. The Indiana bat has a low reproductive rate and roost in colonies during both maternity and hibernation periods, making them susceptible to many threats that typically cause declines in bat populations including disease and human disturbance. The species was listed as endangered by the U.S Department of Interior, Fish and Wildlife Service in 1967 and remains critically imperiled throughout much of its geographic range (USFWS 1996). Current research on Indiana bat landscape ecology emphasizes roosting and summer habitat requirements (Menzel et al. 2001, Britzke et al. 2003, Timpone 2004, Menzel et al. 2005, Carter 2006, Hein et al. 2009, Womack 2012, Chapter 1) with less in regards to interspecies relationships (Lee and McCracken 2004, Bergeson, 2012). Both species are found in abundance throughout our study areas and are morphologically similar; indeed the species were considered the same species until 1928 (Miller and Allen 1928) and the little brown bat is sometimes used as a surrogate of the Indiana bat (Schmidt et al. 2002). Both species also share extremely similar structure in echolocation calls and are known to use aerial hawking foraging strategies (Fenton and Bogdanowicz 2002). Therefore, Indiana bats and little brown bats might select for the same types of summer foraging habitat and compete for food resources. Further, while the Indiana bat struggles to persist, the little brown bat is common, suggesting the

possibility of a competitive interaction between the two acting to underpin failure of Indiana bats to recover.

Working at three conservation areas in northern Missouri, our objective was to determine site occupancy of the Indiana bat and little brown bat and then to develop models that predict whether or not the addition of little brown bat occupancy improves the ability to predict Indiana bat occupancy (and vice versa) based on knowledge of their respective patterns of co-occurrence. In a previous study of Indiana bat landscape occupancy (Chapter 1) we applied a maximum likelihood approach to estimate probability of site occupancy using acoustic detection data by evaluating *a priori* hypotheses relative to both probability of detection and site occupancy using an objective model selection criterion to rank candidate models. This occupancy modeling framework helps to better understand the habitat and management features that best predict the distribution of Indiana bats within our study regions.

Indiana bats are known to be associated with hydric habitats when foraging (Humphrey et al. 1977, Murray and Kurta 2002, Menzel 2005, Sparks et al. 2005, Ulrey 2005, Carter 2006), and reflecting this we found, with high significance, that the amount of bottomland hardwood habitat found within a 7 km. buffered landscape was the single most determining factor predicting Indiana bat occupancy. However, we did note some occupancy of Indiana bats in all habitat types throughout the study area. In addition, Womack (2012) found Indiana bats roosting in upland habitat at one of our study sites. Collectively, this suggests other factors may also influence Indiana bat occupancy.

Little brown bats are a widespread species and are associated with a wide variety of habitats, but have been reported to show a tendency towards the use of hydric habitats

(Belwood and Fenton 1976, Anthony and Kunz 1977, Bergeson 2012). Little brown bats are also known to use anthropogenic roosts in addition to roosting within dead trees whereas Indiana bats tend to avoid using anthropogenic roosts (Schowalter et al. 1979, Barclay and Cash 1985, Bergeson 2012).

Lee and McCracken (2004) suggest that inter-specific competition may cause Indiana and little brown bats to partition resources. By examining habitat use of sympatric populations of these species through occupancy modeling, we attempt to provide more insight into their ecological relationship. Our framework for doing this was to build occupancy models for the little brown bat and use them to quantify site-specific occupancy, and then ask if the predictive value of the Indiana bat model is improved by including our knowledge of little brown bat occupancy. Given that such interactions, if they occur, are potentially bilateral, we also ask the similar question of whether the little brown bat model is improved by incorporating knowledge of Indiana bat occupancy.

STUDY AREA

We studied Indiana and little brown bats on Charlie Heath Memorial Conservation Area (CHMCA), Fox Valley Lake Conservation Area (FVLCA), and Deer Ridge Conservation Area (DRCA) during the summers of 2008-2011. The three sites are in close proximity (< 64 km) (Figure 1) and occupied by both Indiana and little brown bats. These conservation areas, managed by the Missouri Department of Conservation (MDC), represent forest patches surrounded predominantly by agricultural lands. Oak-hickory was the dominate forest type with both upland and bottomland forest represented in each area. Deer Ridge Conservation Area received timber management designed to enhance habitat use by the Indiana bat between 2003 and 2008, prior to our study. Small clear

cuts, uneven aged forest harvest, and retention of snag trees were the dominant practices. Commercial uneven aged forest harvest and post-harvest slashing occurred on FVLCA over the fall and winter of 2008. No timber management had occurred prior or during our study at CHMCA, however, prescribed fires were conducted annually in April on two separate units totaling 33 ha from 2006-2009. For further details on the three sites, see chapter 1.

