

## GEOGRAPHIC VARIATION IN ACTIVITY AND FATALITY OF MIGRATORY BATS AT WIND ENERGY FACILITIES

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Little is known regarding the migratory behavior of bats, due in part to their elusive nature. Recently, however, fatalities of migratory bats at some wind energy facilities across North America have provided the opportunity and impetus to study bat migration at the landscape level. Using acoustic monitoring and carcass searches, we examined variation in activity levels and fatality rates of bats across southern Alberta, Canada, to determine if bat activity and fatality are concentrated in certain areas or evenly distributed across the landscape. To investigate geographical variation in bat activity, we acoustically monitored activity from 15 July to 15 September 2006 and 2007 at 7 proposed or existing wind energy installations across southern Alberta (~155 km between the most westerly wind energy facility and the most easterly). Activity of migratory bats varied among sites, suggesting that, rather than migrating in a dispersed way across a broad area, bats concentrate along select routes. To investigate variation in bat fatality rates among wind energy installations, we compiled fatality data collected between 2001 and 2007 from 6 wind energy facilities and conducted carcass searches at 3 wind energy installations in 2006 and 2007. Fatality rates differed among the 9 sites, partly due to differences in turbine height, but also due to differences in migratory-bat activity and the interaction between bat activity and turbine height. Our results indicate that bats migrate in certain areas and that measuring migratory activity may allow wind energy facilities to be placed so as to minimize bat fatalities.

Key words: hoary bat, *Lasiurus noctivagans*, *Lasiurus cinereus*, migration, silver-haired bat, wind energy

Long-distance migration is relatively rare among bats compared to birds (Barclay and Harder 2003; Fleming and Eby 2003). Bird migration has been studied extensively for hundreds of years, resulting in considerable knowledge and a relatively thorough understanding of bird migratory behavior (e.g. Alerstam et al. 2003; Berthold 2001). The study of bat migration has not been nearly as extensive, and many basic questions remain unanswered. We know something about the broadscale patterns of occurrence (i.e., continental) of a few species (Cryan 2003; Cryan et al. 2004; Findley and Jones 1964; Hutterer et al. 2005; Steffens et al. 2007), but have little information on migration behavior or finer-scale movement patterns (Barclay 1984; Fleming and Eby 2003).

The major components of animal migration are timing, orientation, and navigation: individuals must first decide whether to migrate and when, and then decide where to go and how to get there. Birds use a variety of visual and nonvisual cues for orientation and navigation, and these various maps and compasses interact with genetic cues during

migration (Able 1980; Berthold and Terrill 1991; Wiltschko and Wiltschko 1999). However, research on the sensory systems of bats has focused on echolocation, and information on the use of nonauditory cues and the perceptual abilities of bats is more limited (Altringham and Fenton 2003; Buchler and Childs 1982; Eklof and Jones 2003; Griffin 1970).

Given the high rate of atmospheric attenuation of high-frequency sounds, it is unlikely that bats use echolocation to navigate long distances (Altringham and Fenton 2003; Griffin 1970; Neuweiler 2000). Bats possess excellent spatial memory (Baker 1978; Griffin 1970; Holland et al. 2005; Holler and Schmidt 1996) and are capable of perceiving stars (Childs and Buchler 1981), postsunset glow (Buchler and Childs 1982), the Earth's magnetic field (Holland et al. 2006, 2008), and geographical landmarks and linear features (Ahlén 1997; Barclay 1984; Johnson et al. 2004; Limpens et al. 1989; Racey and Entwistle 2003; Serra-Cobo et al. 2000; Timm 1989) for orientation and navigation. If geographical landmarks are important navigational aids, then migrating bats may concentrate near prominent landscape features, such as rivers and mountains. It seems likely that bats use a combination of sensory systems for orientation and navigation, and that these systems interact with genetic information to provide a map and compass for long-distance migration (Holland 2007).

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Migration is energetically expensive, and long-distance migrants depend on suitable stopover sites to drink, rest, and refuel (Berthold and Terrill 1991; Catry et al. 2004; Fleming and Eby 2003; Schaub et al. 2004). The availability of stopover habitats and daily roosting sites may influence bat migration in the same way they influence bird migration. Although there are historical records of bats migrating during the day (Hall 1946; Howell 1908; Mearns 1898), the majority of bats migrate at night and stop to roost during the day. Therefore, migration ranges, routes, and nightly distance traveled should be affected by the availability and distribution of appropriate stopover and roosting sites (Berthold 2001; Catry et al. 2004; Cryan and Veilleux 2007; Fleming and Eby 2003; Richardson 1978, 1998). If such sites are not distributed uniformly across the landscape, then the distribution of migrating bats is unlikely to be uniform either, but instead, concentrated near appropriate roosting habitat. Interspecific differences in roost selection and flight behavior during migration also may lead to different species of bats migrating along different routes.

