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Migration of bats past a remote island offers clues toward the problem of bat fatalities at wind turbines

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ABSTRACT

Wind energy is rapidly becoming a viable source of alternative energy, but wind turbines are killing bats in many areas of North America. Most of the bats killed by turbines thus far have been migratory species that roost in trees throughout the year, and the highest fatality events appear to coincide with autumn migration. Hoary bats (*Lasiurus cinereus*) are highly migratory and one of the most frequently killed species at wind turbines. We analyzed a long-term data set to investigate how weather and moonlight influenced the occurrence of hoary bats at an island stopover point along their migration route. We then related our results to the problem of bat fatalities at wind turbines. We found that relatively low wind speeds, low moon illumination, and relatively high degrees of cloud cover were important predictors of bat arrivals and departures, and that low barometric pressure was an additional variable that helped predict arrivals. Slight differences in the conditions under which bats arrived and departed from the island suggest that hoary bats may be more likely to arrive on the island with passing storm fronts in autumn. These results also indicate that fatalities of hoary bats at wind turbines may be predictable events, that the species may be drawn to prominent landmarks that they see during migration, and that they regularly migrate over the ocean. Additional observations from this and other studies suggest that the problem of bat fatalities at wind turbines may be associated with flocking and autumn mating behaviors.

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1. Introduction

Wind power is a promising source of sustainable energy. Wind turbines have enormous potential to serve as effective sources of “green” power across the globe (Hoogwijk, 2004), and such efficacy has led to vast increases in the number of turbines currently under construction (AWEA, 2006). The impact of wind turbines on abiotic components of the environment (i.e., air, land, and water) is far less than conventional power sources. However, it is becoming increasingly apparent that the deployment of large wind turbines is creating problems for wildlife, particularly bats (Johnson, 2005; Arnett

et al., in press; Kunz et al., in press). Several recent incidents at turbine sites in North America involved the killing of dozens to hundreds of bats during periods lasting just a few weeks (Fiedler, 2004; Rowland, 2006; Arnett et al., in press; Barclay et al., 2007). These unexpectedly high bat fatalities at anthropogenic structures are unprecedented and the mystery of why bats are so vulnerable to large wind turbines remains unsolved. Despite our lack of a clear understanding of this growing problem, certain patterns are emerging from the fatality data on bats at wind turbines. The first pattern is that the bat species most frequently killed at turbines have similar life history characteristics. Thus far, most reported

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fatalities involve a group of species referred to as “migratory tree bats,” because they roost in the foliage or in cavities of trees throughout the year and make seasonal migrations over several degrees of latitude (Griffin, 1940; Cryan, 2003). In North America, these species are the hoary bat (*Lasiurus cinereus*), the eastern red bat (*L. borealis*), and the silver-haired bat (*Lasionycteris noctivagans*). Hoary bats are killed by turbines at more sites and in greater numbers than most other species, with the exception of eastern red bats in the Appalachian Region of eastern North America (Johnson, 2005; Arnett et al., in press; Kunz et al., in press). In addition to the primary involvement of migratory tree bats, another clear pattern to bat kills at turbines is that peaks in fatalities typically occur during a few weeks in late summer and early autumn (Johnson, 2005; Bailey, 2006). This seasonal peak in fatalities at turbines coincides with the period during which migrating bats are most frequently encountered elsewhere (Strelkov, 1969; Cryan, 2003) and further indicates that migration plays a key role in bat fatalities observed at wind turbines.

Little is known about the behavior of bats during migration and what aspects of this seasonal behavior make them particularly susceptible to wind turbines. One of the greatest difficulties in studying this phenomenon is finding places to observe bats that are actively migrating. We are aware of only one place in North America where tree bats can be observed with any regularity during autumn migration. Tenaza (1966) first reported the occurrence of hoary bats on Southeast Farallon Island (SEFI), which is a small (<2 km²), rocky island, situated more than 30 km from the coast of California in the Pacific Ocean. Since that first report, biologists from the Point Reyes Bird Observatory (PRBO) have noted the presence of hoary bats on the island almost every autumn for the past four decades (PRBO, unpublished data).