METHODS

During the summers of 2008-2011 (from May-early August to coincide with time spent by bats in nursery colonies) and following methods discussed in chapter 1, we collected and analyzed acoustic detection histories for the little brown bat. We also used the same modeling approach described in chapter 1 to then determine the little brown bat's detection probability, patch-scale, and landscape-scale occupancy characteristics.

For detection probability (p) and site occupancy (Ψ) modeling, our general approach was to contrast the *a priori* hypotheses we developed for the Indiana bat (Table 1), which we expressed as models that could be fit to data collected from sample units and ranked in terms of their ability to explain the empirical data relative to little brown bats using an information-theoretic model selection criterion (Akaike's Information Criteria, AIC_c) (Burnham and Anderson 2002).

Environmental conditions and characteristics of a bat echolocation call influence the range of detection (Lacki et al. 2007, Weller 2007). We therefore hypothesized that bat detection would be affected by sound attenuation due to temperature (T), maximum relative humidity (RH), and mean barometric pressure (BP), time within season or Julian Date (JD), and proximity of water (DW) as an attractant. SITE was included as a

covariate for psi because we hypothesized that occupancy would vary by Conservation Area. Sampling visit (V) was included in all models to evaluate species specific seasonal behavioral patterns (Bailey et al. 2004). Keeping T and RH paired, we considered single covariate models and all possible additive combinations for a total of 17 models.

Climatic data were derived from the National Oceanic and Atmospheric Administration's (NOAA) Keokuk, Iowa weather station. Distance to a water feature was calculated using the near tool in ArcGIS 9.

Patch-level occupancy (Ψ) models were assessed always including the most supported p model. We considered single covariate models and all possible additive combinations; while keeping highly correlated tree stocking (TS) and canopy cover (CC) separate, for a total of 46 patch-scale models. Within a 10 factor prism plot surrounding each survey point, we identified tree species, noting their associated diameter at breast height (DBH), and vertical height using this information to calculate TS in program SAS (Johnson et al. 2009). We derived area land cover types and CC from the National Land Cover Database (NLCD 2001) verifying with NAIP 2009 aerial photographs of the study area. Land cover types at each point location were characterized as upland hardwood (ULHD), bottomland hardwood (BLHD), riparian (RIP), or open crop or pasture (OCP). Bats use riparian areas (LaVal et al. 1977, Barclay 1991, Waldien and Hayes 2001) as well as trails or roads (Krusic et al. 1996, Zimmerman and Glanz 2000, Menzel et al. 2002) for flyways and foraging. Therefore, we hypothesized that we would see an increase in Ψ with a decrease in the distance a bat had to travel to reach a permanent water source (DW) or a flyway (DF). We calculated DW and DF using the near tool in ArcGIS 9. Individual Conservation Areas were designated by site (SITE).

We assessed landscape-scale (buffered at 7 km) characteristics along with the most supported p model following hypotheses for the Indiana bat (chapter 1). First we evaluated landscape composition, determined which parameters fell within the top 90% AIC weight, and ran those in all possible combinations with edge density (ED) and forest connectivity (FC). We considered a total of 16 landscape-scale models (Table 5). We used percent upland hardwood (perULHD), percent bottomland hardwood (perBLHD), percent open crop and pasture (perOCP), percent riparian (perRIP) and percent water (perW) to describe landscape composition surrounding each point. We calculated these covariates in ArcGIS 9 and using NLCD 2001 projections. We calculated FC as an index ranging from 0-100, with 100 representing a single contiguous block of forest and 0 representing the maximum possible number of small unconnected forest patches and ED in m/ha between forest and open land in FRAGSTATS 3.3 (MacGarigal et al. 2002).

We estimated the overall covariate effects on probability of occupancy for the little brown bat, using its most supported p model. We combined models found in the top patch-scale and landscape-scale models resulting in all possible combinations totaling 3 models (see results). The models were ranked according to AIC_c outputs. Parameters of highly supported models were examined in more detail by calculating odds ratios and by graphing the relationships of these metrics with Ψ . Because program PRESENCE does not determine goodness-of-fit for multi-season models, we determined goodness-of-fit for our models by running a single season analysis of the global model from our combined patch and landscape effects using the 2008 data for each of our study areas.

To initially assess patterns of co-occurrence and determine whether occupancy of Indiana bats and little brown bats occurred randomly with respect to each other, we

examined our presence/absence of each species at each survey site using Pearson's Chi-square tests. To further determine whether the little brown bat's occupancy affected the ability to predict Indiana bat occupancy, we contrasted our overall top model for the Indiana bat with the same model using occupancy estimates generated for each location of little brown bat included as an additional covariate. We also modeled the reciprocal, contrasting our overall top model for the little brown bat with the addition of the Indiana bat as a covariate.

