INTRODUCTION

Space use in animals is a common focus of ecological research because animals meet their requirements for survival, growth and reproduction by exploiting available resources within a hierarchically selected environment (Johnson, 1980). Management and conservation of animal populations require a scientific understanding of hierarchical resource selection that is attained by viewing animals in their spatial context (Levin, 1992). Movements of many animals, including bats, can be viewed as use of an area representing locations in space and time based on selection of resources that provide for their physical needs. The concept of home range originated by Burt (1943) as the area an animal normally uses throughout its life. This concept has more recently been described as an area used by an individual repeatedly during a certain time period, with a boundary drawn based on proportion of occurrence (Kendall, 2001). The underlying assumptions are that an area with high quality resources will be used more than one with low quality; that availability of, or access to, resources is not uniform; and that use of the home range may change with availability or time frame (Manly et al., 2002; Buskirk and Millspaugh, 2006). Landscape change, such as conversion of forest to agricultural land, affects ecological processes, species, and their home range size (Tscharntke et al., 2005). Knowledge of how species move across the landscape and what resources are needed to meet physiological requirements are crucial for conservation of species, especially for threatened and endangered species. Therefore, assessing home range size is an important topic in mammalian ecology. Bats are good study organisms to assess home range size due to high mobility compared to their small body size and the ability to transverse large areas within diverse landscapes (Hayes and Loeb, 2007).

Myotis sodalis (Indiana bats) were listed as federally endangered in the United States in 1966 under a precursor to the Endangered Species Act (ESA). The general consensus was that human disturbance of hibernating bats was a primary cause of prelisting declines (Barbour and Davis, 1969; Greenhall, 1973). However, even with protection of hibernacula, population numbers continue to decline.
(USFWS, 2007) suggesting factors related to summering resources may also be influencing declines (Kurta and Kennedy, 2002). Kurta (2001) described these ultimate factors as suitable foraging, roosting, and water resources must be available in an area for a maternity colony to be present. Female *M. sodalis* form maternity colonies within forests during summer. Maternity colonies in the Midwest are associated with forest patches in highly fragmented landscapes dominated by agriculture (Murray and Kurta, 2004; Kurta, 2005; Menzel et al., 2005; Sparks et al., 2005b; Womack et al., 2013). *Myotis sodalis* forage along riparian corridors, upland forests, and bottomland forests (Humphrey et al., 1977; Murray and Kurta, 2004; Menzel et al., 2005; Sparks et al., 2005b; Carter, 2006; Tuttle et al., 2006; Womack et al., 2013). This species typically forages 2 to 30 m above the ground, under the forest canopy (Humphrey et al., 1977) and around the tree crowns (Brack, 1983; Sparks et al., 2005b) but will fly across agricultural fields between foraging areas and maternity roosts (Menzel et al., 2005; Sparks et al., 2005b).

*Myotis sodalis* occupy unique home ranges, particularly in the summer (Garner and Gardner, 1992). Knowledge of foraging home range may provide valuable insight into resources needed for survival. Knowledge of *M. sodalis* home ranges comes from a few studies that are based on modest numbers of individuals due to the rarity of this species and have combined individuals of different sex or reproductive condition due to small sample sizes (Rommé et al., 2002; Menzel et al., 2005; Sparks et al., 2005b; Watrous et al., 2006). Mean home range size during summer in the Champlain Valley of New York and Vermont was 83 ha (n = 14; Watrous et al., 2006), in Illinois 161.1 ha (n = 7; Menzel et al., 2005), in Indiana 335 ha (n = 11; Sparks et al., 2005b). Maximum distance from diurnal roosts to foraging areas was 8.37 km in Indiana (Sparks et al., 2005b). Maximum foraging area was 3,026 ha and a maximum commuting distance was 10.3 km during the spring and fall when bats are moving greater distances due to migration to or from hibernacula (Rommé et al., 2002). Murray and Kurta (2004) determined 13 foraging areas for an *M. sodalis* maternity colony in Michigan and found five were used exclusively by pregnant individuals and four were only visited by lactating females, suggesting there may be differential use of space by reproductive classes within the same maternity colony. In a closely related species, *M. lucifugus* (little brown bats), foraging home range size was 40% smaller for lactating versus pregnant bats (Henry et al., 2002), highlighting the potential importance of home range use between reproductive classes to understand resource needs throughout the maternity season. Non-reproductive *Eptesicus fuscus* (big brown bats) had significantly larger foraging ranges compared to reproductive *E. fuscus*; while, no difference was found in foraging range size for *Nycticeius humeralis* (evening bats) at the same study site in Indiana (Duchamp et al., 2004). No significant difference in home range size between pregnant and lactating individuals was noted for another sympatric species, *M. septentrionalis* (northern long-eared bats; Owen et al., 2003). Sample size is likely a factor for the lack of significant differences in space use between reproductive conditions in several of these home range studies (i.e., Owen et al., 2003; Duchamp et al., 2004). Knowledge of changes to home range size between reproductive conditions during summer will provide additional information on the spatial scale resource managers and conservationists need to consider when managing for *M. sodalis*.