Recently, bat fatalities at wind energy installations have offered potential insights into bat migration because the majority of such fatalities around the world involve migratory bats during fall migration (Arnett et al. 2008; Dürr and Bach 2004). In North America, fatalities are mostly migratory tree-roosting bats: hoary bats (*Lasiurus cinereus*), eastern red bats (*L. borealis*), and silver-haired bats (*Lasionycteris noctivagans*—Arnett et al. 2008; Johnson 2005). In Alberta, Canada, the majority of bat fatalities are *L. cinereus* and *L. noctivagans* (Baerwald 2008).

Across North America, fatality rates of bats vary among wind energy installations, at least partly because taller turbines kill more bats (Barclay et al. 2007), but also likely due to other factors, such as spatial variation in the migration activity of each species. There is no information as to whether bats follow specific migratory routes or are more dispersed across the landscape as they migrate. Thus, we examined geographic variation in activity and fatality at several existing and proposed wind energy installations across southern Alberta. Southern Alberta is ecologically diverse, with the Rocky Mountains in the west and dry mixed-grass prairies and badlands in the east. If bats use specific migratory routes, we expect that more bats will be killed at wind facilities along those routes. We hypothesized that migratory bats use specific migration routes associated with landmarks and roost availability. We thus predicted that migratory-bat activity would vary among sites in different habitats. Activity should be greater near the foothills of the Rocky Mountains in the west, where presumably there are more roost sites, than on the prairies in the east. We further predicted that fatalities at wind turbines are correlated with activity rate.

## MATERIALS AND METHODS

*Study species.*—*Lasiurus cinereus* is found throughout North and South America, from northern Canada to southern

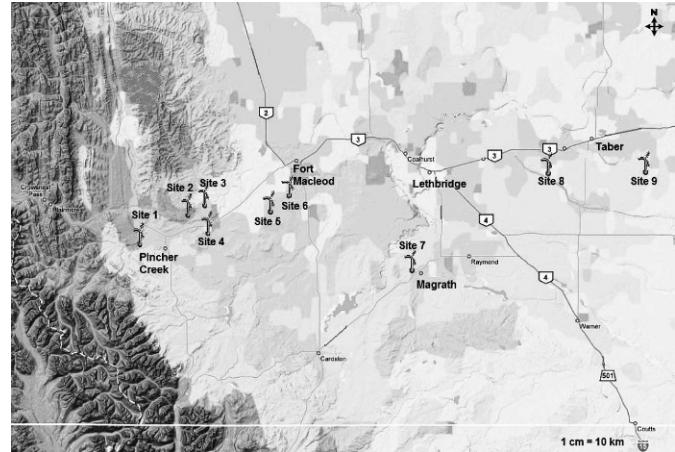


FIG. 1.—Study area in detail. The Rocky Mountains are in the west and the border between the United States and Canada is to the south. Wind energy sites are labeled and their locations are indicated by turbines. Shading depicts levels of vegetation. The numbers on white background indicate highway numbers. We monitored acoustic activity at sites 1, 2, 3, 5, 6, 8, and 9. We compiled fatality data from all sites. Image from Google Maps (<http://maps.google.ca>).

Argentina and Chile (Cryan 2003; Shump and Shump 1982). Although we still do not understand the movement patterns or seasonal distributions of *L. cinereus*, it seems that individuals winter in California, the southern United States, and Mexico then migrate north and east in the spring (Cryan 2003; Cryan et al. 2004; Findley and Jones 1964). In summer, *L. cinereus* is found throughout the aspen parkland and boreal forest of northern Alberta (Smith 1993; van Zyll de Jong 1985). There is some degree of sexual segregation during summer, with females potentially migrating farther than males (Cryan 2003; Cryan et al. 2004; Findley and Jones 1964). Long-distance migration (>2,000 km) of individual *L. cinereus* was recently confirmed by stable-hydrogen isotope analysis of fur (Cryan et al. 2004).

*Lasionycteris noctivagans* ranges from southeastern Alaska through southern Canada, south to central California and northern Mexico and east to Georgia (Hall 1981; Yates et al. 1976). Wintering grounds are in the Pacific Northwest, southwestern states, and middle latitudes of the eastern United States (Cryan 2003; Izor 1979). In spring, *L. noctivagans* from eastern regions migrates north and east, and western *L. noctivagans* migrates northward (Cryan 2003). In summer, *L. noctivagans* is common in aspen parkland, but is found throughout the southern three-fourths of Alberta (Smith 1993; van Zyll de Jong 1985). As in *L. cinereus*, there is some degree of sexual segregation during summer, with females potentially migrating farther than males (Cryan 2003), although adult males also are present in northern Alberta (Crampton and Barclay 1998).

*Study area.*—We monitored bat activity or fatality or both at 1 proposed and 8 existing wind energy installations across southern Alberta (Fig. 1). We used fatality data from 309 wind turbines in 8 wind energy installations and activity data from 7 project sites (Table 1). Wind energy installations ranged in

size from 1 wind turbine to 114 turbines. The height of wind turbines ranged from 50 to 84 m at hub height, with 47- to 80-m-diameter rotors. The site farthest west was located along the Castle River approximately 20 km east of the Rocky Mountains (49°30'11.01"N, 114°2'3.89"W) and 155 km from the easternmost site, which was approximately 20 km southeast of the town of Taber (49°42'25.20"N, 111°55'37.57"W). Distances between sites varied from approximately 5 km to 155 km. Distance to treed riparian habitat, and thus roosts for migrating bats, varied from <1 km to approximately 23 km, and distance to the foothills of the Rocky Mountains varied from approximately 10 km to 165 km (Table 1). All wind energy installations had similar landscape features (e.g., flat and treeless) and were situated in similar habitat, a mosaic of mixed agriculture and native mixed grasslands.