Over the course of their annual migrations, hoary bats range wider than any other small mammal in North America. Progress has been made in recent years toward elucidating the details of migration by hoary bats (Cryan, 2003; Cryan et al., 2004), but there is still much to be learned about the specifics of this phenomenon. For example, available evidence indicates that California is a major wintering area for North American hoary bats, but the natural history of the species in the region during spring, winter, and autumn is poorly understood. For the most part, the location of specific wintering grounds and migration routes of hoary bats in and out of California remain unclear. Occurrence records suggest that both male and female hoary bats winter together in California (Grinnell, 1918; Dalquest, 1943; Vaughan and Krutzsch, 1954), but reproductive females mostly vacate the state during summer (Cryan, 2003). The lack of records of female hoary bats from areas north of California in spring and early summer suggests that they leave the state and move to the eastern half of the continent where they give birth and raise their young; during this same period adult males apparently make shorter migrations and tend to spend the spring and early summer months in mountainous regions of western North America (Cryan, 2003). As autumn progresses, many female hoary bats move back toward the western half of the continent and the previously segregated distributions of males and females begin to overlap as they migrate south and westward toward the Pacific Coast. Thus, both males and females

apparently migrate together along the Pacific Coast as they travel back to wintering grounds in California. These continental movements likely contribute to the widespread fatalities of hoary bats observed at wind energy facilities. Is the occurrence of migrating hoary bats predictable, particularly at specific sites such as wind energy facilities? Answering questions such as this is an important step toward understanding and eventually minimizing the impacts of wind turbines on bats.

Herein, we analyzed the 38-year data set of observations of hoary bats on SEFI to determine if moonlight and weather conditions influenced the occurrence of bats on the island. We also examined the temporal relationships of migration events involving hoary bats and similar species, and then related our findings to observed bat fatalities at wind turbines.

2. Materials and methods

2.1. Study area

Southeast Farallon Island is situated in the Pacific Ocean approximately 32 km due south of Point Reyes, Marin County, California (the nearest land) and 48 km west of San Francisco (37°41'N, 123°00'W; Fig. 1). SEFI is part of the Farallon National Wildlife Refuge and lies within waters of the Gulf of the Farallones National Marine Sanctuary. SEFI is approximately 28 ha in size and was formed by tectonic uplift of granite fault blocks along the western edge of the Continental Shelf (Howard, 1979). The island rises 109 m above sea level to the top of Lighthouse Hill where an active lighthouse has been maintained since 1855 (White, 1995). Much of the island's land area consists of bare granite and low-growing (<0.5 m) non-woody vegetation (Coulter, 1971, 1978). Woody vegetation on the island is sparse and consists of only three individual trees (2 Monterey cypresses [*Cupressus macrocarpa*] and 1 Monterey pine [*Pinus radiata*]), thin stands of tree mallow (*Lavatera arborea*; Coulter, 1971, 1978), and one mirror bush (*Coprosma repens*; J. Clark, pers. comm.). The cypress trees range in height from about 8 to 12 m and grow in the lee of the two residences on the island. The pine grows on the windward side of a small hill and has been contorted by wind so that it is only 3 m in height, but radiates out about 5 m in each direction. Weather on the island was described in detail by Pyle et al. (1993) and is generally described as stable with clear skies and prevailing moderate winds out of the northwest, punctuated by short periods of fog and overcast skies.

2.2. Observations of bats

Personnel from PRBO maintained a continual presence on SEFI since 1968 and recorded daily observations from routine censuses of birds and marine mammals in standardized journals (Desante and Ainley, 1980; Richardson et al., 2003). Although protocols for searching for bats on the island were never established, and thus considered incidental observations, island records include regular observations of hoary bats from as early as 1968. The size and pelage characteristics of hoary bats are distinct among bats in North America and thus island personnel were able to make most observations

