Space use and resource selection by foraging Indiana bats at the northern edge of their distribution

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ABSTRACT: Despite 4 decades of conservation concern, managing endangered Indiana bat (Myotis sodalis) populations remains a difficult wildlife resource issue facing natural resource managers in the eastern United States. After small signs of population recovery, the recent emergence of white-nose syndrome has led to concerns of local and/or regional extirpation of the species. Where Indiana bats persist, retaining high-quality foraging areas will be critical to meet physiological needs and ensure successful recruitment and overwinter survival. However, insight into foraging behavior has been lacking in the Northeast of the USA. We radio-tracked 12 Indiana bats over 2 summers at Fort Drum, New York, to evaluate factors influencing Indiana bat resource selection during night-time foraging. We found that foraging space use decreased 2% for every 100 m increase in distance to water and 6% for every 100 m away from the forest edge. This suggests high use of riparian areas in close proximity to forest and is somewhat consistent with the species’ foraging ecology in the Midwest and upper South. Given the importance of providing access to high-quality foraging areas during the summer maternity season, Indiana bat conservation at the northern extent of the species’ range will be linked to retention of forested habitat in close proximity to riparian zones.

KEY WORDS: Foraging · Home range · Indiana bat · Myotis · New York · Resource utilization function

INTRODUCTION

For over 4 decades, conservation of the federally endangered Indiana bat Myotis sodalis has been a daunting task facing natural resource managers in the eastern United States (Menzel et al. 2001, 2005). Although Indiana bats were one of the first species federally listed as endangered in 1966 under the Endangered Species Preservation Act, they still faced successive years of declines post-listing due to various factors. By the mid-2000s the species had experienced a modest growth in numbers, with much of the species’ increase in numbers occurring in the Northeast. However, since the emergence of white-nose syndrome (WNS) in 2006, caused by the fungal pathogen Pseudogymnoascus destructans, over 40,000 Indiana bats have died, with 95% of populations predicted to decline below extirpation thresholds in the next 50 yr.
ongoing disease-related declines and regional extir-

pation, modeled climate-change impacts predict a
drastic displacement of optimal cave habitat for hiber-
nation and summer maternity habitat from the Mid-
west to the central Appalachians and Northeast over
the next 50 yr (Loeb & Winters 2012), adding uncer-
tainty to the long-term conservation of the species.

With these precipitous declines, knowledge of the
roosting and foraging ecology is needed for conserva-
tion of Indiana bats (Sparks et al. 2005, Womack et
al. 2013). To maximize recruitment during the materni-
ty season and help ensure population persistence, man-
agers need to provide quality foraging and roost-
ing habitat (Humphrey et al. 1977). Indiana bats begin
to emerge from hibernation in caves and mines in
mid-April and migrate to their summer ranges (Cope
& Humphrey 1977, Kurta & Murray 2002). At their
summer ranges, female Indiana bats form day-roost
maternity colonies of 20 to 100 individuals under
exfoliating bark of trees or snags and in cracks or
crevices (Kurta et al. 1993, Menzel et al. 2001, Kurta
2004). During the night, Indiana bats forage on in-
sects in riparian forested areas, and in upland forested
areas and other habitats to a lesser extent (Humphrey
et al. 1977, LaVal et al. 1977, LaVal & LaVal 1980,
Brack 1983, Ford et al. 2005). Accordingly, in the
maternity season, managers must be cognizant of
both roosting and foraging habitat needs (Menzel et
al. 2005). Although many aspects of Indiana day-roost
ecology are understood across the bat’s distribution,
documentation of foraging habitat use is known from
only a few radio-telemetric and acoustical studies
(e.g. LaVal et al. 1977, Menzel et al. 2005, Sparks et