*Activity monitoring.*—To investigate geographical variation in bat activity, we acoustically monitored bat activity from 15 July to 15 September 2006 and 2007 at 7 proposed or existing wind energy installations (Fig. 1; Table 1). We installed a combination of calibrated AnaBat II bat detectors with a Compact Flash ZCA Interface Module (CF ZCAIM), and AnaBat SD1 bat detectors (Titley Electronics, Ballina, Australia), in pairs on meteorological towers. We mounted 1 detector approximately 1.5 m from the ground, and the other 30 m from the ground. For turbines on 65-m towers with 80-m-diameter blades, a height of 30 m is within the blade swept area, or zone of risk. Microphones of all detectors pointed north. We housed all detectors in weatherproof boxes with microphones protruding from a tightly sealed and shielded hole. We powered the units with an external 12-V, 7.5-Ah battery and a 2.2-W solar panel. Detectors recorded all ultrasound from sunset to sunrise at a division ratio of 16 and sensitivity determined during calibration. The detection range of AnaBat detectors varies depending on echolocation call intensity and habitat structure (Patriquin et al. 2003); relatively high-intensity calls emitted by *L. noctivagans* and *L. cinereus* in open habitat should be detectable up to 30–40 m away (Vonhof 2006).

We analyzed all echolocation calls using AnaLookW 3.3q software (Corben 2006). Using a combination of call characteristics (minimum frequency [Fmin], duration, and slope), we visually identified calls as *Myotis* (Fmin ~ 40 kHz, slope steep to gently curving), *L. borealis* (Fmin ~ 35 kHz, relatively shallow slope, calls with terminal upsweep in frequency—Obrist 1995), *Eptesicus fuscus*–*L. noctivagans* (Fmin ~ 25 kHz, calls regularly spaced, duration ~ 9 ms, slope from somewhat steep to almost flat—Barclay 1986), *L. cinereus* (Fmin < 25 kHz, calls erratically spaced and shaped, duration ~10 ms, shallow slope; Barclay 1986), unknown low-frequency bats (Fmin ≤ 25 kHz, duration and slope intermediate, calls usually of poor quality), or unknown bats (Fmin ~ 30 kHz, relatively steep slope, potentially low *Myotis* or high *E. fuscus*–*L. noctivagans*). Because of the difficulty of distinguishing *E. fuscus* from *L. noctivagans* acoustically (Betts 1998), calls that fit the criteria were placed in an *E. fuscus*–*L. noctivagans* group. However, the strong seasonal

TABLE 1.—Description of wind energy installations used in this study. Searcher efficiency and scavenger removal rates with asterisks (\*) were estimated from studies in similar habitat in Alberta, Canada, with similar search techniques. Daggers (†) indicate searcher efficiency and scavenger removal rates we determined experimentally. The remaining values come from unpublished technical reports (denoted by superscripts).

Wind energy site (from west to east)	Years bat activity was sampled	Years bat fatality was sampled	No. turbines	Tower height (m)	Search interval values used (in days)	Searcher efficiency values used (proportion found)	Scavenger removal rates used (average no. days carcass remained)	Approximate distance from riparian roosting habitat (km)	Approximate distance from foothills (km)
1	2006 and 2007	2001	60 (41 searched)	50	7	0.64*	5.5*	<1	10
2	2007	2007	2	65	7	0.78†	5.5†	2.5	25
3	2006 and 2007	2005, 2006 and 2007	39	65	1 and 7	0.97† and 0.78†	5.5†	2.5	30
4	—	2006 and 2007	35	65	7	0.64*	5.5*	2.5	30
5	2006	2003	114	50	5.5	0.60 <sup>a</sup>	5.5*	11	50
6	2007	2006 and 2007	1	67	7	0.78†	5.5†	8	55
7	—	2006	20	65	5	0.40 <sup>b</sup>	8.1 <sup>b</sup>	12	75
8	2006 and 2007	2007	20	80	4	0.64 <sup>c</sup>	8.6 <sup>c</sup>	16	135
9	2006 and 2007	2007	37	84	4	0.64*	8.6*	23	165

<sup>a</sup> Brown, W. K., and B. L. Hamilton. 2004. Bird and bat monitoring at the McBride Lake Wind Farm, Alberta 2003–2004. Vision Quest Windelectric, Inc., Calgary, Alberta, Canada.

<sup>b</sup> Golder Associates, Ltd. 2007. Final report: Macgrath Wind Power Project, 2006 monitoring report. Suncoor Energy Products, Inc., Calgary, Alberta, Canada.