RESULTS

We obtained acoustic data from 576 sites across all three conservation areas (CHCMA = 202; DRCA = 171; FVLCA = 203) during the summers of 2008-2011. All surveys were conducted between 13 May- 21 August (Julian date 133- 234). The range of maximum temperature, maximum relative humidity, and mean barometric pressure documented during our surveys were as follows: 11 - 34 degrees C, 59 - 97%, and 28.95- 29.68 in. Hg. Across all survey points, tree stocking ranged from 0 – 306% (mean = 55%) and canopy cover from 0 – 100% (mean = 48%). Distance to water ranged from 1.02 – 680.76 m (mean = 211.57 m) and distance to flyway from 0.08 – 1239.24 m (mean = 183.77 m).

We detected an Indiana bat at 316 (55%) sites and a little brown bat at 412 (72%) sites during one or more surveys. Within CHMCA we detected Indiana bats at 78% of the survey sites and little brown bats at 64% of the sites. Within DRCA we detected Indiana bats at 79% of the sites and little brown bats at 80% of the sites. Within FVLCA we detected Indiana bats at only 11% of the sites while detecting little brown bats at 72% of the sites. When evaluating patterns of co-occurrence we found strong non-random

patterns both overall and within each of the conservation areas ($P < 0.001$ in all instances except FVLCA for which $P = 0.04$).

Little Brown Bat Probability of Detection

The best supported model for probability of detection of little brown bat included T, RH, and DW. This top model carried 19% of the Akaike weight. The second best supported model carried 17% of the Akaike weight and included the same parameters as the top model with the addition of JD (Table 2). Julian date, T, and DW were positively related to p , while RH was negatively associated. Relative to DRCA, CHMCA was negatively associated and FVLCA positively associated for little brown bat occupancy.

Little Brown Bat Patch-level Effects

Site (Conservation Area) combined with DW and CC represented the top site occupancy model for the little brown bat, carrying 19% of the Akaike weight (Table 3). Site combined with DF, DW, and CC came in second with 17% of the Akaike weight, but the addition of DF was uninformative. Therefore, SITE, DW, and CC were the only parameters carried forward as our “best” model set for the little brown bat. Both DW and CC were negatively associated to Ψ . Relative to DRCA, CHMCA was negatively associated and FVLCA positively associated for little brown bat occupancy.

Little Brown Bat Landscape-level Effects

For the little brown bat, perW combined with ED was the top model affecting Ψ at the landscape-level, carrying 31% of the Akaike weight (Table 4). These were the only 2 variables considered for our final modeling output. Percent water was negatively associated to Ψ while ED was positively associated.

Little Brown Bat Combined Patch and Landscape-level Effects

Site combined with DW and CC represented our top model, carrying 45% of the weight (Table 5). Percent water combined with ED came in second, carrying 33% of the weight. None of the parameters showed significant support when assessing the confidence intervals of calculated model averaged odds ratios (Table 6). A goodness-of-fit test using the 2008 data suggests there may be some unexplained variability with differing results among sites (CHMCA: $P = 0.007$, c-hat = 2.2567; DRCA: $P = 0.5075$, c-hat = 0.9488; FVLCA: $P = 0.0350$, c-hat = 1.7905).

Indiana and Little Brown Bat Interaction

The addition of little brown bat estimated occupancy as a covariate to the Indiana bat model did not improve Indiana bat occupancy with a Δ AICc of 1.94 and carrying 27% of the weight (Table 7). Evidence ratios indicated Indiana bat occupancy was nearly 3x better (2.703) without the influence of little brown bat estimated occupancy. The reciprocal model (the addition of Indiana bat estimated occupancy as a covariate to the little brown bat model) also did not improve the little brown bat occupancy model (Δ AICc = 1.76; $w_i = 29\%$) (Table 8). Evidence ratios indicated little brown bat occupancy was more than 2x better (2.448) without the influence of Indiana bat estimated occupancy.

DISCUSSION

Occupancy modeling indicates that Indiana bats are using bottomland hardwood habitat for foraging (chapter 1), while little brown bats are more general in habitat use while foraging. Though not significant, our top model indicates that less distance to a water source increases the likelihood of little brown bat occupancy. This finding coincides with

those of several studies regarding the Indiana bat (Humphrey et al. 1977, Clawson et al. 2006), and with presumed little brown bat ecology which are also typically deemed to be associated with hydric habitats (Belwood and Fenton 1976, Anthony and Kunz 1977). In our study found no one factor to be truly indicative of little brown bat occupancy. Bergeson (2012) found little brown bats to roost in bottomland hardwood habitat alongside Indiana bats, but fly further distances while foraging. Bergeson (2012) documented little brown bats to have an average home range of $2739 \pm 456\text{ha}$ which is nearly quadruple that of the largest home range (709.8ha) documented by an Indiana bat within our study area (Womack 2012). Because little brown bats forage more extensively across the landscape, this may help explain why we are not finding occupancy of little brown bats to be driven by a certain habitat type as we did with Indiana bats.

