

Long-distance movements of little brown bats (*Myotis lucifugus*)

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Quantifying distributions, home ranges, and individual movements for wildlife species is crucial for understanding their ecology and is important for conservation. This has become especially urgent for bat species affected by white-nose syndrome, a new disease of hibernating bats associated with the fungus *Geomyces destructans*. We studied within- and between-season movements of individual little brown bats (*Myotis lucifugus*) throughout a 337,540-km² study area in Manitoba and northwestern Ontario, Canada. Our objectives were to quantify proportions of male and female bats that relocated from hibernacula and/or summer roosts between years, proportions of males and females captured at swarms that hibernated at those sites versus other hibernacula, and distances traveled by males and females during relocation events. We predicted that bats would exhibit male-biased dispersal, with males significantly more likely to relocate and more likely to travel long distances during relocation events. Between 1989 and 2010, we recaptured 1,459 of 10,432 banded individuals. Seasonal movements from hibernacula and/or swarms to summer colonies ranged widely from 10 to 647 km. Consistent with previous studies we found high fidelity to summer colonies and hibernacula across years. However, some individuals switched sites between years and the median relocation distance was 315 km, with over 20% of individual movements exceeding 500 km. Surprisingly, we found that females were significantly more likely to relocate than males. Our data could help explain apparent jumps in the distribution of *G. destructans*, but more data on transmission of the fungus in the wild are needed.

Key words: Chiroptera, long-distance dispersal, mammals, migration, white-nose syndrome, wildlife disease

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DOI: 10.1644/12-MAMM-A-065.1

Movement of individuals from one place to another is the primary mechanism of gene flow for animals and, therefore, influences spatial distribution, dynamics, and genetic structure of populations (Kokko and López-Sepulcre 2006). Patterns of movement also affect susceptibility of wildlife species and populations to anthropogenic and naturally occurring environmental dynamics like climate change (Grosbois et al. 2008), habitat fragmentation (Debinski and Holt 2000), transport of invasive species (Mooney and Cleland 2001), and emerging wildlife diseases (Kelly et al. 2010). Understanding movements of wildlife species is therefore critical for understanding their ecology and developing strategies for conservation (Diffendorfer et al. 1995; Handley and Perrin 2007).

Sex-biased movements of animals often result from selection pressures to minimize risk of inbreeding (Handley and Perrin 2007; Pusey and Wolf 1996) or to meet habitat requirements, which may vary for males versus females and/or during different life-history stages (Andrews et al. 2010; Bowler and

Benton 2005; Iossa et al. 2009). Among mammals, males are typically considered to disperse or relocate, whereas females are more likely to remain philopatric (Dobson 1982; Greenwood 1980; Handley and Perrin 2007). Some studies on the population genetic structure of bats have reported this sex-biased behavior, where gene flow is often male biased and females show natal philopatry (Arnold 2007; Castella et al. 2001; Rossiter et al. 2012). Long-distance movements by males or females may be especially important to populations at risk of extinction or extirpation (Keller and Waller 2002; Pryde et al. 2005; Willi et al. 2006) because movements can help maintain genetic and social connectivity of isolated populations (Brown and Kodric-Brown 1977; Trakhtenbrot et al. 2005), provide individuals with access to habitats with sufficient



resources (Lowe 2010), and allow for recolonization following regional extirpation (Stoner et al. 2008). Despite these benefits, long-distance movements are also potentially costly because they can increase energetic costs (Diffendorfer et al. 1995; Rousset and Gandon 2002), risk of predation (Bonnet et al. 1999), and exposure to pathogens or parasites (Kelly et al. 2010; Williams et al. 2002). Sex-biased movements of male white-tailed deer, *Odocoileus virginianus*, for example, have significant implications for transmission of chronic wasting disease, with male deer more likely to spread the disease (Kelly et al. 2010).

Despite the importance of understanding individual movements for addressing ecological questions and conservation, seasonal movements of bats remain poorly understood for most species. Understanding seasonal movements has become especially urgent for North American bat species in light of white-nose syndrome (WNS), a new disease that is spreading quickly throughout North America (Frick et al. 2010). Recent evidence suggests that *Geomyces destructans* is an invasive species to North America (Warnecke et al. 2012) and, since its arrival, WNS has spread rapidly throughout the northeastern United States and eastern Canada. Mortality from WNS has been reported in at least 6 species, but the little brown bat (*Myotis lucifugus*) appears to have had the largest population declines (Blehert et al. 2009; Foley et al. 2011; Frick et al. 2010; Wilder et al. 2011). Recent work documents a collapse of little brown bat populations in the affected region (Dzal et al. 2010; Langwig et al. 2012), with regional extinction predicted within 20 years of the arrival of WNS in a given area (Frick et al. 2010). Quantifying movements of the most affected species is critical for predicting contact rates of individuals and the spread of the infection to new regions, as well as potentially developing conservation strategies.