Our goal was to estimate home range size differences between pregnant and lactating female *M. sodalis* within a predominately agricultural landscape in Missouri to provide insight into spatial area needed to acquire resources during pregnancy and lactation. Our objectives were to 1) estimate home range size using a fixed kernel method to calculate utilization distributions (UD) of pregnant and lactating *M. sodalis*, 2) determine maximum distance moved from the diurnal roost by pregnant and lactating *M. sodalis*, and 3) compare home range size and maximum distances traveled between reproductive conditions.

**Materials and Methods**

**Study Area**

We studied *M. sodalis* from 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 (i.e., *Carya ovata* [shagbark hickory], *C. laciniosa* [shellbark hickory], *C. tomentosa* [mockernut hickory], *Quercus alba* [white oak], and *Q. velutina* [black oak]) typically found in northern Missouri and the mature bottomland forest consists of typical mix species for northern Missouri, including *Acer saccharinum* (silver maple), *Platanus occidentalis* (American sycamore), *Populus deltoides* (Eastern Cottonwood), *Betula nigra* (river birch), and bottomland associated oak species (i.e., *Q. palustris* [pin], *Q. bicolor* [swamp], *Q. alba* [white], and *Q. macrocarpa* [bur]). The only recent forest
management on CHMCA were two 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 area around the center of CHMCA was 56% agricultural (corn, soybeans, and pasture), 27.8% forested (mostly CHMCA), 6.8% shrub/grass land, 3.6% developed, and 4.5% wetland based on the National Land Cover Database 2001 (NLCD; Homer et al., 2004).

**Capture and Telemetry**

Bats were captured with mist nets and harp traps (Tuttle, 1974; Kunz and Kurta, 1988) and placed in a muslin bag until processed. Bags and equipment were cleaned following the decontamination protocol recommended by U.S. Fish and Wildlife Service because of the emerging infectious disease, white-nose syndrome (WNS). Radio transmitters were attached weighing 0.43–0.53 g (Holohil Systems Ltd., Carp, Ontario, Canada) to female *M. sodalis* with weights above 8.0 g so that the transmitter did not exceed 5% of the individual’s body mass (Amelon, 2007). Transmitters were optimized for signal strength to last 10–12 days. We trimmed the hair between the scapula with surgical scissors and glued (Osto-Bond, Montreal Ostomy Inc., Vaudreuil-Dorion, Quebec, Canada) transmitters to the skin. Bats with radio transmitters were placed in a holding bag for 15 minutes to allow the glue to cure. Animal procedures were approved under Missouri Department of Conservation permit 14529, Federal permit TE068090A, and University of Missouri Animal Care and Use Committee protocol #4451.

We radio tracked bats by obtaining simultaneous compass bearings from at least two locations and triangulated bat locations (Amelon et al., 2009). Antennas were either roof-mounted on vehicles (RA-4A model, Teleonics) or at a fixed location (9.14 m tower, VHF model, Teleonics). Lenth’s maximum likelihood estimates were used (White and Garrott, 1990) in program GTM3 (Sartwell, 2000) to calculate bat locations from simultaneous compass bearing including error polygon estimates. Digital compasses were calibrated on each vehicle nightly using a stationary radio transmitter at a known azimuth. We determined observer accuracy by using standard deviations (SD) of directional azimuths and azimuth error for each observer based on three receiver locations with stationary transmitters placed in multiple locations throughout the study area. Azimuth SD averaged ± 4.1° and ranged from 1.7° to 7.7° for individual observers. Locations with error polygons greater than 200 m² (mean 42 m² ± 2.66) were excluded from the analysis.