Although the Chi-square results give the appearance of non-randomness and thus an interaction suggestive of competition and resource partitioning, the more sophisticated occupancy modeling do not support a strong interaction that underpins habitat use. Because these bats are morphologically similar, use the same foraging strategies, and consume the same diet, it is still possible they are occurring in different habitat types to partition the available resources. Bergeson (2012) compared the home range and habitat use of both species within the same study sites and found them to partition resources by varying the habitat they selected while foraging. This allowed the two species to avoid foraging within the same habitats for prolonged periods of time. Bergeson (2012) found that although both species roosted in the same bottomland forest, little brown bats would travel large distances to forage in other habitat patches while Indiana bats remained in bottomland hardwood habitat. Our results do not imply that such hypothesized

competition is absent. Rather, it implies that competition, if it does exist between these species is less important than habitat selection in underpinning the patterns of occupancy.

MANAGEMENT IMPLICATIONS

Little brown bats are often considered to be the best surrogate species for Indiana bats.

To make a good surrogate, the little brown bat should similarly match the ecological needs of the Indiana bat. Our research indicates that these species are selecting for different foraging habitat when in sympatry. Because management for endangered species often focuses on the preferred habitat, managers should use caution in assuming the little brown bat is a good surrogate species.

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Table 1. Covariate hypotheses for Indiana bat occupancy.

Affect	Covariate	Measurement	Hypotheses	Model
Detection Probability (p)				
Sound	Temperature (T)	Maximum each night during sampling interval	$> T = >$ attenuation of sound = $<$ detectability of high frequency calls	$p(T)$
	Relative Humidity (RH)	Maximum each night during sampling interval	$> RH = >$ attenuation of sound = $<$ detectability of high frequency calls	$p(RH)$
	Barometric Pressure (BP)	Mean for each night during sampling interval	$> BP = >$ attenuation of sound = $<$ detectability of high frequency calls	$p(BP)$
Temporal	Julian Date (JD)		seasonal affects = $>$ insect noise levels = $<$ detectability of calls	$p(JD)$
Attractant	Distance to Water (DW)	Km	$< DW = >$ bat abundance = $>$ detection	$p(DW)$
Occupancy (ψ)				
Patch	Vegetation Type (VT)	Mixed hardwoods + upland topographic position (ULHD)	$< ULHD = >$ bat occupancy	$\psi(ULHD)$
		Mixed hardwoods + lowland topographic position (BLHD)	$> BLHD = >$ bat occupancy	$\psi(BLHD)$
		Riparian landscape within 30m of permanent streams (RIP)	$> RIP = >$ bat occupancy	$\psi(RIP)$
		Open crop and pasture (OCP)	$< OCP = >$ bat occupancy	$\psi(OCP)$
	Tree Stocking (TS)	Stems per hectare (measured greater than 2.5 cm)	$> TS = >$ bat occupancy	$\psi(TS)$
	Distance to Nearest Permanent Water Source (DW)	Km	$< DW = >$ bat occupancy	$\psi(DW)$
	Distance to Flyways (DF)	km to roads and trails	$< DF = >$ bat occupancy	$\psi(DF)$
	Canopy Closure (CC)	Measured with densitometer	$> CC = >$ bat occupancy	$\psi(CC)$
Landscape (7km)	Vegetative/Water Composition	% Forest (ULHD+ BLHD) (%F)	$> %F = >$ bat occupancy	$\psi(%F)$
		% Open crop and pasture (%OCP)	$< %OCP = >$ bat occupancy	$\psi(%OCP)$
		% Water (%W)	$> %W = >$ bat occupancy	$\psi(%W)$
		% Riparian (%RIP)		
	Forest Connectivity (FC)	Connectivity (FRAGSTATS)	$> FC = >$ bat occupancy	$\psi(FC)$
	Edge Density (ED)	Edge Density (FRAGSTATS)	$> ED = <$ bat occupancy	$\psi(ED)$

Table 2. Ranking of detection probability models assessing temporal and environmental variables for little brown bats in Charlie Heath Memorial Conservation Area, Deer Ridge Conservation Area, and Fox Valley Lake Conservation Area during summer 2008- 2011 surveys. K is the number of parameters in the model, -2*LL is -2*log- likelihood, AIC_c is Akaike's Information Criterion, Δ AIC_c is the difference in AIC_c value from the top model, w_i is the Akaike weight, and ML is the model likelihood.