The little brown bat is one of the most common, widely distributed, and best-studied bats in North America, but many aspects of its biology are still not well understood. Like many temperate bats, little brown bats choose caves and mines as hibernacula, where they form groups of a few to hundreds of thousands of individuals (Fenton and Barclay 1980; Keen and Hitchcock 1980). In spring, they split into smaller, largely sex-segregated groups, with females forming maternity colonies to give birth and raise pups (Fenton and Barclay 1980; Nowak 1994). Males are less gregarious in summer and rarely found in groups (Davis and Hitchcock 1965; Kurta and Kunz 1988). In fall, from August to October, bats gather at swarms, focused at hibernacula, presumably to mate and potentially to familiarize juveniles with hibernation sites (Davis and Hitchcock 1965; Fenton 1969; Thomas et al. 1979). During swarming, bats fly near entrances of hibernacula in large numbers, and often enter sites to roost briefly and mate. Little brown bats appear to exhibit promiscuous mating behavior in fall, with some additional mating during winter, especially in early hibernation (Thomas et al. 1979). Swarms are likely primary sources of gene flow connecting otherwise isolated populations, as reported for similar bat species (Arnold 2007; Glover and

Altringham 2008; Kerth et al. 2003; Rossiter et al. 2012; Stihler et al. 1997; Veith et al. 2004).

Several studies have reported movements of little brown bats between different hibernacula (from a few kilometers to 805 km for 1 individual—Fenton 1969), between summer roosts and hibernacula (2–241 km—Davis and Hitchcock 1965), and between swarms and both summer roosts and hibernacula (119–805 km, Fenton 1969; 10–455 km, Humphrey and Cope 1976). However, to our knowledge, so far there have been no long-term data analyzed to test hypotheses about sex-biased movements of males versus females, or the likelihood of individuals relocating from certain types of sites versus others (e.g., summer roosts versus hibernacula versus swarms or caves versus mines). Moreover, despite several studies based on a few years of mark–recapture data, the large aggregations of bats at specific sites and their long life spans mean that long-term data sets (i.e., decades long) may be needed to fully characterize individual movements for this species.

We studied individual movements of little brown bats throughout a 337,540-km² study area in Manitoba and northwestern Ontario, Canada (Fig. 1) using a 21-year capture–mark–recapture data set (Dubois and Monson 2007). Our objectives were to quantify the proportions of recaptured bats that changed hibernacula and/or summer roosts between years, the proportion of bats captured at swarms that hibernated at those sites versus other hibernacula, and the distances traveled by bats during relocation events, all critical parameters for informing infectious disease models of spread of WNS. Past studies have reported long-distance movements of hundreds of kilometers, but movements on this scale represented a small proportion (12–13%) of all reported relocation events (Davis and Hitchcock 1965; Fenton 1969). Thus, although we expected to observe a few movements on this scale, we predicted that movements exceeding 300 km (the approximate distance that WNS has spread annually since its discovery—Foley et al. 2011) would be rare compared with more local-scale movements. Female philopatry and male-biased dispersal are common in wide-ranging mammals (Handley and Perrin 2007). Female bats are known to exhibit high levels of long-term fidelity to summer maternity roosts (Lewis 1995; Willis et al. 2003; Willis and Brigham 2004), whereas dispersal is often male biased (e.g., Arnold 2007; Castella et al. 2001; Kerth et al. 2002). Therefore, our second prediction was that male bats would be more likely to relocate than females, and that relocating males would travel greater distances than relocating females. Given the importance of swarms for gene flow, we also predicted that a higher proportion of bats captured at swarms would be recaptured at sites other than their swarm, whereas individuals first caught at summer roosts or hibernacula would be more likely to be recaptured at those same locations.