Given their vagility, Indiana bats use much larger
areas than would otherwise be expected for a simi-
larly sized terrestrial mammal (Kelt & Van Vuren
1999), and therefore have a greater ability to select
for areas that maximize foraging efficiency. Previous
studies on resource selection by Indiana bats during
summer foraging periods have shown considerable
foraging use plasticity contingent upon local land-
cscape characteristics throughout the range of the spe-
cies. At the western extent of their range in the central
USA, where forest tracts are relatively small and frag-
mented, Indiana bats forage closer to forested wood-
lots and riparian habitats than to agricultural lands
(Menzel et al. 2005, Womack et al. 2013, Knio
wski 2011). Similarly, in the heavily forested landscapes
of the central Appalachians, within the Allegheny
Plateau of northern West Virginia, Indiana bat forag-
ing activity was highest in mid-order forested riparian
areas with moderate to full canopy cover, with very
little activity elsewhere in the surrounding upland
forests (Ford et al. 2005). Conversely, in the ridge and
valley area of central Pennsylvania, Butchkoski &
Hassinger (2002) observed most Indiana bat foraging
activity in large patches of interior, upland forests on
the valley floor rather than along riparian areas or
surrounding mountain side slopes and ridges. At the
northern extreme of the Indiana bat distribution in
the Champlain Valley of Vermont, Watrous et al. (2006)
documented foraging preference for patchy land-cover types in close proximity to water and east-
face slopes, including some use of agricultural
fields. Collectively there is a fairly consistent theme of
Indiana bats foraging within or near forested areas
and in close association with water. However, it is
clear that Indiana bats display considerable plasticity
in foraging habitat use that reflects local landscape
characteristics. As such, effective Indiana bat conser-
vation in the summer maternity season probably re-
quires region- and site-specific observations on space
use and resource selection.

In this study we evaluated foraging space use and
resource utilization patterns by Indiana bats at the
northern edge of their range. Indiana bat populations
in the Northeast of the USA are arguably the most
imperiled, by virtue of being exposed to WNS for the
longest period, both in terms of time since advent of
the disease and annual duration (longer) of hiberna-
tion (Ford et al. 2011). To better inform managers in
this region about Indiana bat habitat requirements
during the maternity season and to provide insight
for post-WNS habitat conservation and management,
we evaluated multiple competing hypotheses of
habitat-based factors that could influence Indiana bat
foraging space use and resource selection patterns.

MATERIALS AND METHODS

Study area

We conducted our study within and adjacent to
Fort Drum, a >43 000 ha US Army installation in Jef-
ferson and Lewis counties, New York, USA. Located
in the northwestern portion of the state, Fort Drum
lies at the intersection of 3 eco-regions: the Tug Hill
Plateau, the St. Lawrence/Great Lakes Lowlands,
and the foothills of the Adirondack Mountains. Lime-
stone ‘karst’ formations in the Niagara Escarpment
are situated 10 to 15 km west of Fort Drum and con-
tain caves where bats hibernate. Topography is
rolling with some incised water-courses along the
Black and Indian river drainages. Elevations range from 125 to 278 m. Approximately 70% of Fort Drum is forested. Mature forests are northern hardwood associations of sugar maple *Acer saccharum*, American beech *Fagus grandifolia*, white ash *Fraxinus americana*, and American elm *Ulmus americana* mixed with a conifer component of white pine *Pinus strobus* and eastern hemlock *Tsuga canadensis*. In addition to developed areas within the installation’s 4500 ha cantonment area and airfield, open habitats maintained for training such as drop-zones, firing ranges, maneuver areas, and forest regeneration areas occur throughout. Small lakes, beaver (*Castor canadensis*) ponds, and open wet meadows cover approximately 20% of the landscape. Lands adjacent to Fort Drum include similar elevations and forest associations; however, forested areas are highly fragmented and interspersed with agricultural row crops, pastureland, and areas of urban sprawl development.

**Capture and handling**

We captured *Myotis sodalis* in 2008 and 2009 by setting up 6, 9, and 12 m wide double-stacked mesh (38 mm) mist nets (Avinet, Dryden, NY) opportunistically over dirt roads and trails, with some in the interior forest, along edges, and occasionally over water. Mist nets were open for ≥4 h following sunset. Upon capturing a bat, we determined species, sex, age, weight, forearm length, and reproductive condition (Menzel et al. 2002). We used Skin Bond® (Smith and Nephew, Largo, FL) surgical cement to affix a 0.35 g radio transmitter (Blackburn Transmitters, Nacogdoches, TX) between the scapulae of each captured Indiana bat. Bat capture and handling protocols were approved by the Animal Care and Use Committee of West Virginia University (Protocol No. 08-0504) and followed the guidelines of the American Society of Mammalogists (Sikes et al. 2011). The average weight of captured bats was 7.44 g (n = 15, SE = 0.20, range = 6.5–8.9 g), and the average radio-transmitter to body mass ratio was 4.76% (SE = 0.12, range = 3.93–5.38%), below the 5% threshold recommended for minimizing the effects of transmitters on bat movement (Aldridge & Brigham 1988).