<sup>c</sup> S. Glendinning, Golder Associates, Ltd., pers. comm.

timing of *E. fuscus*–*L. noctivagans* passes and the low number of *E. fuscus* fatalities compared to the number of *L. noctivagans* fatalities (Baerwald 2008) suggest that the majority of passes identified as *E. fuscus*–*L. noctivagans* were *L. noctivagans*. For some analyses, we pooled *L. borealis*, *L. cinereus*, and *E. fuscus*–*L. noctivagans* passes into the migratory-bat category. The strong seasonal timing of migratory-bat passes (Baerwald 2008) and the lack of feeding buzzes indicative of foraging activity suggest that the majority of activity detected was from actively migrating bats. We present bat activity as the number of bat passes/detector-night. A bat pass is a sequence of 2 or more echolocation calls recorded as a bat flies within range of a bat detector (Thomas and West 1989; Vonhof 2006). A detector-night is the activity recorded by 1 detector from sunset to sunrise and was used to standardize measures of activity. If more than 1 detector recorded activity at a site, then activity was averaged. We included nights with 0 migratory-bat passes and 0 total-bat passes in our determination of bat passes/detector-night.

To determine if migratory-bat activity varied among sites, we compared the activity of all migratory bats, and of each species, from the 7 sampled sites. Data could not be normalized via transformations, so we analyzed them using Wilcoxon/Kruskal–Wallis tests with site as the main factor and height as the grouping variable. To determine if migratory-bat activity varied with detection height (30 m versus ground), we analyzed activity by detection height using a Wilcoxon 2-sample test.

Given that migratory-bat activity is influenced by weather variables such as temperature and wind speed (Baerwald 2008), we analyzed weather variation among sites. To determine if weather varied among sites, we analyzed minimum nightly temperature, maximum nightly wind speed, and minimum nightly wind speed using 1-way analyses of variance (ANOVAs) with site and night as predictor variables. We obtained hourly weather data from sunset to sunrise for 15 July–15 September 2006 and 2007 from the Environment Canada weather station closest ( $\leq 20$  km) to each wind energy facility where bat activity was monitored ( $n = 7$ ).

**Fatality monitoring.**—To investigate variation in fatality rates of bats among wind energy installations, we compiled fatality data collected between 2001 and 2007 from 9 wind energy facilities (Fig. 1; Table 1). We searched for bat carcasses at sites 3 and 6 from 15 July to 30 September in 2006 and 2007 and at site 2 from 15 July to 30 September 2007, checking 10 randomly chosen turbines every day and the remaining 32 turbines once a week (Table 1). To locate bat carcasses, 1 searcher held the end of a 45-m rope attached to the base of a turbine, and another searcher held the end of a 7-m rope attached to the 1st searcher. Starting with the ropes fully extended (i.e., to 52 m from the turbine base), both searchers walked around the base of the turbine. The rope shortened by 14 m with each rotation thereby creating 2 spiral transects 7 m apart. For each carcass found, we recorded the species and location relative to the base of the turbine. Because the majority of bat fatalities occur during fall

migration at our study sites (e.g., Baerwald 2008) and elsewhere (Arnett et al. 2008), even though we only searched turbines in late summer and early fall, we report bat fatality rates as the number killed per turbine per year. If anything, our estimates underestimate actual fatality rates, but we have no reason to suspect appreciable numbers of fatalities outside of the fall migration, based on data from other years.

To test searcher efficiency, a search team placed discreetly tagged bat carcasses at turbines about to be searched by the other team. Searcher efficiency was the proportion of these carcasses found. Search teams did not know when or where searcher-efficiency trials would occur. We performed 100 trials throughout the 2007 season (July–September).

To determine how long carcasses remained before being removed or fully consumed by scavengers, we performed 3 scavenger removal trials, 1 in 2006 and 2 in 2007 ( $n = 38$  carcasses). For each trial, we placed pairs of previously frozen carcasses (1 *L. cinereus* and 1 *L. noctivagans*) at turbines located throughout the installation. To minimize human disturbance, we placed carcasses at turbines searched once a week and checked for carcass presence once daily. We recorded how long (in days) each carcass remained where placed. If a carcass was still present after 14 days, we removed it.

We corrected fatality rates per turbine for searcher efficiency and scavenger removal rates in 1 of 3 ways. At turbines that we searched weekly, where we performed searcher efficiency and scavenger removal trials, we incorporated a variable from Smallwood's (2007) equation for proportion of carcasses remaining and corrected fatality rates by the equation:

$$F_e = \left[ \frac{(C \div S_e)}{\sum_{l=1}^I R_l} \right] + \left\{ \left( \frac{C}{S_e} - C \right) - S_e \left[ \left( \frac{C}{S_e} - C \right) R_i \right] \right\},$$

where  $F_e$  is estimated number of fatalities,  $C$  is number of carcasses found,  $S_e$  is searcher efficiency,  $R_i$  is percentage of carcasses remaining by the  $i$ th day following the initiation of a scavenger removal trial (Smallwood 2007), and  $I$  is search interval (in days). The 1st term corrects for searcher efficiency and scavenger removal rates of the initial search. The 2nd term adjusts for those bats not found during the initial search that are still available to be found during the subsequent search.