MATERIALS AND METHODS

We captured bats at 3 types of sites between 1989 and 2010: at summer maternity colonies ($n = 22$ sites), which consisted

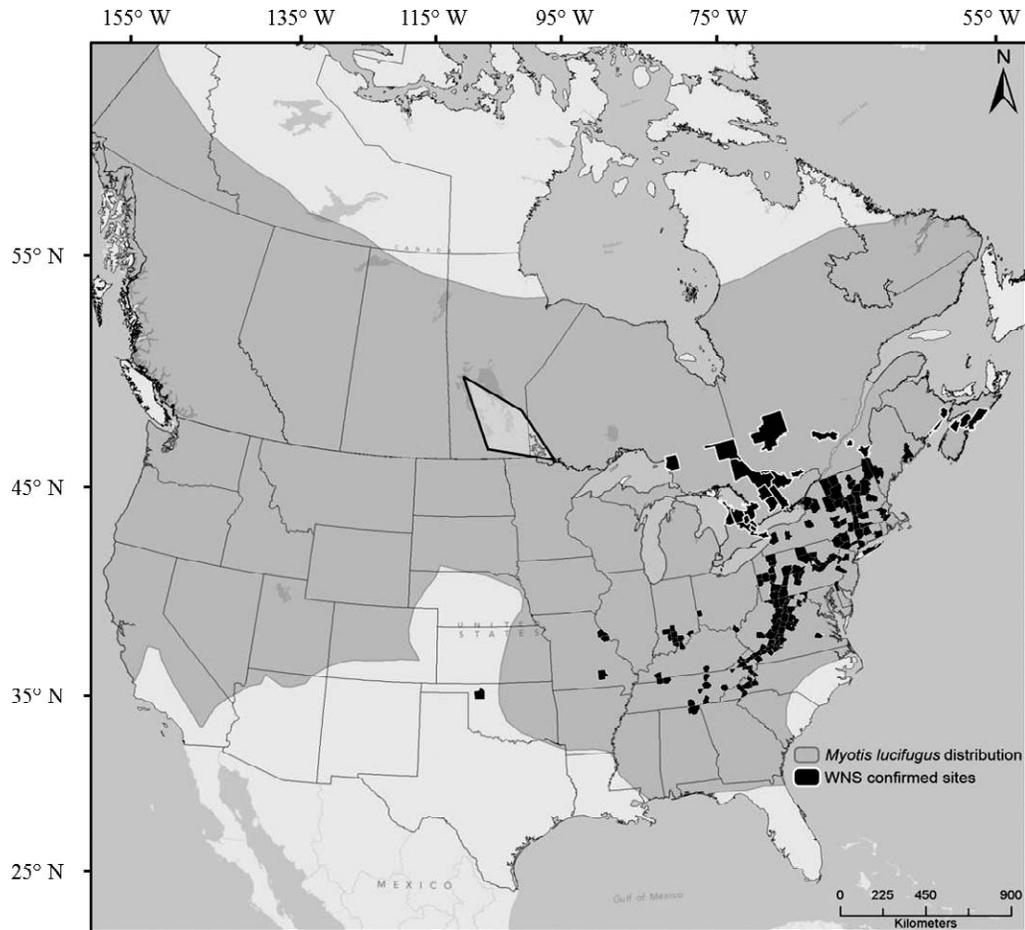


FIG. 1.—Distribution of little brown bats (*Myotis lucifugus*) and counties/districts in North America (in black) where white-nose syndrome (WNS) has been confirmed. The highlighted gray region in Manitoba and Ontario represents our study area, where a total of 10,432 bats were banded from 1989 to 2010. The little brown bat distribution is based on data from United States Geological Survey and Bat Conservation International available through a national atlas (<http://www.nationalatlas.gov/mld/bat000m.html>) and the distribution of WNS is based on information from the United States Fish and Wildlife Service (<http://www.fws.gov/whitenosesyndrome/maps.html>).

primarily of adult females and their young, at swarming sites at known hibernacula ($n = 6$ sites), and during early hibernation and late hibernation within hibernacula ($n = 16$ sites). Summer roosts were identified with the help of home and cottage owners in Manitoba and northwestern Ontario, as well as Manitoba Conservation, the Ontario Ministry of Natural Resources, and other agencies. Hibernacula were first located on the basis of surficial geology, topographical maps, and air photos. Regions were examined for karst features such as caves, sinkholes, and trenches in areas where limestone, dolomite, and gypsum bedrock were near the surface. Promising regions were then searched in a grid pattern using topographic maps, compasses, and handheld global positioning system units. An additional hibernaculum was found with aid from a member of the public. Known hibernacula were then visited in August and September to identify swarms. Swarming sites were defined by the presence of relatively large numbers of bats flying near the entrances of, or entering and exiting, hibernacula (Cope and Humphrey 1977; Davis and Hitchcock 1965; Fenton 1969).