We obtained simultaneous azimuths each night at pre-specified times by an atomic clock to synchronize time. Scheduled location times were offset each night by rotating the order of bats being located so that locations represented the range of times each bat foraged (21:00 to 05:00). Bats were tracked from dusk (around 21:00) to night roost (01:00–02:30) and again from about 03:00 to dawn (around 05:00) monitoring times varied because of variability in individual’s night roost time. All individuals were monitored until the last bat was inactive (i.e., night or day roosting) for at least 30 minutes. We attempted to determine each bat’s location every 5–10 minutes, depending on the number of radio tagged animals. We estimated azimuths as the center of the bisected angle between the nulls (Fuller et al., 2005). Our monitoring schedule was divided into two periods based on the crepuscular nature of foraging activity potentially linked to increased insect availability during these times (Barclay, 1991). We tracked all individuals to roost trees daily for the duration of the transmitter life. Roost tree locations were not included in our foraging home range size estimates; although, roost tree locations were in the 50% core area for all individuals.

**Data Analysis**

The fixed kernel method was used to estimate the utilization distributions (UD) for each individual using program R (v2.12.2 — Gitzen et al., 2006). Utilization distributions represent use of space as a probability distribution calculated in program R is a more accurate method to estimate home range than minimum convex polygons and kernel estimates using the animal movement tool in ArcGIS (Fieberg and Kochanny, 2005). We used the ‘solve-the-equation plug in’ reference bandwidth to calculate an appropriate smoothing factor for each bat (Worton 1987). The plug in reference bandwidth calculates the amount of smoothing unique to each individual based on their movements, which helps eliminate over-smoothing and over estimating the home range size for an individual (Gitzen et al., 2006). We imported UD’s for each individual into ArcGIS (v9.3.3, ESRI, Redlands, CA, USA) and calculated the area in the 50% and 95% probability contour of each bat’s UD using Hawth’s tools in ArcGIS (ESRI, v9.3.3). The 95% contour represents most of the area used by an individual while eliminating outlier locations, which may be a result of exploratory behavior or telemetry error, and the 50% contour is often used to represent a core area most frequently used by an individual (Powell 2000). Furthermore, we used both 50 and 95% probability contours to facilitate comparisons with previous home range estimates. We reported estimates for individuals, summarized, and compared results for lactating or pregnant individuals. Additionally, we calculated the maximum distance traveled from the roost tree for each individual nightly and averaged these maximum distances for each individual to understand the movement potential for all female *M. sodalis* in our study. We used *t*-tests for unequal variances to test for a difference in means and *F*-test to test for equality of variances (Proc TTTEST, SAS 9.2) of home range size and flight distances between pregnant and lactating bats.

**RESULTS**

Home range estimates were calculated for 25 female (13 pregnant and 12 lactating) *M. sodalis* with a range of 32–208 locations per individual and monitored each bat an average of five nights (range 2–7). We tracked 6, 10, and 9 bats in 2008, 2009, and 2010, respectively. Mean area (± SE) for the 50% and 95% probability contours for all individuals was 204.52 ± 28.87 ha and 1,137.13 ± 144.06 ha, respectively (Table 1). The 50% probability contours ranged from 65.32–505.62 ha for pregnant and 71.76–709.78 ha for lactating bats. The 95% probability contours ranged from 522.47–2059.34 ha for pregnant and 1452.9–436.67–3,812.86 ha for lactating bats. There was no difference in home range size between pregnant and lactating bats based on 50% and 95%
Table 1: Home range estimates from the UD calculated using the fixed kernel method (95% and 50% probability contours) and maximum distances traveled from roosts for 25 female Indiana bats in northeastern Missouri in summers 2008–2010