**Monitoring**

To monitor movement of radio-marked Indiana bats, we established a network of radio-telemetry stations, both within and outside of Fort Drum Military Installation. We commenced radio-telemetry after bats emerged from their roost trees at dusk. Given the ability of Indiana bats to move relatively long distances in 5 min periods, we assumed sufficient spatial independence between locations for subsequent space use and resource selection by attempting to locate bats at 5 min intervals (Womack et al. 2013). We attempted to triangulate the location of individual radio-tagged bats by having 2 or 3 observers simultaneously use radio receivers and 3-element Yagi antennae to obtain directional azimuths (White & Garrott 1990). We ceased obtaining azimuths when steady transmitter signals were received, indicating the bat was night-roosting. We estimated point locations where bats were flying by entering radio-telemetry station locations and directional azimuth data into LOCATE 3 (Nams 2006).

**Foraging space use**

We represented foraging space use by creating a utilization distribution (UD) for each bat for which ≥29 nighttime locations were collected. UDs create a 3-dimensional grid based on animal relocations that estimate the probability of use by a bat throughout its home range (Kernohan et al. 2001). We calculated a UD for each bat using the kde package in the program R, Version 2.10.0 (R Core Team 2010), using the plug-in method for bandwidth selection (Gitzen et al. 2006). We then trimmed each UD by its 95% volume contour using Hawthtools extension in ArcGIS, and the resulting perimeter representing the bat's 95% fixed kernel home range.

**Resource selection analyses**

We developed 14 *a priori* hypotheses of factors influencing resource utilization based on a literature review of important habitat features in past Indiana bat resource selection studies throughout their range (Table 1). We categorized habitat into upland mixed forest, forested wetland, shrub wetland, agricultural/field habitats, or developed, based on Northeast Terrestrial Habitat Classification System land-cover maps (Wildlife Management Institute 2012). Dummy variable coding for categorical variables required that 1 category be removed prior to model fitting. Because the upland mixed forest category was the dominant land-cover category, we removed it to serve as a reference category. We also developed 6 continuous variables for use in our resource selection
models (Table 1). Indiana bats have been found to select for foraging areas near forest edge (Brack 1983, Menzel et al. 2001); therefore, we used the Euclidean distance function in ArcGIS 9.3 (ESRI, Redlands, CA) to include a metric for distance to forest edge (DisE; a generalized category for all 3 types of forest listed above). Multiple studies have found that Indiana bats prefer to forage near water (Kurta & Whitaker 1998, Menzel et al. 2005, Watrous et al. 2006). Thus, we included a positive effect of being near open water (i.e. lakes and ponds) or streams (DisW). Also, Indiana bats preferentially forage in wooded areas rather than developed areas at a rural–urban interface in Indiana (Sparks et al. 2005, Menzel et al. 2005). Therefore, we developed distance metrics representing the likely avoidance of developed areas (DisD) (Sparks et al. 2005).

We included measures of both aspect and slope, which have been found to be important factors in Indiana bat space use, particularly in the north and in the Appalachians (Watrous et al. 2006). We obtained slope and aspect measures by downloading US Geological Survey digital elevation models for the study area from the New York State GIS Clearinghouse (www.gis.ny.gov, accessed June 2013). We first hypothesized that Indiana bats would preferentially forage in areas of less topographic complexity (Watrous et al. 2006). Where pronounced relief and topographic complexity existed, we predicted that bats would preferentially forage on or near south-facing slopes due to warmer temperatures. Because aspect is based on circular degrees, we transformed angular data to radians and centered our metric on the south aspect using cos(aspect) + 1 which yielded values that ranged from 0 (at 180°, or S) to 2 (at 0 and 360°, or N). We also hypothesized that space use would decrease with increasing upland elevation (Watrous et al. 2006). Once each of these habitat attributes was spatially defined across our study area, we used ArcGIS to intersect UD grid node points with habitat covariates to extract point-specific covariate values.