Before 1996 all banding during fall was performed by entering hibernacula ($n = 4,996$) and removing bats within reach by hand. Sampling was not necessarily random in a few hibernacula because there were areas we could not reach. However, this was only an issue for the largest hibernacula with hundreds to thousands of bats and, in these sites, our sample only represented a small proportion of the accessible individuals, so it is unlikely to have strongly influenced our results. From 1997 to 2010 fall banding was performed by capturing bats at swarms, with the exception of banding in late October and November from 1997 to 2002 ($n = 1,401$). Between 1989 and 2007, 9,505 bats were banded using numbered, split-ring aluminum bands (National Band and Tag Co., Newport, Kentucky). From 2007 to 2010 an additional 927 bats were marked using lipped, numbered aluminum bands (Porzana Ltd., 2.9 mm, Icklesham, East Sussex, United Kingdom, $n = 364$), or by subcutaneously injecting a passive integrated transponder tag (Trovan Ltd. ID 100-01, Douglas, United Kingdom, $n = 653$). Of the total 10,432 bats captured, 7,922 (76%) were banded at 16 winter hibernacula, 999 (10%)

TABLE 1.—Summary of the types of movements of little brown bats (*Myotis lucifugus*) from sites where they were first captured to sites where they were later recaptured. Numbers in parentheses indicate total sample sizes of recaptures at a given type of site (i.e., including bats that did not relocate).

Type of movement	Median relocation distance per type of movement (km)	Number of relocated bats per type of site
Between summer roosts	431	5 (41) ^a
Between hibernacula	315	54 (1,349) ^a
Between swarm and hibernacula	314	5 (43)
Between summer roost and hibernacula	463	24 (41)
Between swarm and summer roost	298	2 (43)
Total		88 (1,459)

^a One bat from each of these categories completed 2 movements.

were banded at 22 summer locations, and 1,511 (14%) were banded at 6 swarms located near the entrance of known hibernacula. The greatest proportion of banding (5,002 bats, 48%) occurred at St. George's Bat Cave in central Manitoba, where over 9,000 bats spend the winter. The 2nd largest proportion of bats we banded (2,932 bats, 27%) were captured at 9 caves located 30 to 60 km north of Grand Rapids, Manitoba. A total of 1,190 bats was marked at a 3rd hibernaculum at Richard Lake near Kenora in northwestern Ontario. Sex was recorded for each bat, whereas age (adult or juvenile) was recorded for 539 individuals captured from 2007 to 2010. Juveniles (<1 year) were identified on the basis of the degree of epiphyseal ossification in the metacarpal-phalangeal joints of the wing (Kunz and Anthony 1982), in combination with an estimate of tooth wear (Grinevitch et al. 1995; Stegeman 1956). In females, the presence of bare patches around the nipples indicating lactation status helped rule out juvenile status (Racey 1974). Body condition was quantified as mass/forearm length (Pearce et al. 2008; Reynolds et al. 2009). All recaptures occurred during regular banding activities at summer roosts, swarms, and hibernacula.

Fieldwork was conducted under Manitoba Conservation and Ontario Ministry of Natural Resources Wildlife research permits, approved by the University of Winnipeg Animal Care Committee in 2006 and adhered to the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011). We took care to minimize disturbance to bats, only entering hibernacula at most once per year and by minimizing the duration of entries into hibernacula to 1 h. All bats were released at the site of capture after data collection. Although none of the study sites is, as yet, affected by WNS, since 2007 we closely followed United States Fish and Wildlife Service guidelines for decontamination of *G. destructans*.

Distances were calculated by measuring the straight-line distance between sites using Google Earth 6.2 (Google Inc.). We used chi-square tests to assess differences between frequency of recapture and relocation for males and females. We used nonparametric Mann-Whitney *U*-tests in SYSTAT 13 (Systat Software Inc., Chicago, Illinois) to compare distances traveled by males and females because distances traveled appeared to be limited by the nonrandom spatial distribution of hibernacula and summer roosts. Significance was assessed at an alpha level of 0.05. Sample sizes refer to number of

movements unless otherwise indicated (i.e., in a small number of cases individual bats were recaptured, and observed relocating, more than once).