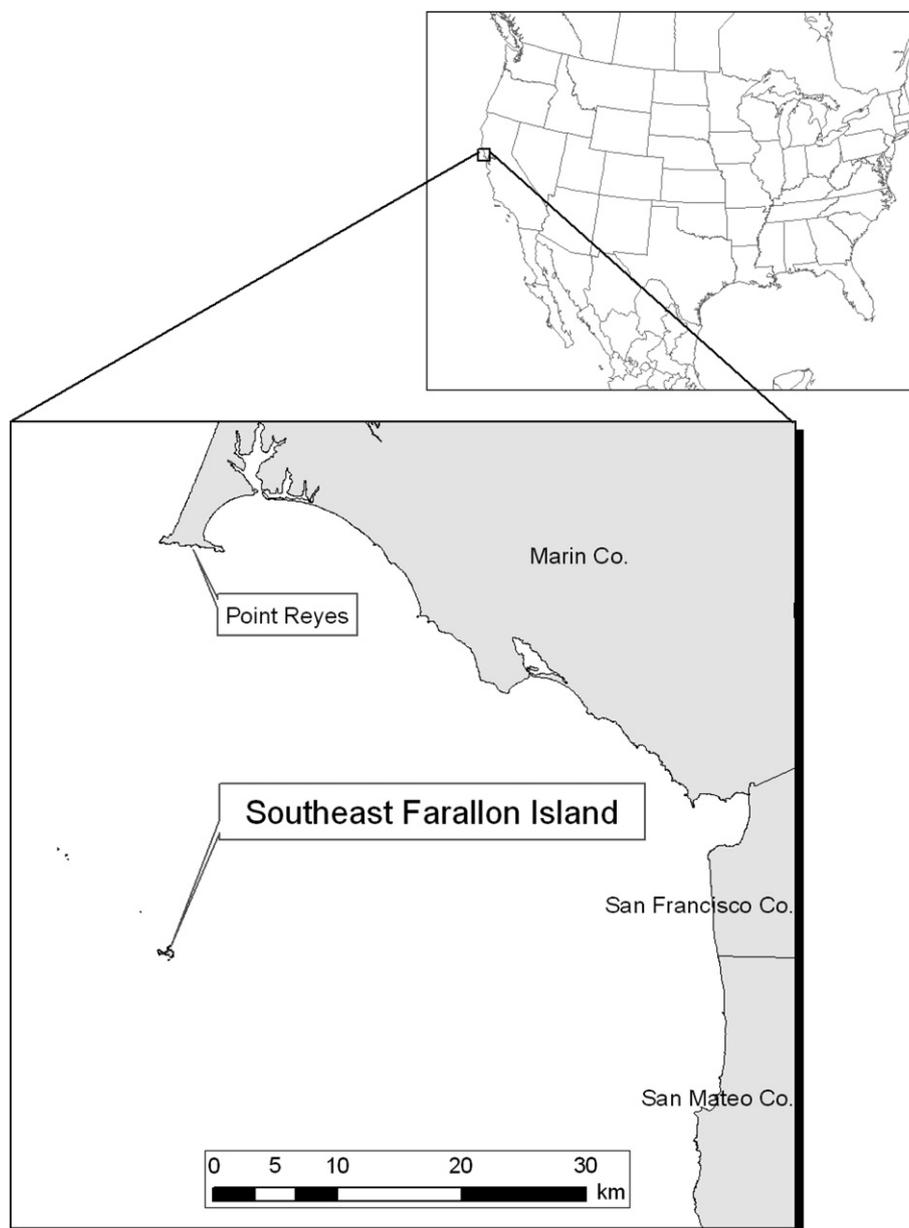


Fig. 1 – Map of the coast of California near San Francisco showing the location of Southeast Farallon Island and its relation to Point Reyes.

from within 1 to 10 m of roosting bats. Specimens of hoary bats were also taken on the island as early as 1965 (Tenaza, 1966) and thus are familiar to island biologists. For these reasons, we have little reason to doubt the reliability of species identification. All of the trees and vegetated areas known to be used by hoary bats on SEFI were surveyed multiple times per day throughout the year for birds (DeSante and Ainley, 1980; DeSante, 1983; Pyle and Henderson, 1991).

