Activity of tree bats at anthropogenic tall structures: implications for mortality of bats at wind turbines

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Conserving migratory species is difficult because wide-ranging animals are challenging to study and aspects of their annual cycles occur in geographically distant areas. This challenge is illustrated by the hundreds of thousands of migratory bats killed annually during autumn migration by industrial wind turbines. It is unknown why bats are killed at turbines because they are so difficult to observe during migration. A conservation behaviour approach has potential to explain what is, arguably, the most significant environmental impact of wind energy. We tested predictions of two hypotheses to explain the presence of bats at turbines: (1) bats are attracted to visually conspicuous tall structures during autumn migration; (2) attraction is linked to social behaviour rather than foraging. We compared acoustic activity of migratory tree bats at conspicuous tall structures (telecommunication towers) to activity at two types of control sites (woodlot edges: consistently attractive to bats; open fields: consistently unattractive) before and during migration. Activity of migratory bats increased dramatically at towers during migration, from low premigration levels, to exceed that at open fields and match that at woodlots. Moreover, the proportion of feeding calls at towers remained low while the proportion of events during which multiple bats visited the towers simultaneously increased during migration to surpass that at woodlots and open fields. This suggests that migratory bats actively visit tall structures during migration for reasons other than foraging. Exploiting this behaviour, and the abundance of communication towers on the landscape, could reveal critical information about migratory behaviour of bats and help guide site selection for wind energy projects. Our findings demonstrate the importance of understanding the behaviour of migratory species at all stages of their annual cycle for effective conservation.

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The field of conservation behaviour aims to apply behavioural approaches to questions relevant for conservation of animal populations (e.g. Angeloni, Schlaepfer, Lawler, & Crooks, 2008; Sutherland, 1998). These efforts often focus on behavioural events and human impacts occurring during the reproductive season (e.g. Walker, Boersma, & Wingfield, 2005), but for species that perform long-range seasonal migrations, critical behavioural events and potentially dramatic human impacts can occur at multiple times throughout the year in geographically disjunct locations (Martin et al., 2007). Animals are particularly difficult to study during the process of migration, so we know relatively little about how migratory behaviour may place animals at risk, despite the importance of understanding behaviour throughout the annual cycle for effective conservation (Martin et al., 2007; Wilcove & Wikelski, 2008).

Mortality of bats at wind turbines typifies this challenge for conservation of migratory species. As many as half a million bats are killed annually in the U.S. and Canada, making bat mortality arguably the most significant environmental impact of industrial wind power (Arnett & Baerwald, 2013; Cryan, 2011; Hayes, 2013; Smallwood, 2013). Despite their sensitive echolocation, bats fail to avoid collisions presumably because tips of modern turbine blades spin too fast (up to 300 km/h) for bats to detect and avoid (Kunz, Arnett, Erickson, et al., 2007). In contrast to birds, for which mortality is distributed among many species with relatively low rates per species, in North America, high rates of mortality occur in only a few bat species, primarily hoary, Lasiurus cinereus, eastern red, Lasiurus borealis, and silver-haired bats, Lasionycteris noctivagans, creating the potential for significant population impacts (Barclay, Baerwald, & Gruver, 2007; Johnson et al., 2002; Kunz, Arnett, Cooper, et al., 2007; Smallwood, 2013; Willis et al., 2010). These species roost alone or in small groups in trees, undertake

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long-distance seasonal migrations and, in the case of *L. cinereus* and *L. borealis*, fly higher and faster than nonmigrants (Kunz, 1982; Shump & Shump, 1982a, 1982b). As a result, little is known about the behaviour of 'tree bats', especially during migration.

Given the high rates of mortality, the demographic and species composition of fatalities and the seasonal pattern of mortality, it is unlikely that fatalities result from random encounters between turbines and flying bats (Cryan & Barclay, 2009). Bats are not attracted to aviation lights on turbines (Arnett et al., 2008; Bennett & Hale, 2014; Horn, Arnett, & Kunz, 2008). Moreover, while turbines produce ultrasound, its intensity may be too low to attract bats from long distances (Szewczak & Arnett, 2006) and there is no evidence to suggest bats are attracted to sounds from turbines. Bats may be attracted to insects that might concentrate around turbines or they could mistake turbines for potential roosts (Cryan & Barclay, 2009; Kunz, Arnett, Erickson, et al., 2007), but this predicts that mortality should be more evenly distributed seasonally and demographically. On the contrary, the large majority of fatalities occur in late summer/early autumn, when southward migration and mating occur, with dramatically less mortality during spring migration and summer (Cryan, 2008). Many studies have also found a larger proportion of adults among fatalities of some tree bat species (Arnett et al., 2008; Cryan, 2008; Jameson, 2011; Jameson & Willis, 2012). These nonrandom aspects of bat mortality at turbines led Cryan (2008) to hypothesize that bats are actively attracted to turbines during autumn migration and that mortality may be linked to social behaviour, although no direct evidence of an attraction exists.