<table>
<thead>
<tr>
<th>Radio frequency</th>
<th>Reproductive condition</th>
<th>n</th>
<th>Probability contour (ha)</th>
<th>Maximum distance (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>95%</td>
<td>50%</td>
</tr>
<tr>
<td>150000</td>
<td>Lactating</td>
<td>93</td>
<td>605.25</td>
<td>87.50</td>
</tr>
<tr>
<td>150181</td>
<td>Lactating</td>
<td>43</td>
<td>1611.25</td>
<td>221.22</td>
</tr>
<tr>
<td>151078</td>
<td>Lactating</td>
<td>99</td>
<td>784.23</td>
<td>177.39</td>
</tr>
<tr>
<td>151177</td>
<td>Lactating</td>
<td>144</td>
<td>2075.89</td>
<td>362.52</td>
</tr>
<tr>
<td>151440</td>
<td>Lactating</td>
<td>208</td>
<td>597.45</td>
<td>95.49</td>
</tr>
<tr>
<td>151481</td>
<td>Lactating</td>
<td>33</td>
<td>1037.51</td>
<td>203.62</td>
</tr>
<tr>
<td>151538</td>
<td>Lactating</td>
<td>87</td>
<td>1733.33</td>
<td>302.83</td>
</tr>
<tr>
<td>151578</td>
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<td>151</td>
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</tr>
<tr>
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<td>Lactating</td>
<td>75</td>
<td>3812.86</td>
<td>709.78</td>
</tr>
<tr>
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<td>160</td>
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</tr>
<tr>
<td>151839</td>
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<td>99</td>
<td>860.87</td>
<td>210.72</td>
</tr>
<tr>
<td>151900</td>
<td>Lactating</td>
<td>130</td>
<td>436.67</td>
<td>71.76</td>
</tr>
<tr>
<td>151018</td>
<td>Pregnant</td>
<td>118</td>
<td>837.39</td>
<td>157.46</td>
</tr>
<tr>
<td>151098</td>
<td>Pregnant</td>
<td>82</td>
<td>1024.85</td>
<td>203.05</td>
</tr>
<tr>
<td>151118</td>
<td>Pregnant</td>
<td>51</td>
<td>964.36</td>
<td>161.36</td>
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<tr>
<td>151238</td>
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<td>115</td>
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<tr>
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<td>115</td>
<td>971.02</td>
<td>215.79</td>
</tr>
<tr>
<td>151970</td>
<td>Pregnant</td>
<td>101</td>
<td>1294.24</td>
<td>159.42</td>
</tr>
</tbody>
</table>

probability contours (Table 2). There was also no difference in the variances between pregnant and lactating bats based on 50% probability contour but the variance based on the 95% probability contour was significantly greater for lactating than pregnant bats (Table 2).

The mean maximum distance individuals were triangulated from their roost tree ranged 1.89–5.13 km for pregnant and 2.17–9.40 km for lactating bats (Table 1). There was no significant difference in mean maximum distance, and a marginally significant ($P$-value = 0.076) difference in the variance in maximum distances, between pregnant and lactating bats (Table 2).

**DISCUSSION**

Understanding the home range size of reproductive female *M. sodalis* has important implications for management of this species (Thogmartin et al., 2012, 2013). Our study took place in an agriculturally dominated landscape in which over 50% of the landscape within 10 km of our site was in agricultural crop production. *Myotis sodalis* maternity colonies are often associated with agriculturally dominated landscapes particularly in the Midwest and Ozark-Central Recovery Units (Menzel et al., 2005; Sparks et al., 2005b; USFWS, 2007). We found *M. sodalis* home ranges were, on average, 3.3 times larger than those found in any previous *M. sodalis* maternity season study (Menzel et al., 2005; Sparks et al., 2005b; Watrous et al., 2006). Our home ranges were much larger than those reported for *M. lucifugus* during the maternity season, where the mean 90% home range size was calculated using the fixed kernel method for pregnant females was 30.1 ha and 17.6 ha for lactating bats (Henry et al., 2002). In another closely related species, the mean 95% home range size using adaptive kernels was 65 ha for nine *M. septentrionalis* (four pregnant, five lactating) in West Virginia (Owen et al., 2003) and no differences were found between reproductive conditions. Rommé et al., (2002) spring and fall *M. sodalis* home range and maximum foraging distance estimates from the Missouri Ozarks, were the most similar to what we documented. Difference between estimates from our study and previous studies could result from a larger number of individuals, greater numbers of locations per individual, intensity of the monitoring...
schedule, different home range estimators, home ranges differing geographically across the range of a species, or because of habitat availability and fragmentation.