Table 1. Foraging resource use models developed from a literature review, based on factors we hypothesized to influence Indiana bat (Myotis sodalis) foraging resource use near Fort Drum, New York, 2008 to 2009

<table>
<thead>
<tr>
<th>Model no.</th>
<th>Hypothesis</th>
<th>Model</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Use decreases as distance from water increases</td>
<td>DisW</td>
<td>Menzel et al. (2005), Watrous et al. (2006)</td>
</tr>
<tr>
<td>2</td>
<td>Use decreases as distance from forest edge increases</td>
<td>DisF</td>
<td>Brack (1983), Menzel et al. (2001)</td>
</tr>
<tr>
<td>3</td>
<td>Use decreases as proximity to disturbed/developed areas decreases</td>
<td>DisD</td>
<td>Sparks et al. (2005), Menzel et al. (2005)</td>
</tr>
<tr>
<td>4</td>
<td>Use decreases on steep slopes and high elevation</td>
<td>SLP – ELEV</td>
<td>Watrous et al. (2006)</td>
</tr>
<tr>
<td>5</td>
<td>Use decreases on north-facing slopes</td>
<td>ASP</td>
<td>Watrous et al. (2006)</td>
</tr>
<tr>
<td>6</td>
<td>Use increases in upland forest as well as forested wetland; decreases in shrub wetland, agricultural, and developed areas</td>
<td>LAND</td>
<td>Bowles (1981), Menzel et al. (2005), Womack et al. (2013)</td>
</tr>
<tr>
<td>7</td>
<td>Use increases in upland and wetland forest, particularly in areas near forest edges</td>
<td>LAND – DisF</td>
<td>Menzel et al. (2001)</td>
</tr>
<tr>
<td>8</td>
<td>Use increases in upland and wetland forest along south-facing slopes</td>
<td>LAND + ASP</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>Use increases in upland and wetland forest, particularly in areas near water</td>
<td>LAND – DisW</td>
<td>Bowles (1981), Womack et al. (2013)</td>
</tr>
<tr>
<td>10</td>
<td>Use increases in flat, upland, and wetland forest, and decreases at high elevation</td>
<td>LAND – SLP – ELEV</td>
<td>Watrous et al. (2006)</td>
</tr>
<tr>
<td>11</td>
<td>Use increases in upland and wetland forest that is in close proximity to water and further away from development</td>
<td>LAND + DisD – DisW</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>Use increases in upland and wetland forest that is in close proximity to forest edge and open water</td>
<td>SLP + ASP – DisF – DisW</td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>Use increases in upland and wetland forest that is in close proximity to forest edge, open water, flat slopes, and away from development</td>
<td>DisD – DisF – DisW – SLP</td>
<td></td>
</tr>
</tbody>
</table>
Model fitting and selection

We developed a resource utilization function (RUF) to examine the relationship between space use and resource attributes for each of our 12 individual bats. Through the RUF calculation we used the height (z-value) of the UD at each grid point as the response variable in a multiple regression analysis that included combinations of predictor variables that represent the hypotheses outlined above (Marzluff et al. 2004). Prior to analysis, we clipped each bat UD by its 99% volume contour and re-standardized the values of each bat UD into 100 UD percentiles, so that the probability of use was on a scale of 0 to 100, with 100 representing the highest probability of use (Jachowski et al. 2013, Montgomery et al. 2013). We evaluated support for our models (Table 1) using Akaike’s Information Criteria corrected for small sample size (AIC_c) (Burnham & Anderson 2002) in the program R (Version 2.10.0). We were unable to evaluate all models across the larger Fort Drum landscape.