Cryan (2008) proposed the reproductive landmarks hypothesis, which posits that bats perceive turbines and other visually conspicuous tall structures as sites at which to find potential mates. Since tree bats roost alone or in small groups, are presumably spread out across the landscape during summer and migrate long distances, selection should favour behavioural mechanisms that help them find conspecifics for mating. Tall structures on the landscape could be landmarks that remain visually conspicuous against the horizon while bats migrate at night. Historically, such landmarks would have been tall trees, but more conspicuous tall structures are now common. Although rare, collisions of migratory tree bats have been reported at other tall anthropogenic structures including lighthouses (Saunders, 1930), cooling towers at nuclear facilities (Ryback, Jackson, & Vessey, 1973), television towers (Van Gelder, 1956) and even the Empire State Building (Terres, 1956). As with turbines, all such collisions have occurred during autumn migration/mating.

We addressed two hypotheses arising from the reproductive landmarks hypothesis. (1) Tree bats are attracted to visually conspicuous tall structures at the same time of year (i.e. autumn mating/migration) that they are killed at wind turbines. (2) Bats visit tall structures for some function other than foraging (e.g. social/mating behaviour). We compared acoustic activity and types of vocalizations of bats at conspicuous tall structures (i.e. telecommunication towers) to activity at control habitats (i.e. woodlot edges and open fields; Barclay, 1989; Downs & Racey, 2006; Gehrt & Chelsvig, 2003) to evaluate the following predictions. (1) Prior to autumn migration, activity of migratory bats at tall structures is comparable to that at open fields (which are unattractive to bats) and lower than activity along woodlot edges close to a source of fresh water (which are consistently attractive to bats; de Jong & Ahlén, 1991; Ethier & Fahrig, 2011; Grindal & Brigham, 1998; Rainho & Palmeirim, 2011). (2) During the migration period, activity of migratory bats increases sharply at tall structures to exceed that at open fields and approach that at woodlot edges, while activity at control habitats does not change dramatically. (3) A smaller proportion of the activity of nonmigratory bat species occurs at tall structures compared to the activity of migratory bat species. (4) Proportion of feeding buzzes, a distinctive sequence of echolocation pulses produced by bats when they attempt to capture prey (Griffin, 1958) and which can be used to make inferences about foraging behaviour (Brigham, Grindal, Firman, & Morissette, 1997; Russo & Jones, 2003), are lower at tall structures than at woodlot edges because bats visit tall structures for social purposes rather than for foraging. (5) The proportion of recorded passes that include calls from multiple individuals increases at tall structures during migration when multiple bats visit towers simultaneously.

METHODS

We conducted this study from 9 July to 17 September 2008 and 2 June to 30 September 2009 near the 99 MW St Léon Wind Energy facility in south-central Manitoba (49°22′01″N, 98°35′24″W). The area is a forest-agricultural matrix of small woodlots, wetlands, cultivated cropland and cattle pasture. Woodlots were dominated by trembling aspen (*Populus tremuloides*) and bur oak (*Quercus macrocarpa*).

All methods were approved by the University of Winnipeg Animal Care Committee and were consistent with the ASAB/ABS Guidelines for the treatment of animals in research. We selected four (2008) or five (2009) Manitoba Telecom Services towers (towers) to serve as visually conspicuous tall structures. Towers were located at least 24 km from the wind energy facility, so that wind turbines were not visible in the distance, but within 45 km of the facility to ensure they were all within a 1- to 2-night flight distance for tree bats. Within 1.5–6.5 km of each tower we selected both a 10–25 ha woodlot and a 500–1300 ha open field. We assumed that this distance would be close enough to control for local variation in topography but far enough to ensure that our sample of bat activity at one habitat was not influenced by activity at another in the same group. We monitored bat activity simultaneously at each habitat type within a given site. We had a limited number of bat detectors (described below), so we used a blocked, repeated measures design and rotated equipment among sites at 3-day intervals from as early in the spring/summer as possible until bats were no longer detected in the study area during autumn. We defined one 'recording cycle' as beginning with the onset of sampling at the first site (i.e. the first group of habitats: tower, woodlot, open field) and ending with the end of sampling at the last site. We completed two of our recording cycles in 2008 and six cycles in 2009. We defined each cycle as occurring during either 'premigration' or 'migration', delineated based on when we began finding dead bats at the nearby wind energy facility (Jameson, 2011). We were unable to sample during premigration in 2008 because of a delay in site access, so both cycles from that year occurred during migration. In 2009, recording cycles 1–2 coincided with premigration and recording cycles 3–6 coincided with migration.

Towers in our study area were lattice towers. These provided a good proxy for wind turbines as they were, by far, the tallest structures (70–111 m) in the area after turbines (120 m) and were visible against the horizon from up to 14 km away at ground level. In general, towers also have no moving parts and generate no heat or noise, all factors hypothesized as possible direct or indirect attractants of bats to wind turbines (Cryan & Barclay, 2009; Kunz, Arnett, Erickson, et al., 2007). Both turbines and towers have aviation lighting, but there is no evidence that these lights attract bats (Arnett et al., 2008; Bennett & Hale, 2014; Horn et al., 2008). Thus, towers provide an opportunity to test whether bats are attracted to visually conspicuous tall structures.