Detection Probability (p) Model	K	-2*LL	AIC_c	Δ AIC_c	w_i	ML
psi(SITE),gamma(),eps(),p(V+T+RH+DW)	24	4278.78	4326.78	0	0.19	1
psi(SITE),gamma(),eps(),p(V+JD+T+RH+DW)	25	4277	4327	0.22	0.17	0.8958
psi(SITE),gamma(),eps(),p(V+JD+DW)	23	4281.74	4327.74	0.96	0.12	0.6188
psi(SITE),gamma(),eps(),p(V+DW)	22	4284.17	4328.17	1.39	0.10	0.4991
psi(SITE),gamma(),eps(),p(V+T+RH+BP+DW)	25	4278.64	4328.64	1.86	0.08	0.3946
psi(SITE),gamma(),eps(),p(V+JD+T+RH+BP+DW)	26	4276.97	4328.97	2.19	0.06	0.3345
psi(SITE),gamma(),eps(),p(V+T+RH)	23	4283.37	4329.37	2.59	0.05	0.2739
psi(SITE),gamma(),eps(),p(V+JD+T+RH)	24	4281.6	4329.6	2.82	0.05	0.2441
psi(SITE),gamma(),eps(),p(V+JD+BP+DW)	24	4281.74	4329.74	2.96	0.04	0.2276
psi(SITE),gamma(),eps(),p(V+BP+DW)	23	4284.16	4330.16	3.38	0.04	0.1845
psi(SITE),gamma(),eps(),p(V+JD)	22	4286.63	4330.63	3.85	0.03	0.1459
psi(SITE),gamma(),eps(),p(V+T+RH+BP)	24	4283.14	4331.14	4.36	0.02	0.113
psi(SITE),gamma(),eps(),p(V)	21	4289.38	4331.38	4.6	0.02	0.1003
psi(SITE),gamma(),eps(),p(V+JD+T+RH+BP)	25	4281.51	4331.51	4.73	0.02	0.0939
psi(SITE),gamma(),eps(),p(V+JD+BP)	23	4286.63	4332.63	5.85	0.01	0.0537
psi(SITE),gamma(),eps(),p(V+BP)	22	4289.37	4333.37	6.59	0.01	0.0371
psi(SITE),gamma(),eps(),p(.)	6	4359.36	4371.36	44.58	0.00	0

Table 3. Ranking of occupancy models assessing vegetative and spatial variables, while incorporating the most supported detection (p) model, for little brown bats in Charlie Heath Memorial Conservation Area, Deer Ridge Conservation Area, and Fox Valley Lake Conservation Area during summer 2008- 2011 surveys. K is the number of parameters in the model, -2*LL is -2*log- likelihood, AIC_c is Akaike's Information Criterion, Δ AIC_c is the difference in AIC_c value from the top model, w_i is the Akaike weight, and ML is the model likelihood.

Patch-scale Occupancy (Ψ) Model	K	-2*LL	AIC_c	Δ AIC_c	w_i	ML
psi(SITE+DW+CC),gamma(),eps(),p(V+T+RH+DW)	26	4270.56	4322.56	0	0.19	1
psi(SITE+DF+DW+CC),gamma(),eps(),p(V+T+RH+DW)	27	4268.76	4322.76	0.2	0.17	0.90
psi(SITE+TS+DW),gamma(),eps(),p(V+T+RH+DW)	26	4271.46	4323.46	0.9	0.12	0.63
psi(SITE+DF+DW+TS),gamma(),eps(),p(V+T+RH+DW)	27	4269.72	4323.72	1.16	0.11	0.56
psi(SITE+DF+DW),gamma(),eps(),p(V+T+RH+DW)	26	4272.73	4324.73	2.17	0.06	0.33
psi(SITE+CC),gamma(),eps(),p(V+T+RH+DW)	25	4274.9	4324.9	2.34	0.06	0.31
psi(SITE+DW),gamma(),eps(),p(V+T+RH+DW)	25	4275.14	4325.14	2.58	0.05	0.28
psi(SITE+TS),gamma(),eps(),p(V+T+RH+DW)	25	4275.99	4325.99	3.43	0.03	0.18
psi(SITE+DF+CC),gamma(),eps(),p(V+T+RH+DW)	26	4274.33	4326.33	3.77	0.03	0.15
psi(SITE),gamma(),eps(),p(V+T+RH+DW)	24	4278.78	4326.78	4.22	0.02	0.12
psi(SITE+DF+TS),gamma(),eps(),p(V+T+RH+DW)	26	4275.43	4327.43	4.87	0.02	0.09
psi(SITE+DF),gamma(),eps(),p(V+T+RH+DW)	25	4277.77	4327.77	5.21	0.01	0.07
psi(SITE+DF+VT+DW+CC),gamma(),eps(),p(V+T+RH+DW)	30	4268.02	4328.02	5.46	0.01	0.07
psi(SITE+VT+DW+CC),gamma(),eps(),p(V+T+RH+DW)	29	4270.09	4328.09	5.53	0.01	0.06
psi(SITE+DF+VT+DW),gamma(),eps(),p(V+T+RH+DW)	29	4270.22	4328.22	5.66	0.01	0.06
psi(SITE+VT+DW),gamma(),eps(),p(V+T+RH+DW)	28	4272.22	4328.22	5.66	0.01	0.06
psi(SITE+VT+CC),gamma(),eps(),p(V+T+RH+DW)	28	4272.35	4328.35	5.79	0.01	0.06
psi(SITE+VT),gamma(),eps(),p(V+T+RH+DW)	27	4274.36	4328.36	5.8	0.01	0.06
psi(SITE+VT+DW+TS),gamma(),eps(),p(V+T+RH+DW)	29	4270.44	4328.44	5.88	0.01	0.05
psi(SITE+DF+VT+DW+TS),gamma(),eps(),p(V+T+RH+DW)	30	4268.61	4328.61	6.05	0.01	0.05
psi(SITE+VT+TS),gamma(),eps(),p(V+T+RH+DW)	28	4272.65	4328.65	6.09	0.01	0.05
psi(SITE+DF+VT+CC),gamma(),eps(),p(V+T+RH+DW)	29	4270.95	4328.95	6.39	0.01	0.04
psi(SITE+DF+VT),gamma(),eps(),p(V+T+RH+DW)	28	4272.99	4328.99	6.43	0.01	0.04
psi(SITE+DF+VT+TS),gamma(),eps(),p(V+T+RH+DW)	29	4271.42	4329.42	6.86	0.01	0
psi(CC),gamma(),eps(),p(V+T+RH+DW)	23	4287.84	4333.84	11.28	0	0
psi(DW+CC),gamma(),eps(),p(V+T+RH+DW)	24	4286.23	4334.23	11.67	0	0