RESULTS

Significantly more males than females were banded at hibernacula (5,382 males versus 2,402 females, 69% male, 31% female, $\chi^2 = 1,122.2$, $P < 0.001$, $d.f. = 1$) and swarms (867 males versus 634 females, 58% male, 42% female, $\chi^2 = 36.2$, $P < 0.001$, $d.f. = 1$). The majority of bats banded at summer roosts were female (179 males versus 820 females, 18% male, 82% female, $\chi^2 = 409.3$, $P < 0.001$, $d.f. = 1$).

Overall, 14% ($n = 1,459$) of bats were recaptured during 155 recapture sessions over 20 years. Six percent of these recaptured bats (0.8% of the total 10,432 banded bats) were found at sites other than their original capture site ($n = 88$). Bats relocated between every possible combination of sites (Table 1). The rate of relocation for bats first captured at summer roosts and later recaptured at a different summer roost in a subsequent year was 12% (5/41), whereas the relocation rate of bats first captured at hibernacula and later recaptured at different hibernacula in a subsequent year was only 4% (54/1,349). Of bats first captured at swarms, 12% (5/43) were later recaptured in a different hibernaculum but the large remaining majority were recaptured in the hibernaculum at which they swarmed. Fidelity to hibernacula was significantly higher than fidelity to maternity colonies ($\chi^2 = 7.4$, $P = 0.006$, $d.f. = 1$) and swarms ($\chi^2 = 6.8$, $P = 0.009$, $d.f. = 1$). Males were significantly more likely to be recaptured at hibernacula than females ($\chi^2 = 82.5$, $P < 0.001$, $d.f. = 1$).

Due to the spatial distribution of hibernacula and summer colonies on the landscape, the frequency distribution of distances traveled by bats was nonnormal and fell into 3 obvious bins: <100 km ($n = 27$), 200–320 km ($n = 42$), and >430 km ($n = 23$) (Fig. 2a). Bats that relocated from one capture site to another were found 6 to 569 km (median = 298, $n = 90$) from their original capture site. Bats that relocated from one hibernaculum to another (Fig. 2b) traveled 6 to 563 km (median = 315, $n = 54$). A surprisingly large proportion of movements between hibernacula (25%, 13/54) covered distances greater than 500 km (Fig. 2b), whereas only 19% (10/54) covered short distances of 6 to 25 km (median = 16 km) among the group of hibernacula north of Grand Rapids. Bats

Richard Lake Mine came from hibernacula 51 to 554 km away. Relocating bats first captured in Richard Lake Mine and then found at another site, or vice-versa (range = 48 to 569 km, median = 552, $n = 23$), traveled significantly farther than bats moving to or from St. George's Bat Cave (range = 80 to 308 km, median = 266 $n = 34$, $U = 570.5$, $P = 0.003$, $df = 1$). Nineteen bats traveled from one of these sites to the other and were excluded from this analysis.

The distances traveled during relocation from one hibernaculum to another by males (range = 6 to 569 km, median = 267, $n = 38$) and females (range = 6 to 569 km, median = 315, $n = 16$; $U = 273.5$, $P = 0.403$, $df = 1$; Fig. 3a) were not significantly different. However, in contrast to our predictions, males were significantly less likely than females to relocate from one hibernaculum to another ($\chi^2 = 4.3$, $P = 0.038$, $df = 1$). Bats that moved between swarms and hibernacula, or vice-versa, included both males ($n = 2$) and females ($n = 3$), whereas bats that moved between maternity roosts included 4 females and 1 male.

Not all sites were monitored each year so we are unable to determine the average rate of movement for individuals in most cases (i.e., if a given bat undertook the movement we observed within 1 year as a single dispersal event or over multiple years). However, 2 individuals recaptured in consecutive years demonstrated that little brown bats are able to travel great distances within a short time frame. One of these individuals traveled 562 km in only 5 months, from May, when it was captured at a hibernaculum north of Grand Rapids, to October when it was captured in Richard Lake Mine in northwestern Ontario. This same bat was recaptured again, back in Grand Rapids the following May. Therefore, this individual traveled at least 1,124 km within a 12-month period. The other bat traveled 569 km in less than 1 year, captured in one of the hibernacula north of Grand Rapids in mid-October and recaptured in Richard Lake Mine the following May.