In contrast to towers, the edges of forest fragments or woodlots are landscape features known to concentrate bats for roosting and foraging throughout the active season (Ethier & Fahrig, 2011;

Grindal & Brigham, 1998). Proximity to open water also leads to higher bat activity (de Jong & Ahlén, 1991; Rainho & Palmeirim, 2011). We therefore sampled activity at woodlots less than 200 m from a source of open water. We assumed this distance would be close enough to water to influence bat activity since the probability of occurrence of bats remains comparatively high even up to a few kilometres of a water source (Rainho & Palmeirim, 2011). In contrast to woodlots, where relatively high bat activity would be expected, open fields are expected to have consistently low levels of bat activity (Barclay, 1989; Downs & Racey, 2006; Gehrt & Chelsvig, 2003).

We used full-spectrum bat detectors (Pettersson D240X, Pettersson Elektronik AB, Sweden) with a sample rate of 305 kHz connected to digital media devices (iRiver H320, iRiver Limited, Seoul, Korea) to record time-expanded signals ($10\times$ expansion factor). We mounted each recording unit on a 3 m pole in a weather-proof container. Monitoring at 3 m provides a good approximation of overall activity of our study species at turbine height (Baerwald & Barclay, 2009; Reynolds, 2006). Detectors were calibrated once a month in an anechoic chamber. We used an arbitrary waveform generator (20 MHz Function; Agilent 33220A, Agilent Technologies Canada Inc., Mississauga, ON, Canada) to design a calibration signal resembling an echolocation call (logarithmic curve, 50 kHz maximum frequency, 34 kHz middle frequency, 28 kHz minimum frequency, 6 ms pulse duration). The signal was generated at a strength of 2.07 V peak to peak and repeatedly played back using a free-field magnetic speaker with flat frequency response (± 8 dB from 1 to 50 kHz, maximum output: 108 dB at 10 cm, ± 4 V peak input, 4 Ω load) (Tucker-Davis Technologies, Alachua, FL, U.S.A.). We positioned detectors 1.4 m from, and facing directly towards, the loudspeaker during calibration. Gain was set such that recordings of the signal by all detectors were of equal strength and the trigger was set just above the threshold of detection for the signal.

We inspected spectrograms of all audio files visually (Sonobat 2.6, Arcata, CA, U.S.A.) and removed files that did not contain bat calls. Because of the memory limitations of the acoustic recorders, or occasional equipment malfunctions, on some nights we only recorded for ~90% of the night. To eliminate this potential bias, we included the proportion of time recorded between sunset and sunrise on each sampling night as a random effect in statistical analyses (see below) and present data as bat passes/h rather than passes/night. Acoustic data cannot provide information on absolute abundance of bats and it is usually impossible to determine whether multiple passes represent many individuals or a single bat passing many times (unless multiple, overlapping calls are recorded in the same files, see below). However, acoustic data are known to correlate with number of bats in an area, and acoustic recording is a standard technique for estimating patterns of relative abundance of bats (Ethier & Fahrig, 2011; Ford, Britzke, Dobony, Rodrigue, & Johnson, 2011; Gehrt & Chelsvig, 2003; Walsh, Barclay, & McCracken, 2004).

We identified calls to species using automated software (Sonobat 3.0) that relies on a discriminant analysis procedure to classify calls based on more than 30 spectral and temporal parameters (Szewczak, 2009). We only analysed calls that were designated to have a recording quality of at least 80% of the optimum quality determined by the software, and up to eight calls per bat pass were used to identify species. We also specified a discriminant probability threshold of 90%. Automated call identification is objective, repeatable and more rapid than manual methods (Skowronski & Fenton, 2008), but to ensure the software accurately identified calls, we manually identified 1266 call files recorded in 2008 to species and confirmed the match between manual and automated identification. We manually identified calls by visually inspecting

call spectrograms (using the default filter settings of the acoustic analysis software). By examining a number of quantitative and qualitative acoustic parameters, we compared the calls we recorded to a collection of reference calls of known species (Waters & Gannon, 2004). Parameters included call duration, frequency with most energy, minimum frequency, maximum frequency and the overall time–frequency shape of the call (Fenton, 2004). The collection of reference calls included call recordings obtained from captured bats in our study area and reference calls provided with the acoustic analysis software.

Not all passes could be identified to species so, to include a greater proportion of our data in the analyses, we also classified calls as belonging to either high-frequency (HF) bat species (minimum frequency >35 kHz) or low-frequency (LF) bat species (minimum frequency <35 kHz). High-frequency calls have been used to represent nonmigratory species, and LF calls have been used to represent migratory species in previous studies (Weller & Baldwin, 2011). However, since *L. borealis*, a migratory species known to occur in our study area, also emits HF echolocation calls, and probably accounted for a large proportion of unidentified HF passes in our study, we did not analyse data for HF bats as this group would not solely represent nonmigratory species. We used feeding buzzes to estimate foraging activity at sample sites as this call type is predominantly associated with attempting to capture prey (Arlettaz, Jones, & Racey, 2001; Brigham et al., 1997; Schnitzler, Moss, & Denzinger, 2003). Feeding buzzes can be difficult to detect in spectrograms generated by the software we used, so we listened for them in all recordings. Feeding buzzes were readily identifiable by an increase in call rate, a decrease in call duration and an increase in frequency (Griffin, 1958) compared to search phase calls, which generally preceded feeding buzzes.