Model validation

We evaluated the predictive ability of our foraging RUF for Fort Drum using 2 approaches. We first used a k-fold cross-validation approach (Boyce et al. 2002), where we randomly selected 20% of UD cells (the testing set) from the UD of an individual bat and recalculated the RUF using the remaining data (the training set). We then iteratively repeated this procedure 5 times to produce 5 sets each of training and testing data for each bat. We then used the estimated coefficients from the training data to predict RUF values for the withheld testing (20%) data set. We classified RUF scores into 20 equal-interval categories or bins based on distribution of values in each sampling subset and examined the correlation between training and testing data using a Spearman-rank correlation (Jachowski et al. 2011). We expected a model with good predictive ability to have a high, positive cross-validated Spearman-rank correlation value (r).

RESULTS

In 2008, we conducted surveys for the bats between 12 May and 16 September, mist netting for 28 nights at 23 locations. In 2009, we conducted surveys between 11 May and 22 September, mist netting for 59 nights at 24 locations. We captured 11 Indiana bats in 2008 and 4 Indiana bats in 2009. We attached radio-transmitters to the 15 Indiana bats captured over the 2 field seasons. On average, we were able to radio-track each Indiana bat for 6.83 nights (SE = 0.85, range = 3–15), gaining 70.75 radio-fix locations per bat (SE = 13.82, range = 14–200) (Table 2). Overall, we col-

<table>
<thead>
<tr>
<th>Bat ID</th>
<th>Age</th>
<th>Sex</th>
<th>Year</th>
<th>Month</th>
<th>No. of nights tracked</th>
<th>No. of locations</th>
<th>No. of roosts</th>
<th>95% fixed kernel home range size (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>A</td>
<td>M</td>
<td>2008</td>
<td>May</td>
<td>4</td>
<td>29</td>
<td>5</td>
<td>18.94</td>
</tr>
<tr>
<td>2</td>
<td>A</td>
<td>F</td>
<td>2008</td>
<td>May</td>
<td>5</td>
<td>33</td>
<td>8</td>
<td>95.25</td>
</tr>
<tr>
<td>3</td>
<td>A</td>
<td>F</td>
<td>2008</td>
<td>Jul</td>
<td>6</td>
<td>47</td>
<td>4</td>
<td>318.02</td>
</tr>
<tr>
<td>4</td>
<td>A</td>
<td>F</td>
<td>2008</td>
<td>Jul</td>
<td>5</td>
<td>33</td>
<td>5</td>
<td>75.46</td>
</tr>
<tr>
<td>5</td>
<td>J</td>
<td>M</td>
<td>2008</td>
<td>Aug</td>
<td>8</td>
<td>84</td>
<td>3</td>
<td>282.98</td>
</tr>
<tr>
<td>6</td>
<td>J</td>
<td>F</td>
<td>2008</td>
<td>Sep</td>
<td>9</td>
<td>52</td>
<td>9</td>
<td>111.89</td>
</tr>
<tr>
<td>7</td>
<td>A</td>
<td>F</td>
<td>2009</td>
<td>Jul</td>
<td>7</td>
<td>76</td>
<td>7</td>
<td>150.37</td>
</tr>
<tr>
<td>8</td>
<td>A</td>
<td>F</td>
<td>2009</td>
<td>Jun</td>
<td>6</td>
<td>91</td>
<td>3</td>
<td>43.56</td>
</tr>
<tr>
<td>9</td>
<td>A</td>
<td>F</td>
<td>2009</td>
<td>Jul</td>
<td>7</td>
<td>134</td>
<td>4</td>
<td>243.6</td>
</tr>
<tr>
<td>10</td>
<td>J</td>
<td>M</td>
<td>2009</td>
<td>Aug</td>
<td>15</td>
<td>200</td>
<td>8</td>
<td>64.54</td>
</tr>
<tr>
<td>11</td>
<td>A</td>
<td>M</td>
<td>2008</td>
<td>Sep</td>
<td>7</td>
<td>40</td>
<td>8</td>
<td>38.32</td>
</tr>
<tr>
<td>12</td>
<td>J</td>
<td>F</td>
<td>2008</td>
<td>Aug</td>
<td>3</td>
<td>30</td>
<td>1</td>
<td>122.67</td>
</tr>
</tbody>
</table>
Although small sample sizes prohibited us from mak-
ing sex-specific generalizations, across both sexes we found some support for the inclusion of each of our predictive covariates in our most supported models: land cover, slope, aspect, elevation and distance to water, forest, and development. Therefore, our population-level model contained all predicted covariates (i.e. the global model). We found further evidence of support for the global model through k-fold cross validation of our averaged, population-level model, where the mean cross-validated Spearman-rank correlation values ($r_s$) were ≥0.9345 ($p < 0.0001$) (Table 4).