At turbines that we searched daily, we corrected fatality rates using carcass recovery rates estimated by combining searcher efficiency and scavenger removal data. We generated values of carcass recovery rate by calculating the number of available carcasses lost to scavengers each day: we found 78% (searcher efficiency) of the remaining carcasses every day until there were no more carcasses available to be found (Table 2).

For fatality rates that we compiled from other sources (Table 1), we used an equation proposed by Shoensfeld (2004):

$$F_e = \frac{N \times (S_i \times S_e + I) \times C}{K \times S_i \times S_e},$$

where  $F_e$  is estimated number of fatalities,  $N$  is number of

**TABLE 2.**—Recovery rate of bat carcasses at turbines searched daily. Data for estimated daily scavenger losses and number of carcasses found come from scavenger removal and searcher efficiency trials we performed in 2006 and 2007. Overall carcass recovery rate at turbines searched daily was 97%.

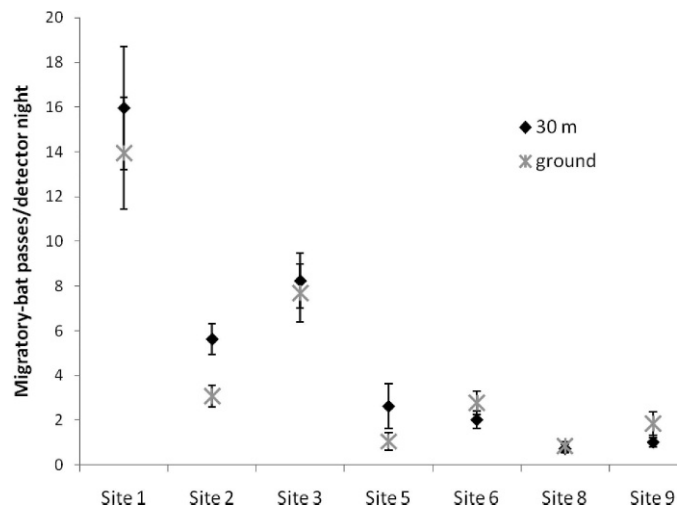
Day	No. available	Minus scavenger losses	No. actually available	No. carcasses found
1	100.00	0.00	100.00	78.00
2	22.00	1.74	20.26	15.81
3	4.46	0.64	3.82	2.98
4	0.84	0.17	0.67	0.52
5	0.15	0.02	0.12	0.10
6	0.03	0.01	0.02	0.02
7	0.00	0.00	0.00	0.00
				97.43/100

turbines,  $S_i$  is mean carcass removal time (in days),  $S_e$  is searcher efficiency,  $I$  is search interval (in days),  $C$  is number of carcasses found, and  $K$  is number of turbines searched. If previous studies had performed searcher efficiency and scavenger removal trials, we used their estimates for these correction factors. If they had not performed such trials, then we assumed that searcher efficiency and scavenger removal rates were the same as rates from trials performed at adjacent sites with similar habitat and search methods. The searcher efficiency and scavenger removal rates we used for our analyses are summarized in Table 1.

Fatality data could not be normalized and thus to determine if bat fatality rates varied among sites, we analyzed corrected bat fatalities/turbine/year among sites using a Wilcoxon/Kruskal–Wallis test (Zar 1999). To investigate the relationship between migratory-bat activity and fatality, we square-root transformed the corrected fatality rates using  $\sqrt{x} + \sqrt{x+1}$  (Zar 1999), then analyzed fatality rates and migratory-bat activity using a generalized linear model with a log-link function (for Poisson distributions). Corrected fatalities/turbine/year was the response variable, and migratory-bat activity at ground level and 30 m, and turbine height (as a continuous variable) were predictor variables. We included the interactions between bat activity and turbine height and corrected for overdispersion. We excluded site 6 from this analysis because it is a single turbine and therefore lacks variance. Data on fatality by species by turbine were not available for all sites, so we did not analyze variation in fatality rates at the species level. To further investigate the correlation between migratory-bat activity at 30 m and fatalities at tall turbines, we analyzed the activity and fatality data from 5 sites (sites 2, 3, 6, 8, and 9; Fig. 1) using a linear regression with a 0-constrained intercept. We conducted statistical analyses with JMP 7.0.1 (SAS Institute, Cary, North Carolina) and present means  $\pm$  SE.