We identified all passes containing the calls of at least two individuals and, for each habitat, calculated the average proportion of passes that included at least two bats. We were conservative in our identification of these passes to avoid misclassifying echoes as calls produced by multiple individuals. Specifically, we only counted passes as including multiple individuals if more than one species was detected or at least two echolocation pulses of the same species overlapped in time and differed in their minimum frequencies or time–frequency patterns.

We conducted separate analyses for each species and year, and for the LF bat group and year, using generalized linear mixed models (GLMMs) with GLIMMIX in SAS 9.2 (SAS Institute, Cary, NC, U.S.A.). We compared numbers of passes with night as the experimental unit and habitat type (open, woodlot, or tower), period (premigration or migration) and an interaction between habitat type and period as fixed effects. Site (sites 1–4 for 2008 or 1–5 for 2009) and the proportion of available time sampled each night were included as random effects. If the habitat*period interaction was nonsignificant, it was excluded from the model. If we detected a significant effect of habitat, we used *t* tests comparing least squares means (LSMEANS statement) for pairwise comparisons of bat activity among habitat types. If we detected a significant habitat*period interaction, we used pairwise comparisons to compare activity between periods within each habitat and among habitats within each period. We used Bonferroni correction to adjust *P* values for multiple comparisons. We also used GLMMs to compare numbers of feeding buzzes per hour among habitat types. Numbers of buzzes recorded per night is likely correlated with the amount of bat activity per night, so cumulative activity of all bat species was included as a covariate. We transformed dependent variables and specified error distributions and link functions in all models to maximize model fit, which we assessed using scaled Pearson χ^2 (value/df) and residual log pseudolikelihood values. We obtained the best fit for all models by specifying a Poisson

distribution and log-link function. We transformed the number of passes by *L. noctivagans* in 2009, *L. cinereus* in 2009, LF bats in 2008 and LF bats in 2009 according to $\sqrt{y+1}$. We also transformed the activity of *L. noctivagans* in 2008 according to $\log(y+1)$, the activity of *L. cinereus* in 2008 according to $y+0.5$, and the number of buzzes in 2008 and 2009 according to $y+0.01$. We compared proportions of passes containing calls from more than one individual using equality of two proportions tests in SYSTAT 12 (SYSTAT Software, Inc., San Jose, CA, U.S.A.). In all cases we assessed significance at $\alpha + 0.05$.

In addition to acoustic surveys, we conducted carcass surveys on 12 mornings during 1 August–14 September 2008 and on 31 mornings during 5 June–28 September 2009 to determine whether towers posed a mortality risk to bats. We searched below any potential collision point including a circular area of radius 20 m centred on each tower and a rectangular area (width = 8 m) centred on each set of guy wires (total search area of 2500 m^2).

RESULTS

We recorded 2621 detector-hours of acoustic data (i.e. where a detector-hour = one detector deployed for 1 h at a given site) over 110 nights. We did not record at every habitat type on all 110 nights due to occasional equipment malfunctions but still recorded an average of 96 ± 3 nights at each habitat type. During migration in 2008 we recorded a total of 17 nights at open fields, 18 nights at woodlots and 13 nights at towers. During premigration in 2009 we recorded for 29 nights at open sites, 24 nights at woodlots and 22 nights at towers, and during migration in 2009 we recorded for 54 nights at open fields, 56 nights at woodlots and 54 nights at towers. We recorded 1187 passes in 2008, 93% of which ($N = 1105$) were of suitable quality for analysis. In 2009 we recorded 6008 passes, 84% of which ($N = 5032$) were suitable for analysis. Of the high-quality calls in 2008, all could be assigned to the LF or HF group, with 64% (711/1105) identified to species. Of the high-quality calls in 2009, all could be assigned to the LF or HF group and 68% (3442/5032) could be identified to species. Of passes assigned to species in 2008, 64% (456/711) were *L. noctivagans* and 8.6% (61/711) were *L. cinereus*. In 2009 63% (2168/3442) were *L. noctivagans* and 25% (845/3442) were *L. cinereus*.

Activity of *L. noctivagans* differed among habitat types during migration in 2008 (GLMM: $F_{2,45} = 6.86$, $P = 0.003$), with greater activity at woodlots and towers compared to open fields and no difference between towers and woodlots (Fig. 1, Table 1). In 2009, *L. noctivagans* activity differed among habitat types (GLMM: $F_{2,228} = 22.71$, $P < 0.001$), with an interaction between habitat and period (GLMM: $F_{2,228} = 5.75$, $P = 0.004$; Fig. 1). Consistent with our predictions, during premigration, activity at woodlots exceeded that at open fields and towers, with no difference between open fields and towers. However, activity at towers increased by 4.3 times during migration to match that at woodlots and exceed that at open fields (Table 1). Only activity at towers increased from premigration to migration, while activity at open fields and woodlots remained consistent (Table 1, Fig. 1).