psi(DF+CC),gamma(),eps(),p(V+T+RH+DW)	24	4287.83	4335.83	13.27	0	0
psi(DF+CC+DW),gamma(),eps(),p(V+T+RH+DW)	25	4286.18	4336.18	13.62	0	0
psi(VT+CC),gamma(),eps(),p(V+T+RH+DW)	26	4284.86	4336.86	14.3	0	0
psi(VT+CC+DW),gamma(),eps(),p(V+T+RH+DW)	27	4283.41	4337.41	14.85	0	0
psi(TS),gamma(),eps(),p(V+T+RH+DW)	23	4291.53	4337.53	14.97	0	0
psi(VT),gamma(),eps(),p(V+T+RH+DW)	25	4287.79	4337.79	15.23	0	0
psi(DW+TS),gamma(),eps(),p(V+T+RH+DW)	24	4290.06	4338.06	15.5	0	0
psi(TS+VT),gamma(),eps(),p(V+T+RH+DW)	26	4286.48	4338.48	15.92	0	0
psi(DW+VT),gamma(),eps(),p(V+T+RH+DW)	26	4286.66	4338.66	16.1	0	0
psi(DW+VT+TS),gamma(),eps(),p(V+T+RH+DW)	27	4285.21	4339.21	16.65	0	0
psi(DF+VT+DW+CC),gamma(),eps(),p(V+T+R+DW)	28	4283.27	4339.27	16.71	0	0
psi(DF+TS),gamma(),eps(),p(V+T+RH+DW)	24	4291.51	4339.51	16.95	0	0
psi(DF+VT),gamma(),eps(),p(V+T+RH+DW)	26	4287.74	4339.74	17.18	0	0
psi(DF+TS+DW),gamma(),eps(),p(V+T+RH+DW)	25	4290.04	4340.04	17.48	0	0
psi(DF+VT+DW),gamma(),eps(),p(V+T+RH+DW)	27	4286.53	4340.53	17.97	0	0
psi(),gamma(),eps(),p(V+T+RH+DW)	22	4296.57	4340.57	18.01	0	0
psi(DF+VT+DW+TS),gamma(),eps(),p(V+T+R+DW)	28	4285.14	4341.14	18.58	0	0
psi(DW),gamma(),eps(),p(V+T+RH+DW)	23	4296.01	4342.01	19.45	0	0
psi(DF),gamma(),eps(),p(V+T+RH+DW)	23	4296.53	4342.53	19.97	0	0
psi(DF+DW),gamma(),eps(),p(V+T+RH+DW)	24	4295.86	4343.86	21.3	0	0

Table 4. Modeling landscape-scale factors for little brown bats in Charlie Heath Memorial Conservation Area, Deer Ridge Conservation Area, and Fox Valley Lake Conservation Area during summer 2008- 2011 surveys. K is the number of parameters in the model, -2*LL is -2*log- likelihood, AIC_c is Akaike's Information Criterion, Δ AIC_c is the difference in AIC_c value from the top model, w_i is the Akaike weight, and ML is the model likelihood.