## RESULTS

**Activity monitoring.**—At the 7 sites we acoustically monitored (Table 1), we detected a total of 4,097 migratory-bat passes over 820 detector-nights. The number of detector-



**FIG. 2.**—Mean ( $\pm$  SE) migratory-bat passes/detector-night by site and detection height (ground level or 30 m) across southern Alberta, Canada. Site 1 is the westernmost site and site 9 is the easternmost site; they are approximately 155 km apart.

nights and the total number of migratory-bat passes detected varied among sites from 161 detector-nights at site 9 to 35 detector-nights at site 5, and from 1,807 migratory-bat passes at site 1 to 67 migratory-bat passes at site 5, respectively. We did not detect migratory-bat activity every night we sampled and the percentage of nights with 0 migratory-bat passes varied among sites from 9.8% at site 1 to 65.2% at site 8. Total acoustic activity of migratory bats varied among sites from  $14.81 \pm 1.84$  passes/night at the westernmost site (site 1), to  $0.78 \pm 0.12$  passes/night at an eastern site (site 8). Migratory-bat activity varied among sites at both ground level and 30 m (ground level, Kruskal–Wallis,  $\chi^2 = 156.5$ ,  $d.f. = 6$ ,  $P < 0.0001$ ; 30 m,  $\chi^2 = 119.6$ ,  $d.f. = 6$ ,  $P < 0.0001$ ; Fig. 2). Total activity of *L. noctivagans* was typically greater than that of *L. cinereus*, but total activity for both species varied among sites and was greater at the western sites than the eastern sites: *L. noctivagans* from  $9.75 \pm 1.69$  to  $0.46 \pm 0.16$  passes/night, and *L. cinereus* from  $5.02 \pm 0.88$  to  $0.14 \pm 0.04$  passes/night. Activity of *L. cinereus* and *L. noctivagans* varied among sites at both ground level and 30 m (*L. cinereus*, ground level,  $\chi^2 = 107.7$ ,  $d.f. = 6$ ,  $P < 0.0001$ , 30 m,  $\chi^2 = 138.6$ ,  $d.f. = 6$ ,  $P < 0.0001$ ; *L. noctivagans*, ground level,  $\chi^2 = 87.8$ ,  $d.f. = 6$ ,  $P < 0.0001$ , 30 m,  $\chi^2 = 104.3$ ,  $d.f. = 6$ ,  $P < 0.0001$ ).

Pooled across all sites, total migratory-bat activity did not differ between detection heights (ground level =  $5.08 \pm 0.56$  migratory-bat passes/detector-night, 30 m =  $4.93 \pm 0.49$  migratory-bat passes/detector-night, Wilcoxon 2-sample test,  $Z = 0.77$ ,  $d.f. = 1$ ,  $P = 0.44$ ). However, when separated by species, activity of both *L. cinereus* and *L. noctivagans* differed between the 2 detection heights with *L. cinereus* being less common at ground level ( $1.17 \pm 0.18$  passes/detector-night) than at 30 m ( $2.21 \pm 0.27$  passes/detector-night;  $Z = 4.02$ ,  $d.f. = 1$ ,  $P < 0.0001$ ), and *L. noctivagans* more common at ground level ( $3.89 \pm 0.52$  passes/detector-night) than at 30 m ( $2.70 \pm 0.39$  passes/detector-night;  $Z = 4.32$ ,  $d.f. = 1$ ,  $P < 0.0001$ ).

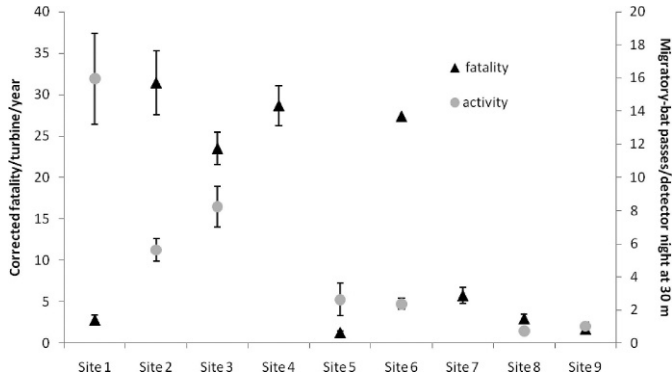


FIG. 3.—Mean  $\pm$  SE activity of migratory bats at 30 m and corrected bat fatalities/turbine/year across sites in southern Alberta, Canada. Heights of turbine towers varied: sites 1 and 5 = 50 m; sites 2, 3, 4, and 7 = 65 m; site 6 = 67 m; site 8 = 80 m; and site 9 = 84 m.

Mean nightly minimum temperature varied among sites from  $7.41^{\circ}\text{C} \pm 0.33^{\circ}\text{C}$  at the westernmost site (site 1) to  $9.02^{\circ}\text{C} \pm 0.36^{\circ}\text{C}$  at site 2 (ANOVA,  $F = 3.68$ ,  $d.f. = 7$ , 812,  $P < 0.001$ ; site,  $F = 3.62$ ,  $d.f. = 6$ , 182,  $P < 0.005$ ; night,  $F = 5.89$ ,  $d.f. = 1$ , 812,  $P = 0.02$ ). On average, site 2 was warmer than the other sites, whereas sites 1 and 9 were colder than the other sites (Tukey's tests  $P < 0.05$ ). Although mean maximum nightly wind speed varied among sites from  $6.28 \pm 0.17$  m/s at site 3 to  $5.62 \pm 0.16$  m/s at site 9 (ANOVA,  $F = 2.18$ ,  $d.f. = 7$ , 812,  $P = 0.03$ ; site,  $F = 2.34$ ,  $d.f. = 6$ , 812,  $P = 0.03$ ; night,  $F = 0.07$ ,  $d.f. = 1$ , 812,  $P = 0.80$ ), no sites were statistically different from others (Tukey's tests  $P > 0.05$ ). Mean minimum nightly wind speed did not vary (ANOVA,  $F = 1.91$ ,  $d.f. = 7$ , 812,  $P = 0.06$ ).