During migration in 2008, the effect of habitat type on activity of *L. cinereus* approached but did not reach significance (GLMM: $F_{2,45} = 3.17$, $P = 0.052$). Mean activity at towers was qualitatively similar to that at woodlots but more than three times greater than that at open sites (Fig. 2). In 2009, activity of *L. cinereus* differed among habitats (GLMM: $F_{2,228} = 11.68$, $P < 0.001$) with an interaction between habitat and period (GLMM: $F_{2,228} = 5.39$, $P = 0.005$; Fig. 2). During premigration, activity did not differ among habitats, but during migration, activity at towers exceeded that at open fields and matched that at woodlots (Table 1). From premigration to migration, activity remained more or less constant at woodlots,
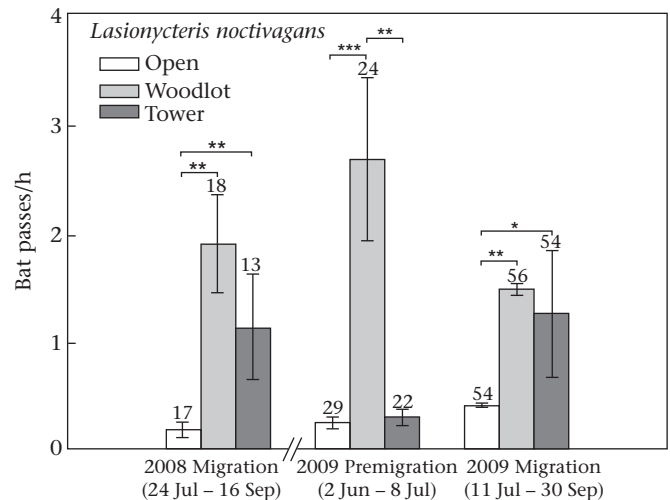

Figure 1. Mean $\pm$ SE activity of *Lasionycteris noctivagans* at three habitat types during the 2008 migration period and during the 2009 premigration and migration periods in south-central Manitoba. The *X* axis denotes the time range of each period. Number of nights sampled and significant pairwise differences are indicated above the bars ($^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$).

with a 2.5-fold reduction in activity at open fields but a 4.5-fold increase in activity at towers, although these differences were not significant after Bonferroni correction (Table 1).

During 2008 migration, activity of LF bats differed among habitats (GLMM: $F_{2,45} = 11.16$, $P < 0.001$) and was higher at towers and woodlots compared to open fields but similar between towers and woodlots (Table 1, Fig. 3). In 2009, activity of LF bats differed among habitats (GLMM: $F_{2,228} = 28.25$, $P < 0.001$) and between periods (GLMM: $F_{1,228} = 5.78$, $P = 0.017$), with an interaction between habitat and period (GLMM: $F_{2,228} = 6.91$, $P = 0.001$). During premigration, activity of LF bats at woodlots exceeded that at open fields and towers, with no difference between open fields and towers. However, activity during migration only increased at towers to surpass that at open fields and match that at woodlots (Table 1, Fig. 3).

Table 1
Results of pairwise comparisons for activity of *Lasionycteris noctivagans*, *Lasiurus cinereus* and all low-frequency (LF) bats at three habitat types during the 2008 migration and during the 2009 premigration and migration periods in south-central Manitoba

	L. noctivagans		*L. cinereus*		LF bats	
	t	*P*	*t*	*P*	*t*	*P*
2008 Migration (*df*=45)						
Tower vs open	−2.91	**0.017**	—	—	−3.61	**0.002**
Tower vs woodlot	−0.81	>0.999	—	—	−1.03	0.930
Open vs woodlot	−3.69	**0.002**	—	—	−4.69	**<0.001**
2009 Premigration (*df*=228)						
Tower vs open	−0.35	>0.999	−0.37	>0.999	−0.44	>0.999
Tower vs woodlot	−4.24	**0.001**	−1.64	>0.999	−4.35	**<0.001**
Open vs woodlot	−5.00	**<0.001**	−2.16	0.481	−5.19	**<0.001**
2009 Migration (*df*=228)						
Tower vs open	−3.32	**0.016**	−6.00	**<0.001**	−5.22	**<0.001**
Tower vs woodlot	−0.78	>0.999	1.56	>0.999	−0.20	>0.999
Open vs woodlot	−4.07	**0.001**	−4.67	**<0.001**	−5.44	**<0.001**
2009 Premigration vs Migration (*df*=228)						
Tower vs tower	−2.97	**0.049**	−2.49	0.203	−3.89	**0.002**
Woodlot vs woodlot	1.51	>0.999	0.51	>0.999	0.92	>0.999
Open vs open	−1.10	>0.999	2.04	0.637	−0.64	>0.999

P values are Bonferroni-corrected for multiple comparisons. Significant values ($\alpha = 0.05$) are shown in bold.
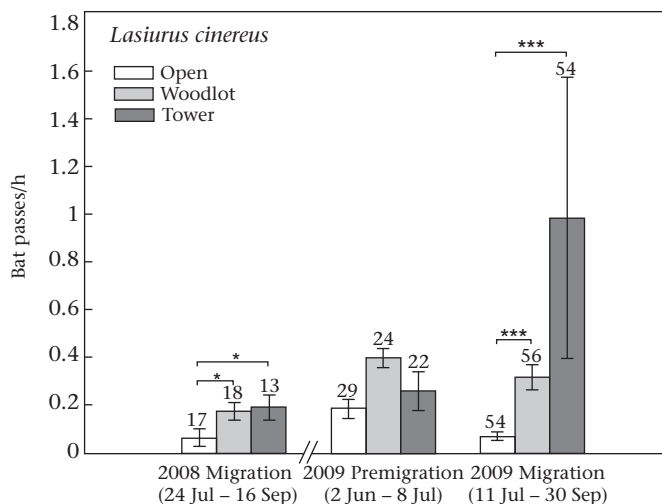
Figure 2. Mean ± SE activity of *Lasiurus cinereus* at three habitat types during the 2008 migration period and during the 2009 premigration and migration periods in south-central Manitoba. The *X* axis denotes the time range of each period. Number of nights sampled and significant pairwise differences are indicated above the bars (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