DISCUSSION

Although a few banding studies have reported on movements of little brown bats (e.g., Davis and Hitchcock 1965; Fenton 1969; Humphrey and Cope 1976), this study provides information on the basis of longer-term banding data and is the first to test specific hypotheses about differences in relocation frequencies of males versus females and of bats from different types of sites. Consistent with past studies on little brown bats (e.g., Humphrey and Cope 1976), we found that most individuals (94%) exhibited philopatry to both maternity colonies and hibernacula, which suggests that costs associated with relocation often outweigh benefits. Individual dispersers may have higher mortality rates than nondispersers, due to increased risk of predation and heightened energetic costs. In yellow-bellied marmots (*Marmota flaviventris*), for example, dispersers had a 16% lower survival rate (0.73) than philopatric individuals (0.87—Van Vuren and Armitage 1994).

Despite strong philopatry, patterns of movement by bats in our study varied among different categories of sites. For

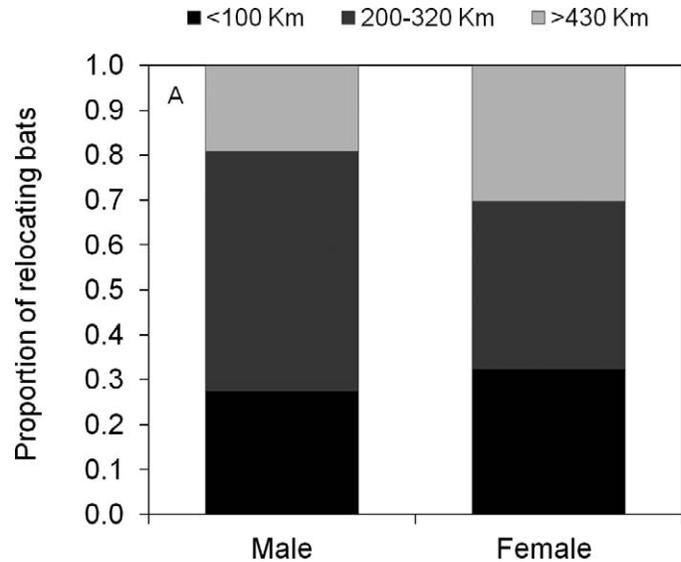


FIG. 3.—a) Proportions of relocating male and female little brown bats (*Myotis lucifugus*) by distance. Shades indicate the relative proportions of short (<100 km), medium (200–320), and long (>430 km) distance movements, with these categories defined on the basis of the frequency distribution of all relocation events (i.e., Fig. 2a).

instance, fidelity to hibernacula we observed (96%) was significantly higher than fidelity to summer roosts (88%). Although bats can exhibit strong fidelity to even relatively impermanent structures such as foliage (Willis and Brigham 2005) or tree hollows (Willis et al. 2003), they tend to show greater fidelity to roosting sites that are relatively permanent and/or rare (Brigham 1991; Lewis 1995). Our results are consistent with this observation, as caves or mines with suitable microclimate characteristics are likely to be less common than potential maternity roosts. Fidelity to swarms was also low (88%) relative to hibernacula, which is likely more reflective of the function of swarms (i.e., mating and gene flow) as opposed to their abundance or permanence.

Although the proportion of bats that relocated was low, our results highlight the ability of little brown bats to travel long distances and suggest that patterns of movement by little brown bats may differ in different parts of their range. Even though a large proportion of the sites we repeatedly sampled was in close proximity (i.e., 9 hibernacula in Grand Rapids, Manitoba are within 17 km of each other), 72% of bats that we observed relocating traveled distances exceeding 200 km and 23% traveled more than 500 km. Maximum distance traveled by bats was just over 560 km ($n = 7$ movements by 6 bats), which is less than the maximum reported for little brown bats in southern Ontario (805 km) by Fenton (1969). However, the 72% of bats that we observed moving distances greater than 200 km was much higher than reported in past studies (e.g., 13% by Fenton 1969; 12% by Davis and Hitchcock 1965). Humphrey and Cope (1976) reported a range of relocation distances for bats from summer to winter roosts in Indiana and north-central Kentucky (6 to 455 km) that was similar to values we observed (35 to 554 km). They observed bats over

a similar period of sampling (17 years) with a similarly sized study area and sample size of sites. They also recorded 10 times more recaptures than in our study. However, median distance traveled by bats in our study (463 km) was more than 4 times greater than the average relocation distance they reported (100 km). This could reflect spatial distribution of hibernacula in our study area. Suitable hibernacula may be rarer in central and western North America, compared with the eastern part of the continent. Western hibernacula also appear to house smaller numbers of bats, with most studies reporting groups of less than 500 individuals per site (Hendricks 1998; Nagorsen et al. 1993; Perkins et al. 1990). The largest group of hibernating bats known in Manitoba numbers just over 9,000 bats, substantially less than the pre-WNS population of overwintering bats reported in many sites in eastern North America that ranged in the tens to hundreds of thousands (Davis and Hitchcock 1965; Fenton 1970). Reduced availability of hibernacula and the smaller size of available sites may force bats to travel longer distances in central and western North America.