**Fatality monitoring.**—During searcher efficiency trials, we found 78 of the 100 bats available to be found, for a searcher efficiency of 78%. Carcasses lasted an average of 5.6 days ( $n = 34$ ). Only 1 carcass remained to be removed on day 14. At turbines searched daily, cumulatively, we recovered an estimated 97% of bat carcasses.

Corrected fatality rates varied among the 9 sites sampled, from  $31.41 \pm 3.04$  bats/turbine/year to  $1.26 \pm 0.18$  bats/turbine/year (Kruskal–Wallis 1-way test,  $\chi^2 = 192.74$ ,  $d.f. = 8$ ,  $P < 0.0001$ ; Fig. 3). Fatality rates were generally highest at western wind energy facilities and lowest at eastern facilities. The generalized linear model that assessed variation in corrected fatality rate explained a significant proportion of the variation (overdispersed Poisson distribution,  $n = 6$  sites,  $\chi^2 = 502.9$ ,  $d.f. = 5$ ,  $P < 0.0001$ ). Fatality rate increased with turbine height ( $\chi^2 = 49.14$ ,  $d.f. = 1$ ,  $P < 0.0001$ ) and with the interaction between migratory-bat activity at 30 m and turbine height ( $\chi^2 = 10.16$ ,  $d.f. = 1$ ,  $P = 0.001$ ; Fig. 3). Fatality rate was not influenced by migratory-bat activity at ground level ( $\chi^2 = 1.77$ ,  $d.f. = 1$ ,  $P = 0.18$ ), migratory-bat activity at 30 m ( $\chi^2 = 2.96$ ,  $d.f. = 1$ ,  $P = 0.09$ ), or the interaction between migratory-bat activity at ground level and turbine height ( $\chi^2 = 2.75$ ,  $d.f. = 1$ ,  $P = 0.10$ ).

Across the 7 sites with both fatality and activity data, we did not find a correlation between activity at 30 m and fatality ( $r^2$

$= 0.02$ ; Fig. 3). However, when we compared just the 5 sites with fatality and activity data, and tall turbines (towers  $\geq 65$  m), there was a significant relationship between activity and fatality ( $r^2 = 0.31$ ; ANOVA,  $F = 12.85$ ,  $d.f. = 1$ , 4,  $P = 0.023$ ). For every migratory-bat pass recorded per detector-night, bat fatalities varied from 1.7 to 13.5 fatalities/turbine/year, depending on the site.

## DISCUSSION

During fall migration, activity of migratory bats varied among sites in southern Alberta, suggesting that, rather than being dispersed randomly or evenly over a wide east–west area, bats concentrated along select routes. Activity rates of both *L. cinereus* and *L. noctivagans* were higher near the foothills of the Rocky Mountains to the west than on the prairie grasslands farther east. If migration ranges, routes, and nightly travel distances are limited by the availability and distribution of appropriate stopover and roosting sites (i.e., trees—Berthold 2001; Catry et al. 2004; Cryan and Veilleux 2007; Fleming and Eby 2003; Richardson 1978, 1998) and geographical landmarks (e.g., rivers and foothills or mountains), then this may explain the higher level of migratory-bat activity we observed at sites located near these features compared to more-distant sites.

Trees are scarce on the prairies. *L. noctivagans* prefers large trees with heavily furrowed bark with crevices to crawl into, such as tall poplars (*Populus*) in early to mid stages of decay (Barclay et al. 1988; Barclay and Kurta 2007; Crampton and Barclay 1998). During migration *L. cinereus* has been found in cherry (*Prunus*), pine (*Pinus*), and cypress trees (*Cupressus*—Constantine 1959; Tenaza 1966). We suggest that bats starting their migration in the aspen parkland or boreal forest of northern Alberta are unlikely to fly south across the open prairie. Rather, routes following the availability of roosts along riparian zones and the foothills of the Rocky Mountains may be optimal. Although flying west to the foothills of the Rocky Mountains before flying south may add extra distance to the migratory route, roosting options in the foothills are less sporadic and more predictable than on the prairies. Depending on where migration originates, the benefit of predictable roosting options in the foothills may outweigh the cost of the extra distance travelled. In addition to providing important roosting habitat (Holloway and Barclay 2000), riparian areas and foothills may serve as navigational landmarks along migratory paths (Serra-Cobo et al. 2000).

Activity of both *L. cinereus* and *L. noctivagans* differed between detection heights, but the relationship between activity and height were opposite for the 2 species; *L. cinereus* was more commonly detected at 30 m, whereas *L. noctivagans* was more commonly detected at ground level. This difference may be due to species differences in morphology and foraging strategies. Although we do not know about the feeding behavior of bats as they migrate, or the relationship of prey distribution and height, morphological differences among bats may interact and combine with their foraging strategies to

influence flight heights. *L. cinereus* has relatively high wing-loading and aspect ratio and is thus adapted for fast, relatively unmaneuverable flight in open spaces (Norberg and Rayner 1987). In contrast, *L. noctivagans* is smaller, slower, and more maneuverable (Norberg and Rayner 1987). Although these differences influence foraging behavior, it is unknown how they influence migratory behavior.