The activity we recorded at towers was composed almost exclusively of migratory bats. Only eight passes in 2008 and 24 passes in 2009 were identified as little brown bats, *Myotis lucifugus*, an abundant nonmigratory species with several colonies in buildings within our study area. Nine per cent (3/32) of these passes occurred at towers versus the other habitats, a 3.3-fold smaller proportion than for *L. noctivagans* (31%, 818/2624, $Z = 3.2$, $P = 0.002$) and a 6.6-fold smaller proportion than that for *L. cinereus* (62%, 558/906, $Z = 6.6$, $P < 0.001$). A small number of passes (53 in 2008; 102 in 2009) were also assigned to big brown bats, *Eptesicus fuscus*, 32% of which (50/155) were recorded at towers. However, most of these calls were likely mistakenly assigned calls of *L. noctivagans* (see Discussion). Only 17.4% of all high-quality calls (1069/6137) were made by HF bats. *Lasiurus borealis* probably made up most of the HF passes we detected since 93% (436/468) of passes

by HF bats that we could identify to species were made by *L. borealis*. More than half of these *L. borealis* calls (58%; 255/436) were recorded at towers.

We recorded 305 passes that included feeding buzzes. These could not be confidently identified to species, so we conducted a single analysis on all feeding passes. Identifying buzzes to species was not necessary to determine the relative frequency of foraging at the towers and, as most recorded passes were made by tree bats, we were confident that the majority of buzzes were also made by this species group. During migration in 2008, nightly rate of buzz production differed among habitats (GLMM: $F_{2,42} = 4.46$, $P = 0.018$; Fig. 4). Buzz rate at open fields did not differ from that at towers or woodlots but was lower at towers compared to woodlots (Table 2). Similarly, in 2009, buzz rate differed among habitats (GLMM: $F_{2,230} = 6.43$, $P = 0.002$) but not between periods, with no interaction between habitat and period (Fig. 4). Again, buzz rate at towers was below that at woodlots (Table 2).

In 2008, passes that clearly included calls from multiple individuals accounted for 0% (0/52) of passes at open fields, 4.4% (28/630) at woodlots and 3.4% (17/505) at towers, with no difference between woodlots and towers ($Z = 0.93$, $P = 0.35$). During premigration in 2009, the proportion of passes including multiple individuals at towers was 1.5% (2/130) and matched that at woodlots (4.5%, 37/815; $Z = 1.91$, $P = 0.056$) and open fields (0.7%, 1/147; $Z = 0.69$, $P = 0.49$). However, during migration in 2009, when our sample size was largest, the proportion of passes including multiple individual at towers (8.2%; 190/2314) was more than three times that at woodlots (2.5%, 55/2183; $Z = 8.8$, $P < 0.001$) and eight times that at open fields (1.0%, 4/419; $Z = 5.32$, $P < 0.001$).

We found two dead birds but no dead bats at towers during 42 morning carcass searches throughout the study.

DISCUSSION

Our results provide the first experimental evidence that migratory tree bats are attracted to visually conspicuous, anthropogenic tall structures at the same time of year they are killed at turbines. Over two seasons, we recorded high levels of activity at towers for *L. noctivagans* and *L. cinereus*, two of the species most frequently killed at turbines. We also recorded qualitatively higher activity of *L. borealis* at towers compared to control sites, although
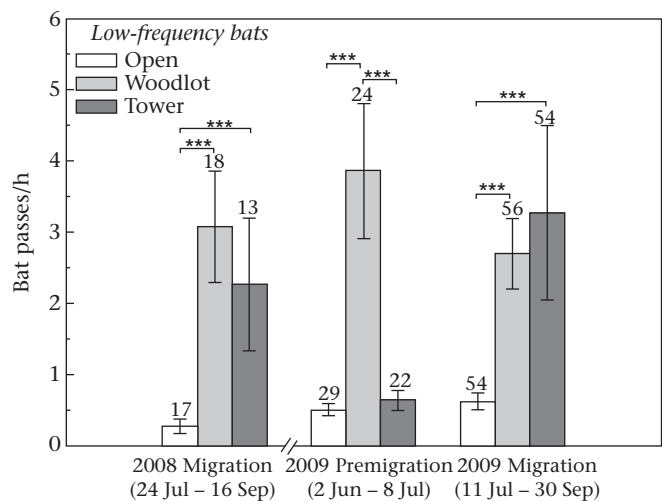