The interspersion of forested habitat and open water was correlated with patterns in Indiana bat resource selection. In comparison to the upland mixed forest land-cover type that dominated our study area on and surrounding Fort Drum, Indiana bat probability of use during foraging bouts was consistently lower in agricultural habitats and shrub wetland habitats (Table 5). We found that most bats

### Table 3. Number of times each model of Indiana bat (Myotis sodalis) resource utilization function received the most support for explaining resource selection of an individual Indiana bat (n = 12) near Fort Drum, New York, 2008 to 2009. na: not applicable

<table>
<thead>
<tr>
<th>Model</th>
<th>Females</th>
<th>Males</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. times</td>
<td>Avg. Akaike weight</td>
</tr>
<tr>
<td>(9) LAND − DisW</td>
<td>1</td>
<td>1.00</td>
</tr>
<tr>
<td>(10) LAND − SLP − ELEV</td>
<td>0</td>
<td>na</td>
</tr>
<tr>
<td>(11) DisD − DisF − DisW − SLP</td>
<td>4</td>
<td>0.98</td>
</tr>
<tr>
<td>(12) DisD − DisF − DisW + DisF + ASP − SLP − ELEV</td>
<td>2</td>
<td>1.00</td>
</tr>
<tr>
<td>(14) LAND − DisF − DisW + DisF + ASP − SLP − ELEV</td>
<td>1</td>
<td>1.00</td>
</tr>
</tbody>
</table>

We observed a low amount of model uncertainty but a relatively high amount of variation in resource utilization by individual Indiana bats (Table 3). Although small sample sizes limited our ability to test for an effect of bat sex or age class on home range size.

### Space use

The mean 95% fixed kernel home range size for the 12 bats was 130.47 ha (SE = 28.75, range = 18.94–318.02) (Table 2). Unfortunately, small sample sizes limited our ability to test for an effect of bat sex or age class on home range size.

### Resource selection

We observed a low amount of model uncertainty but a relatively high amount of variation in resource utilization by individual Indiana bats (Table 3). Although small sample sizes prohibited us from mak-
were less likely to forage in developed areas and that predicted foraging use increased as distance from development increased (Table 5). Use of forested wetlands varied among bats, and coefficient standard errors overlapped zero, suggesting that use of these habitat types could be equivalent with upland mixed forest (Table 5). Predicted foraging space use decreased 6% and 2% for every 100 m away from forest edge and open water sources respectively. Although standard errors of these 2 population-level parameter coefficients overlapped zero, 8 of the 11 bats showed a negative association with increased distance from open water, suggesting higher use of areas near water (Table 5).

For the 6 bats that retained topographic features in their top predictive model, we observed a high amount of variation in the effect of percent slope, aspect, and elevation among individual bats. Standard errors for population-level coefficients overlapped 0 for each topographic feature, and positive or negative effect on resource use varied considerably among individual bats, preventing us from making any population-level generalizations (Table 5). Further, bats remained in the southern portion of the study area and exhibited limited variability in elevation compared to the higher northern section of the installation, limiting our ability to effectively evaluate the role of elevation in resource utilization.

**DISCUSSION**

Given the high vagility of the species, the similarity of Indiana bat home range size estimates among previous studies throughout its distribution suggests that the species can adjust space use within their home ranges to meet energetic requirements rather than expand their home ranges in relation to site-specific attributes. Although differences in methodology exist among studies, our home range estimates are fairly congruent with those of others (Romme et al. 2002, Menzel et al. 2005, Sparks et al. 2005, Watrous et al. 2006). Therefore, it is likely that a maximum home range size threshold exists to fulfill their physiological and behavioral requirements (McNab 1963) and that resource selection likely occurs at fine spatial scales within home ranges.