Weather variables that likely influence bat activity (e.g., minimum temperature and maximum wind speed) varied among sites, but not in ways that would explain the difference in activity of migratory bats among sites. Activity of migratory bats is generally reduced at low ambient temperatures (Baerwald 2008; Erickson and West 2002; Fiedler 2004) and in high wind speeds (Arnett et al. 2008; Baerwald 2008; Cryan and Brown 2007). Despite this, site 1 had both the lowest mean minimum temperature and the 2nd-highest maximum wind speed, but the highest bat activity.

Our acoustic sampling locations were not randomly located across southern Alberta. To sample bat activity at 30 m, and to address the issue of bat activity at wind energy facilities, all acoustic monitoring was done from meteorological towers at existing or proposed wind energy facilities. Wind energy sites are only proposed or built in areas of relatively high and consistent wind speeds, and although the prevailing wind direction is not conducive to southward migration, this may influence the level of migratory-bat activity and introduce bias to the study. However, southwestern Alberta is generally windy, and with another 1,523 MW of wind energy facilities proposed in the study area by 2011 (Government of Alberta 2008), much of the area has been prospected for wind energy sites, thus any differences between wind energy sites and non-wind energy sites are unlikely.

Fatality rates of bats varied among the 9 sites, partly due to differences in turbine tower height (see also Barclay et al. 2007), but also due to differences in activity of migratory bats at 30 m. The interaction between bat activity at 30 m and tower height predicted fatality rate such that sites with high activity but relatively short towers had low fatality rates (e.g., site 1), as did sites with low activity but tall towers (e.g., sites 8 and 9). At sites with little bat activity, we expect fatality rates also will be low because there are few bats to be killed, and tower height is inconsequential. However, at sites with high bat activity, an increase in tower height also increases the probability of fatality. There was no clear relationship between activity of migratory bats recorded at ground level and fatality rates, perhaps because bats detected from the ground are below the blade-swept area and out of the zone of risk. This suggests that acoustic monitoring at ground level is not appropriate for presiting assessments of fatality risk. Although we did not analyze fatality rates at the species level, at a landscape level, species-specific patterns of activity closely resembled patterns of fatality.

At sites with tall turbines, 31% of the variation in fatality rate was explained by migratory-bat activity at 30 m. Examination of the data indicates that, at sites in southern Alberta with tall turbines, for every migratory-bat pass

recorded (at 30 m) on average per detector-night, there were between 1.7 and 13.5 migratory-bat fatalities/turbine/year. Kunz et al. (2007a) found that 79% of the variation in bat fatality rate at 5 wind energy sites in the United States was explained by bat activity, with ratios of fatality to activity lower than those we recorded, and varying between 0.59 and 1.05. However, fatality data were from both short (<65 m) and tall ( $\geq 65$  m) turbines, and bat passes were recorded at various heights, including ground level, and included nonmigratory species (Kunz et al. 2007a). Further studies with larger sample sizes, in different habitat types, with different species compositions, and with bat activity monitored at consistent heights ( $\geq 30$  m) are needed to determine whether a relationship can be found that is generally applicable. If such a relationship is found, it may provide a means of risk assessment for proposed wind energy facilities.

Our results indicate that factors in addition to turbine height and migratory-bat activity influence fatality rates at wind turbines. We suggest that the number of turbines may play a role. Several hypotheses propose that bats are attracted to wind turbines (Cryan 2008; Cryan and Barclay 2009; Kunz et al. 2007b). If so, then facilities with many turbines may experience a dilution effect in terms of attraction, with lower fatality rates per turbine than facilities with few turbines. Examination of our data from sites 2, 3, and 6 supports this hypothesis. Sites 2 and 3 are only 5 km apart and have the same size and make of turbines, but site 2 has only 2 turbines, whereas site 3 has 39. Site 2 had fewer migratory-bat passes/detector-night than site 3, but had a higher corrected fatality rate. Site 6, a single, tall turbine, had a relatively low number of migratory-bat passes/detector-night but a relatively high bat fatality rate.

Migrating *L. cinereus* and *L. noctivagans* were concentrated in some parts of our study area and not others. If such migratory routes are typical of these species, and the specific landscape features they follow can be determined, minimizing fatalities may be possible by building wind facilities in areas with relatively low migratory activity. However, our results demonstrate that it is not only bat activity levels that influence fatality rates at wind energy facilities, but also characteristics of the facilities themselves (e.g., tower height). Additional work with larger sample sizes would help to clarify the importance of such project characteristics either in general or in certain regions and habitats.

The recent proliferation of wind energy facilities and their accompanying environmental assessments has afforded the opportunity to study migratory-bat behavior at the landscape level. This study provides a clear indication that bats, like some birds, follow select routes while migrating, but further studies are needed to fully understand the determinants of these routes.

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