Landscape-scale Occupancy (Ψ) Model	K	-2*LL	AIC _c	Δ AIC _c	w _i	ML
psi(perW+ED),gamma(),eps(),p(V+T+RH+DW)	24	4275.15	4323.15	0	0.31	1
psi(perW+perULHD+ED),gamma(),eps(),p(V+T+RH+DW)	25	4275.03	4325.03	1.88	0.12	0.39
psi(perW+ED+FC),gamma(),eps(),p(V+T+RH+DW)	25	4275.15	4325.15	2	0.12	0.37
psi(perW+perULHD),gamma(),eps(),p(V+T+RH+DW)	24	4277.16	4325.16	2.01	0.11	0.37
psi(perW),gamma(),eps(),p(V+T+RH+DW)	23	4279.4	4325.4	2.25	0.10	0.32
psi(perW+perULHD+FC),gamma(),eps(),p(V+T+RH+DW)	25	4276.48	4326.48	3.33	0.06	0.19
psi(perW+FC),gamma(),eps(),p(V+T+RH+DW)	24	4278.76	4326.76	3.61	0.05	0.16
psi(perW+perULHD+ED+FC),gamma(),eps(),p(V+T+RH+DW)	26	4274.81	4326.81	3.66	0.05	0.16
psi(perULHD),gamma(),eps(),p(V+T+RH+DW)	23	4282.03	4328.03	4.88	0.03	0.09
psi(perULHD+ED),gamma(),eps(),p(V+T+RH+DW)	24	4280.61	4328.61	5.46	0.02	0.07
psi(perULHD+ED+FC),gamma(),eps(),p(V+T+RH+DW)	25	4279.48	4329.48	6.33	0.01	0.04
psi(perULHD+FC),gamma(),eps(),p(V+T+RH+DW)	24	4282.03	4330.03	6.88	0.01	0.03
psi(FC),gamma(),eps(),p(V+T+RH+DW)	23	4289.42	4335.42	12.27	0	0
psi(ED+FC),gamma(),eps(),p(V+T+RH+DW)	24	4288.71	4336.71	13.56	0	0
psi(,),gamma(),eps(),p(V+T+RH+DW)	22	4296.57	4340.57	17.42	0	0
psi(ED),gamma(),eps(),p(V+T+RH+DW)	23	4296.07	4342.07	18.92	0	0

Table 5. Final modeling output for little brown bats in Charlie Heath Memorial Conservation Area, Deer Ridge Conservation Area, and Fox Valley Lake Conservation Area during summer 2008- 2011 surveys. K is the number of parameters in the model, -2*LL is -2*log- likelihood, AIC_c is Akaike's Information Criterion, Δ AIC_c is the difference in AIC_c value from the top model, w_i is the Akaike weight, and ML is the model likelihood.

Final Model Output	K	-2*LL	AIC_c	Δ AIC_c	w_i	ML
psi(SITE+DW+CC),gamma(),eps(),p(V+T+RH+DW)	26	4270.56	4322.56	0	0.45	1
psi(perW+ED),gamma(),eps(),p(V+T+RH+DW)	24	4275.15	4323.15	0.59	0.33	0.74
psi(SITE+DW+CC+perW+ED),gamma(),eps(),p(V+T+RH+DW)	28	4267.96	4323.96	1.4	0.22	0.50

Table 6. Model averaged parameter estimates of the top model set for little brown bats in Charlie Heath Memorial Conservation Area, Deer Ridge Conservation Area, and Fox Valley Lake Conservation Area during summer 2008- 2011 surveys. SE is unconditional standard error, LCL is lower confidence level, UCL is upper confidence level, SITE is conservation area relative to Deer Ridge Conservation Area: s1= Charlie Heath Conservation Area, s2 = Fox Valley Lake Conservation Area, DW is distance to water, CC is canopy cover, perW is percent water within the 7 km landscape, and ED is forest edge density.

	Parameter Coefficient	Odds Ratio	LCL	UCL
CHMCA	-0.595	0.5514	0.1666	1.8258
FVLCA	0.25051487	1.284686693	0.508104905	3.2481873
DW	-0.001542672	0.998458518	0.995960899	1.0009624
CC	-0.00621465	0.993804618	0.983219454	1.00450374
perW	-0.988365	0.3821846	0.033945	4.080764
ED	0.091318533	1.09561794	0.915024007	1.311854838

Table 7. Indiana bat/ little brown bat interaction modeling output for Charlie Heath Memorial Conservation Area, Deer Ridge Conservation Area, and Fox Valley Lake Conservation Area during summer 2008- 2011 surveys. K is the number of parameters in the model, -2*LL is -2*log- likelihood, AIC is Akaike's information criterion, Δ AIC is the difference in AIC value from the top model, w_i is the Akaike weight, and ML is the model likelihood.

Indiana Bat/ Little Brown Bat	K	-2*LL	AIC	Δ AIC	w	ML
psi(perBLHD),gamma(),eps(),p(V+JD+T+RH+DW)	24	3307.93	3355.93	0	0.73	1
psi(perBLHD+MYLU),gamma(),eps(),p(V+JD+T+RH+DW)	25	3307.87	3357.87	1.94	0.27	0.38

Table 8. Little brown/ Indiana bat interaction modeling output for Charlie Heath Memorial Conservation Area, Deer Ridge Conservation Area, and Fox Valley Lake Conservation Area during summer 2008- 2011 surveys. K is the number of parameters in the model, -2*LL is -2*log- likelihood, AIC is Akaike's information criterion, Δ AIC is the difference in AIC value from the top model, w_i is the Akaike weight, and ML is the model likelihood.