Figure 3. Mean ± SE activity of low-frequency (LF) bats at three habitat types during the 2008 migration period and during the 2009 premigration and migration periods in south-central Manitoba. The *X* axis denotes the time range of each period. Number of nights sampled and significant pairwise differences are indicated above the bars (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).
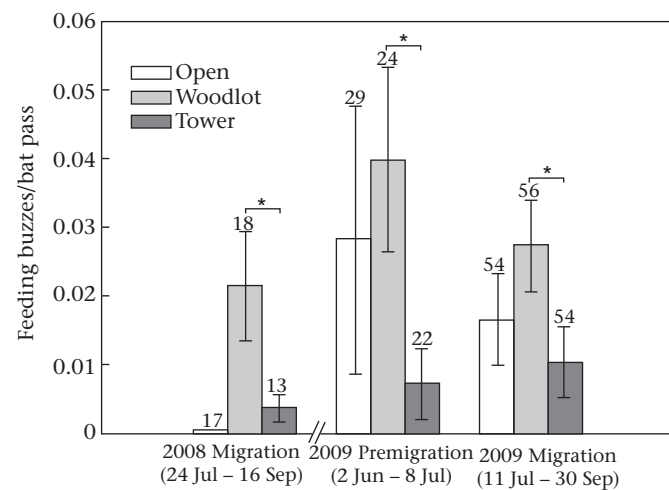

Figure 4. Mean ± SE proportion of feeding buzz production at three habitat types during the 2008 migration period and during the 2009 premigration and migration periods in south-central Manitoba. The *X* axis denotes the time range of each period. Number of nights sampled and significant pairwise differences are indicated above the bars (*$P < 0.05$).

Table 2
Results of pairwise comparisons for proportions of recorded bat passes that contained one or more feeding buzzes at three habitat types during the 2008 migration and during the 2009 premigration and migration periods in south-central Manitoba

	2008		2009	
	t_{42}	P	t_{230}	P
Open vs tower	−0.84	>0.999	1.91	0.170
Tower vs woodlot	−2.62	**0.036**	−2.51	**0.038**
Open vs woodlot	−1.46	0.452	−1.64	0.305

P values are Bonferroni-corrected for multiple comparisons. Significant values ($\alpha = 0.05$) are shown in bold.

data for this species were insufficient for statistical analyses. In general, tree bat activity at towers during premigration was relatively low but increased during autumn migration/mating to vastly exceed that at open fields, which tend not to concentrate bats (Barclay, 1989; Downs & Racey, 2006; Gehrt & Chelsvig, 2003), and to match that at woodlot edges near open water, habitat known to concentrate bats for foraging and roosting (de Jong & Ahlén, 1991; Furlonger, Dewar, & Fenton, 1987; Rainho & Palmeirim, 2011). It is not possible to quantify numbers of individual bats based on acoustic recordings, but the large number of calls we recorded at towers on many nights, and the fact that we often recorded overlapping calls from multiple bats at towers, suggests that many individual bats visited towers. Moreover, compared to both migratory bat species, a much smaller proportion of calls recorded at towers were made by the nonmigratory species in our study area (*M. lucifugus*), which is killed much less often at most wind facilities (Arnett & Baerwald, 2013). Although the proportion of calls that we recorded at towers and assigned to *E. fuscus* was comparable to that for *L. noctivagans*, only 3.7% of passes identified to species were assigned to *E. fuscus*. Moreover, these were probably made by *L. noctivagans* since calls of these two species are difficult to distinguish (Betts, 1998) and because *E. fuscus* has never been captured in our study area (C. Willis, n.d.). These results are consistent with our first three predictions and the hypothesis that tree bats are attracted to tall structures during migration, which could explain mortality of bats at wind turbines.

In contrast to the hypothesis that turbines attract insects, which, in turn, attract bats (Cryan & Barclay, 2009), we observed a smaller proportion of feeding buzzes at towers compared to woodlots during all study periods despite the dramatic increase in overall activity at towers during autumn. We also found that a greater proportion of passes recorded at towers during migration included calls from multiple bats simultaneously, compared to passes recorded at other habitats. Taken together, these findings support our fourth and fifth predictions and are consistent with the hypothesis that activity at towers is linked to social behaviour. Cryan and Brown (2007) reported mating by *L. cinereus* during annual autumn visits to South Farallon Island ~30–40 km from the California mainland, a small (~0.3 km²) but ~100 m tall island that would be visually conspicuous to bats from long distances. Cryan (2008) hypothesized that the tallest trees on the horizon (like those atop South Farallon) could serve as lekking sites where males attract females, or as roosting resources that males might defend to attract females. In this sense, migratory bats might gather at tall structures in the same way as hibernating bats, which mate during autumn swarms and use entrances of hibernacula as reproductive landmarks. Alternatively, tall structures could also serve as staging locations that promote cohesion of migratory groups or 'flocks' (Cryan & Barclay, 2009). However, if bats visit towers solely to promote group cohesion, then this would predict equal visiting rates by adults and juveniles, but mortality at turbines often consists mostly of adults (Arnett et al., 2008; Cryan, 2008; Jameson,

2011; Jameson & Willis, 2012). Despite these possibilities, no study has yet found direct evidence of mating behaviour at turbines (e.g. Cryan et al., 2012), and we did not find direct evidence of social behaviour. For example, we recorded very few social calls. Nevertheless, our results support the hypothesis that tree bats are actively attracted to tall structures, and the low frequency of feeding buzzes combined with high frequency of multiple individuals visiting towers simultaneously are consistent with a link between tall structure attraction and social behaviour.