Within Indiana bat home ranges, foraging space use likely varies based on site-specific patterns in the availability and arrangement of forested and nonforest habitats. In the heavily agricultural settings of the Midwest, Indiana bats have been shown to prefer foraging in closed canopy forests versus open agricultural (Womack et al. 2013) or developed areas with a significant residual forested component (Sparks et al. 2005). By contrast, in the Northeast, where forests dominate the landscape, Watrous et al. (2006) observed that Indiana bats forage more in open or patchy habitats, even selecting agricultural fields in some instances. In our study area, we found evidence for avoidance of open shrub wetlands, agricultural habitats, and disturbed areas, but found a positive association of use with proximity to forest edge. Collectively, this suggests that forested habitats and edges of forest habitat are important foraging areas for Indiana bats in the northern portion of their range. One caveat to this observation is that, given the need for bats to access roost trees during the day (and even during periods of the night), our attempt to monitor ‘foraging’ movements could have been biased due to including movement to and from roost trees that were located primarily in forest stands composed of select deciduous tree species, such as sugar maple and American elm (C. Dobony unpubl. data). This suggests the need for subsequent analyses to evaluate the potential effect of the proximity of daytime roost locations on foraging space use, particularly if forest stands with suitable roost conditions in terms of intra-stand composition and decadent condition/structure are limited in their distribution at Fort Drum. Otherwise the availability of high-quality foraging habitat for Indiana bats may, potentially be overestimated.

Nonetheless, use of forested environments that are in close proximity to water as foraging areas is highly congruent with previous observations that Indiana bats in the northern portion of their range forage for insects associated with aquatic environments (Humphrey et al. 1977, Kurta & Whitaker 1998, Watrous et al. 2006). Indiana bats and other Myotine species have relatively low wing loading; this enables a greater ability to maneuver and forage in such areas of structural complexity (Norberg & Rayner 1987, Kalcounis & Brigham 1995). Within these structurally complex foraging environments along riparian zones, our failure to differentiate use among forest types suggests that Indiana bats were selecting forested habitats near water based more on structure and canopy cover, as opposed to forest type or tree species composition. Therefore, we suggest that managers focus on ensuring the availability of forested habitats of high structural complexity near open water sources.

The impact of land development can negatively affect Indiana bats by removing roost trees (Menzel et al. 2001), but our findings suggest that it is unlikely
that land development alone will deter Indiana bat foraging, provided forest and edge habitats near open water remain available. Our mixed support for development having a negative effect on Indiana bat foraging behavior is supported by previous studies from highly developed landscapes in the Midwest, where Indiana bats tolerate and forage over nearby agricultural fields (Menzel et al. 2005, Womack et al. 2013) and even airport runways (Sparks et al. 2005). Therefore, minimization and mitigation of human disturbance (particularly near riparian and forest habitats) seems prudent, but small amounts of human disturbance are unlikely to negatively impact Indiana bat foraging activity.

Management implications

Clearly, in comparison to WNS, roosting and foraging habitat may not be as strong a limiting factor impacting Indiana bats at present. However, persistence and recovery of remnant populations will rely on awareness of local or regional requirements of Indiana bats. Whereas considerable focus is placed on the identification and retention of suitable roost trees for Indiana bats, because the availability of high-quality foraging areas is critical to meeting the physiological needs of individual bats and ensuring recruitment and overwinter survival, foraging areas should also be an important conservation concern during the summer maternity season (Menzel et al. 2005, Womack et al. 2013). Accordingly, retention of a forest and water association should be a primary concern in the northern portion of the range. Where wetland and/or water associations change through succession or altered hydrology and only upland forests are retained, Indiana bat foraging use may decline or cease altogether. Future attempts to better elucidate conservation strategies for Indiana bats should account for year-round bat resource requirements, including overwinter hibernacula, spring and fall movement corridors, summer roost trees, and high-quality foraging habitat conditions during the summer maternity season.

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