We predicted that males would be more likely to relocate than females and travel farther than females because, in general, promiscuous or polygynous mammals tend to display male-biased dispersal and female philopatry (Dobson 1982; Greenwood 1980; Handley and Perrin 2007). There are exceptions to this trend, including female-biased dispersal in the polygynous sac-winged bat (*Saccopteryx bilineata*) and the polygynous hamadryas baboon (*Papio hamadryas hamadryas*; Hammond et al. 2006; Nagy et al. 2007). Advantages to dispersal can include inbreeding avoidance and avoidance of local competition for mates or resources (Greenwood 1980; Pusey 1987). Local mate competition tends to favor male-biased dispersal because males have greater reproductive potential than females (Clutton-Brock 1991; Perrin and Mazalov 1999). On the other hand, females usually have higher reproductive energetic demands than males so high local resource competition tends to favor female-biased dispersal (Perrin and Mazalov 1999). Interestingly, females in our study had significantly higher relocation rates between hibernacula, almost double those of males, and females traveled just as far as males when they relocated (Fig. 3a). This observation is consistent with the hypothesis that local resource competition influences interannual movements of females and that the costs of this resource competition exceed the costs of local mate competition experienced by males (Perrin and Mazalov 1999). Local competition for high-quality hibernacula may drive this pattern for female bats as females appear to face intense selection pressure to retain as much fat as possible throughout hibernation (Kunz et al. 1998). Jonasson and Willis (2011) showed that female little brown bats lost mass more slowly than males during winter, presumably because females are under greater selective pressure to conserve fat in support of spring reproduction. Taken together, these findings suggest that high-quality hibernacula are not just important for overwinter survival of bats, in general, but are also critical habitats important for female reproduction.

In other bat species, genetic diversity is significantly higher among bats at swarms in comparison with summer roosts, suggesting that swarms are focal points for gene flow (e.g., Kerth et al. 2003; Rivers et al. 2005; Veith et al. 2004). Consistent with these observations, and past work (Fenton 1969), bats captured at swarms had among the highest movement rates of all individuals we studied, with 12% later found in hibernacula other than their capture site. Female little brown bats appear to mate indiscriminately with males, which led Thomas et al. (1979) to hypothesize that, as in other promiscuous mammals, males face selection pressure to inseminate as many females as possible. One way to do this would be to visit multiple swarming sites each fall. However, although our sample size of bats relocating between swarms was very small ($n = 5$; 2 females, 3 males), the fact that we also observed females relocating long distances between swarms suggests that movements of bats among swarms does not simply reflect male mating behavior. Female movements from swarms to different hibernacula could reflect an additional function of swarms: to familiarize juveniles with potential hibernacula (Fenton 1969). Although age was not recorded for most of our study, it is possible that bats we observed relocating from swarms were juveniles visiting multiple hibernacula before choosing a site in which to hibernate. Despite these movements, a large proportion of bats captured at swarms (88%) were later found hibernating at those same sites and, of these, 37% (14/38) were found during the winter immediately following 1st capture. This suggests that many individuals focus their activity at swarms locally, at sites where they intend to hibernate.

Movements among summer roosts were more common than expected, supporting results from a recent study on maternity colonies of little brown bats in Minnesota (Dixon 2011). On the basis of genetic markers, Dixon (2011) found low but significant population genetic structure, supporting the occurrence of some female natal philopatry. However, he also estimated a relatively high overall migration rate among summer colonies, which is consistent with our observations of relatively frequent movements of females among maternity roosts. Our results demonstrating high rates of movement among summer roosts may also reflect juvenile dispersal or influences of weather/climate. Syme et al. (2001) found that large colonies of little brown bats increased in size during summers with low temperatures, whereas small colonies decreased in number. Such fluctuations may reflect trade-offs between benefits of social thermoregulation, important for roost selection and development of juveniles (Kurta and Kunz 1988; Tuttle 1975; Willis and Brigham 2007) and potential costs of communal roosting, including increased parasite load and disease risk (Reckardt and Kerth 2007). Our sampling areas are close to the northern limit of the little brown bat's distribution (Fenton and Barclay 1980) and high numbers of movements among maternity colonies could reflect unpredictable or unfavorable weather patterns. Humphrey and Cope (1976), for example, found much lower relocation rates (1.3%)

than we observed (6%), in their more southern study sites in Indiana and Kentucky.