Home range size of bats may reflect the distribution of prey and the behavior of individuals or may reflect habitat selection of both roosting and foraging resources that may be separated in highly modified landscapes. Flight can increase energy expenditure by 14.5 times over basal metabolic rate (Racey and Speakman, 1987) which requires high quality foraging resources to support longer range travel. Bats select habitats that provide for foraging, roosting, and water resource needs (Hayes and Loeb, 2007). We previously reported resource selection by *M. sodalis* on CHMCA and found forested areas with contiguous canopy and understories thinned by prescribed fire were selected by individuals, while agricultural land was avoided (Womack et al., 2013). In addition, water resources were not a limiting factor across the greater CHMCA area since water sources were no further than 1.5 km from known telemetry locations (Womack et al., 2013).

Many factors could have simultaneously influenced space use over the summer including changes in habitat conditions and prey densities. Prey distribution and abundance are likely highly variable in highly modified landscapes (Lacki et al., 2009). Total prey biomass was similar in agricultural, upland hardwood, and bottomland hardwood forests but lower in upland hardwood forests that were managed with prescribed fire within CHMCA (Womack, 2011). If prey resources are evenly distributed, size of home range should reflect metabolic requirements and would be expected to be greater in bats with higher energy demands (i.e., reproductive females).

Differences in home range size and movement between reproductive classes were not significant ($P < 0.05$), they were suggestive of greater areas of use during lactation, which could reflect greater caloric needs and lower body mass during this stage. Lactating individuals had the largest home ranges, which contrast studies where lactating females had smaller ranges, perhaps reflecting the need for females to visit and care for their young during the night (Racey and Swift, 1985; Fuhrmann and Seitz, 1992; Henry et al., 2002). There was significant individual variation in the 95% probability contour among lactating individuals that may be linked to time from parturition as developmental stage of the young would influence adult female behavior. For example, lactating individuals further from parturition may be weaning their young (Kurta et al., 1989) and potentially use areas further from roosts since they do not have to nurse young as frequently. Pregnant *M. sodalis* in general had smaller maximum distances traveled than lactating females, although variation within reproductive condition was not significant. This may be linked to the high variability of resource selection used by individuals within each reproductive condition (Womack et al., 2013). Similarly, Sparks et al. (2005b) found that distances traveled from roosts to foraging areas were highly variable (0.80–8.37 km) between individuals and reproductive classes along an urban-rural gradient in Indiana. We found *M. sodalis* moved greater distances nightly in Missouri than Indiana (Sparks et al., 2005b), but further study of prey and landscape factors would be needed to better understand if this was driven by proximity of roosting and foraging habitat or some other factor.

While due to the limitations of small transmitters we can only assess home range over small time intervals, it is clear from our results that in some landscapes, female *M. sodalis* use larger areas than previously reported. Bats are highly mobile species and may be able to adapt to some level of landscape modification by either selecting roost sites closer to foraging areas or by commuting greater distances between these resources, but there are energy consequences for either of these options. We suggest that *M. sodalis* home range be examined on larger landscape scales with multiple study areas.
and include measures of prey availability and abundance to better understand the summer ecology of this endangered species.

We found that home ranges were larger than previously recorded which may be a factor of larger sample sizes for both individuals and telemetry locations. We also found considerable individual variation in space use for bats within and between reproductive conditions. Knowledge about home ranges are important in understanding the effects that forest management practices and landscape change will have on bat species. If resource managers and conservationists are managing species at a smaller spatial scale than individuals are using they may not have enough resources to meet all of their energetic needs during the maternity season. We suggest that differences in home range size between pregnant and lactating individuals should receive further study to elucidate resource needs for both foraging and roosting habitats and the relative proximity of these resources during the breeding season. This is not just an issue for *M. sodalis* but for all bat species of conservation concern since reproductive failure will result in further decreases in population.

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**LITERATURE CITED**


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