The mechanism underlying tall structure attraction in tree bats could be a tendency to select tall trees for roosting (Cryan, 2008; Cryan & Barclay, 2009). While towers and turbines do not resemble trees, tree height is important for roost selection by tree bats and correlates with other optimal roost features (Kalcounis-Rüppell, Psyllakis, & Brigham, 2005). Barclay et al. (2007) showed that bat mortality increases exponentially with turbine height, which is consistent with attraction to tall trees. Taller, more conspicuous trees will attract more bats, which could also explain the higher mortality rates that occur at taller, more modern turbines (Barclay et al., 2007). Older model turbines are still relatively tall structures on the landscape but are less conspicuous than modern turbines. If tree bats investigate tall trees and other tall structures for roosting opportunities, it seems unlikely that they are searching for day roosts since Baerwald (2008) found that bats were active at turbines all night, not just at the end of the night when bats should be most motivated to find day roosts. Instead, perhaps bats perceive turbines as potential night roosts for resting during migration. Bats may detect distant tall structures visually and mistakenly perceive them as potential high-quality roost trees, after which they may approach these structures to investigate more closely.

An alternative, although in our view unlikely, interpretation of our data could be that a change in echolocation behaviour during the migration/mating period increases detectability of tree bats at tall structures at the same time as a coincidental increase in their susceptibility to collision at turbines (Cryan & Barclay, 2009). For example, we might have detected more calls at towers than at open sites during migration if tree bats echolocate less frequently during migration but are startled and begin echolocating when they encounter a tall structure in their flight path to avoid collision (Cryan & Barclay, 2009). This seems unlikely to us for several reasons. First, towers and turbines would probably both be visually obvious to bats from long distances on all but the darkest nights during autumn migration. Therefore, it seems unlikely that bats would be startled into echolocating when approaching a tower. Second, detectors at all three habitat types were positioned 3 m from the ground, and tree bats are likely to use echolocation similarly close to the ground. Third, if tree bats do occur in equal numbers at towers and open habitats, and our results reflect a difference in detectability, density of tree bats would have to be extremely high across the landscape (i.e. at both sets of habitats) to account for the high call rates we detected at towers, which seems equally unlikely. Fourth, and finally, the increase in calls by *L. noctivagans* and the low-frequency bat group from premigration to migration was only observed at towers. The absence of a similar increase in calls at open fields and woodlots counters the hypothesis that our results reflect an overall influx of migrants into the study area. Thus, we argue that our data provide strong, if indirect, evidence of an active attraction to towers with a seasonal pattern that matches mortality at wind turbines.

Despite an extensive survey effort, we found no evidence of bat mortality at towers, even though relatively high rates of mortality occur at the wind energy facility nearby (Jameson, 2011; Jameson & Willis, 2012). Communication towers are now ubiquitous on the North American landscape with more than 15 000 distributed across Canada (Loxcel, 2012) and more than 200 000 in the U.S.

(CTIA, 2012). Given our evidence that bats are attracted to towers and wind turbines in a similar way and that we found no bat mortality at towers, we argue that telecommunication towers represent a potential tool for improving our understanding of migratory behaviour in tree bats. Preconstruction bat surveys are typically conducted at proposed wind energy sites to help guide placement of turbines and, presumably, reduce postconstruction mortality. However, if bats are attracted to tall structures from long distances, they may not be present in the survey area until after turbines are constructed. Thus, with some additional information, (see below) preconstruction surveys could be more informative if conducted near telecommunication towers in the vicinity of proposed wind energy sites.

We advocate for future studies aimed at determining how features of towers (e.g. height, diameter, proximity to other landscape elements) influence tall structure attraction in tree bats. Also critical will be to quantify distances from which bats are attracted to tall structures, to understand how tall structures influence the behaviour of individuals and the relationship between activity before and after construction. Acoustic recording equipment is sometimes mounted on meteorological towers at proposed or operating wind energy facilities to monitor tree bats but, to our knowledge, no studies have accounted for the possibility that bats may be actively attracted to these towers. Meteorological towers are shorter and more slender than communication towers and are likely less conspicuous to bats, but future studies should examine how attraction is influenced by the size and shape of different structures. Studies should also aim to draw firm conclusions about the motivations underlying bats' attraction to tall structures. Additional predictions of the reproductive landmarks hypothesis that we were not able to test include: (1) the proportion of social calls associated with mating activity is greater at towers and turbines during migration compared to control habitats; (2) the proportion of captures of mating bats is greater near towers and turbines during the autumn than at control sites; (3) territorial behaviours of bats are more frequent at towers; (4) social interactions between individuals occur with greater frequency at towers (Cryan & Barclay, 2009). All of these predictions will be difficult, at best, to evaluate, but they will be useful for understanding bats' attraction of tall structures. Thermal infrared imaging may prove useful for testing these predictions.

Our results highlight the importance of understanding behaviour of migratory animals not just during the reproductive season but throughout their annual cycle (Martin et al., 2007; Wilcove & Wikelski, 2008). Wind turbines kill bats during a period of the year when behaviour of individuals is difficult to study, so tall structures like communication towers could improve our understanding of their migratory behaviour. Understanding more about interactions of individual bats with tall structures will improve preconstruction surveys for proposed wind energy sites and help reduce what is arguably the most significant environmental impact of renewable wind energy.

Acknowledgments

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