Davis and Hitchcock (1965) found that bats from the cave they examined tended to travel farther than bats from 3 mines that they also surveyed, leading them to hypothesize that mines serve more local populations than caves because mines are more recent landscape features that have had less time to be discovered by bats. We did not find evidence for this hypothesis. Bats from St. George's cave had shorter dispersal distances (median = 266.5 km) than bats from Richard Lake Mine (median = 555.6 km). This likely reflects, in part, the central location of St. George's Cave in our study area (Fig. 2b) but it is clear that bats hibernating in the mine we studied regularly travel long distances.

Although more data are needed on the nature of *G. destructans* transmission in the wild, our results have implications for the spread of WNS in North America. Given that bat-to-bat transmission of *G. destructans* has been demonstrated in the laboratory (Lorch et al. 2011), relatively frequent long-distance movements of hundreds of kilometers in a year provide a biological (i.e., nonanthropogenic) mechanism to explain rapid spread of this emerging epizootic but only if the kinds of movements we observed occur when bats are infectious. Movements we observed most commonly (i.e., interannual movements from one hibernacula to another) could be important for transmission if bats can harbor infectious fungal material obtained in one hibernaculum over the summer and then infect bats or substrates in a new hibernaculum when they relocate the following autumn. Hibernacula may serve as environmental reservoirs for *G. destructans* (Lindner et al. 2011) and bats are known to enter hibernacula during swarming (Thomas et al. 1979), which means that movements from one swarm to another (which we never observed) or movements from a swarm to a different hibernaculum (which we did observe, albeit infrequently) may be more important in terms of *G. destructans* transmission than interannual movements. On the other hand, individual bats more likely to perform long-distance, interannual movements may also be more likely to visit multiple hibernacula before hibernation in the fall, in which case these individuals could be most likely to spread *G. destructans*.

Our data on relative distances traveled by bats in Manitoba and northwestern Ontario, compared with data from eastern North America, also suggest possible scenarios for transmission of *G. destructans*. If only small fungal loads (and only 1 or a few infectious bats) are needed to spread infection to a new site, greater apparent distances between suitable hibernacula in central and western North America and a tendency for longer distance movements by bats could allow WNS to expand in greater leaps than previously observed. However, even though long-distance movements are occurring in our study area, fewer total numbers of individuals may be moving among sites compared with eastern North America due to smaller cave populations. This may reduce the rate at which *G. destructans* will colonize new hibernacula in the west, even if proportions of bats switching among sites is higher, particularly if large fungal loads are needed to result in new infections. In light of

these hypotheses, it is urgent that we determine the occurrence and prevalence of fungal conidia on bats at swarms and in hibernacula, and test whether fungal conidia can remain viable in maternity roosts or on bats during summer (Jonasson and Willis 2011).

Our data indicate that, although fidelity of individuals to summer roosts, hibernacula, and swarms is high, movements of hundreds of kilometers occur routinely (i.e., every year) for both male and female little brown bats. Surprisingly, fidelity to hibernacula was higher among males, which could reflect local resource competition for hibernacula among females, and selection pressure for females to seek out the highest-quality sites. This finding, combined with the fact that hibernacula are also likely hot spots for gene flow and information transfer, emphasizes the importance of protecting these critical habitats for bats. The movements we observed have important ecological and conservation implications, especially in light of WNS, and highlight the need for data on the progression of disease in bats affected by WNS and the viability of *G. destructans* on bats and in the environment throughout the year.

ACKNOWLEDGMENTS

We thank members of the Manitoba Speleological Society, especially D. Brown, and the University of Winnipeg Bat Lab for help with fieldwork, and Manitoba Conservation for providing lodging in the field. We also thank the Misipawistik Cree Nation for the opportunity to study bats on their traditional territory. A. M. Kilpatrick and W. F. Frick provided very helpful comments on an earlier draft of the manuscript. Funding was provided by the Natural Sciences and Engineering Research Council (NSERC, Canada), Canada Foundation for Innovation, Manitoba Research and Innovation Fund, and Manitoba Hydro Forest Enhancement Program.

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Submitted 13 March 2012. Accepted 21 September 2012.

Associate Editor was Richard D. Stevens.