Little Brown Bat/ Indiana Bat	K	-2*LL	AIC	Δ AIC	w	ML
psi(SITE+DW+CC),gamma(),eps(),p(V+T+RH+DW)	26	4270.56	4322.56	0	0.71	1
psi(SITE+DW+CC+MYSO),gamma(),eps(),p(V+T+RH+DW)	27	4270.32	4324.32	1.76	0.29	0.41

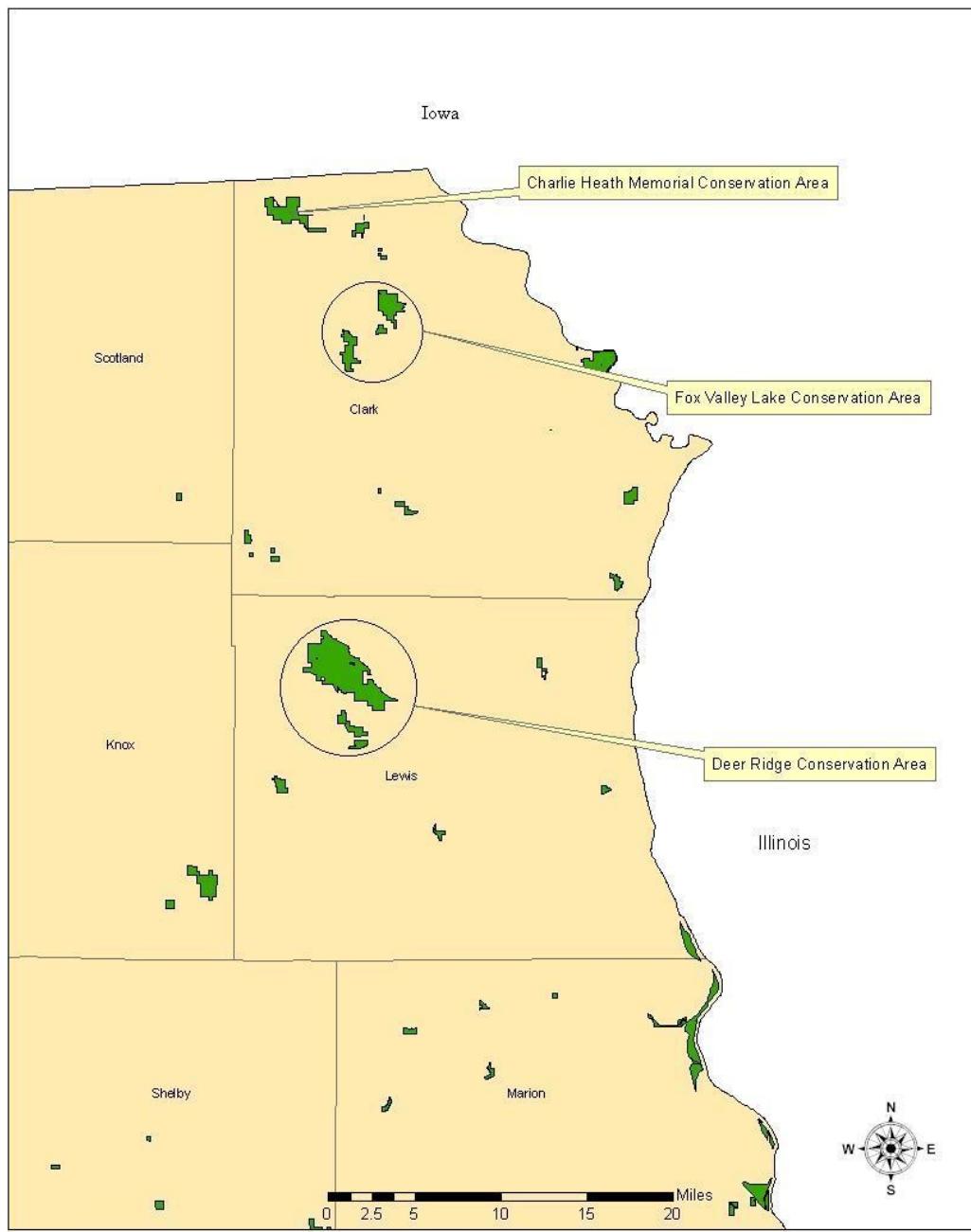


Figure 1. Northeast corner of Missouri showing Missouri Department of Conservation owned land including the 3 proposed study sites (T. Elliot, Missouri Department of Conservation).