2.3. Statistical analysis

We modeled the influence of weather and moonlight on bat occurrence using logistic regression (Proc GENMOD in SAS, SAS Institute, Inc., Cary, NC). Two separate logistic regression analyses were conducted: the first examined the probability

of bat arrival to the island and the second modeled the probability of bat departure from the island. We defined arrivals as the appearance of bats on the island after not being observed during >3 previous days, or days when the number of bats observed on the island increased by ≥ 5 individuals. We defined departures as the last day during which bats were observed on the island before an absence of >3 days or when the number of bats observed decreased by ≥ 5 individuals. In both analyses, we modeled bat presence (1) or absence (0) on the island as a binomial response variable, and abiotic conditions as independent predictor variables. Independent predictor variables were wind speed (m/s; WIND), visibility (km; VISI), barometric pressure (kPa; BARO), cloud cover (%; CLOU) and moon face illumination (%; MOON). We constructed 26 candidate regression models comprised of ≤ 5 independent

variables that were of biological interest. We ran the same 26 models on both arrival and departure data sets. Goodness-of-fit tests were performed using Pearson χ^2 values generated by PROC GENMOD to assess the validity of global models. In the analyses of arrival and departure days, we independently compared conditions on 1934 evenings between 1 August and 31 October 1971–2003 when bats were not observed on the island to conditions on 86 evenings prior to the arrival of bats and 82 evenings of bat departure. We limited our analysis to the days of 1 August through 31 October because that is the period when hoary bats mostly have been observed on the island (97% of days observed). We acknowledge that bats may have been present on some of the days they were not observed, but given the limited number of potential roosts and the degree to which those sites were closely examined on a daily basis, we suspect that detection probability was >95%. PRBO personnel occupying the island gathered all weather data used for this study, and we used readings taken at 20:00 h each night. We excluded the years 1998, 2004, and 2005 from our analysis because weather data from 20:00 h were not available during those years. We included all available data with complete records (all variables present). The online moon phase calculator of the U.S. Naval Observatory, Astrological Applications Department (available online at http://aa.usno.navy.mil/data/docs/RS_OneDay.html) was used to calculate percentage of the moon face illuminated each night, using values derived for San Francisco, CA. We calculated Pearson correlation coefficients to examine the relationships between the independent predictor variables used in regression models.

We ranked logistic regression models using Akaike's Information Criterion (AIC; (Burnham and Anderson, 2002). We calculated differences in AIC values between candidate models (Δ_i ; a measure of the i th model relative to the top-ranked model) and Akaike weights (w_i ; the weight of evidence in favor of model i as being the best model in the candidate set). Top-ranking models were those with $\Delta_i < 2$ and with the greatest number of parameters with confidence intervals that do not cover zero.

We did not include data on wind direction in regression models because when wind speed = 0 m/s wind direction data are not available and would thus confound analysis (logistic regression models omit records with missing variables). However, data for wind direction are provided as summary statistics. Because data for wind direction were recorded in a vector format (degrees), we transformed these data to and from X and Y-axial components before and after compiling summary statistics.

2.4. Literature records

In an effort to summarize the seasonal timing of known events involving migration by species of *Lasiurus* (*L. cinereus*, *L. borealis*, and *L. ega*) we compiled records from the literature. We chose to include species of *Lasiurus* other than hoary bats in this review because their migration behaviors appear to be similar in seasonal timing (Cryan, 2003). These records involved incidents where bats or groups of bats: landed on ships at sea (Nichols, 1920; Thomas, 1921; Haagner, 1921; Allen, 1923; Norton, 1930; Griffin, 1940; Carter, 1950; Brown, 1953;

Mackiewicz and Backus, 1956; Peterson, 1970); were encountered in situations suggesting they had been traveling over large bodies of water (Rhodes, 1903; Murphy and Nichols, 1913; Brown, 1935; Mumford, 1973); were encountered on remote islands (Miller, 1897; Saunders, 1930; Van Gelder and Wingate, 1961; Koopman and Gundmundsson, 1966; Tenaza, 1966; Hill and Yalden, 1990); died after colliding with buildings or communication towers (Terres, 1956; Van Gelder, 1956; Anonymous, 1961; Ganier, 1962; Elder and Hansen, 1967; Avery and Clement, 1972; Zinn and Baker, 1979; Crawford and Baker, 1981; Timm 1989); or were observed in concentrated groups flying during the day (Merriam, 1884; Mearns, 1898; Howell, 1908; Hall, 1946; Mumford, 1973). We tabulated the timing of fatalities for species of *Lasiurus* (*L. cinereus* and

Table 1 – Timing and frequency of autumn observations of hoary bats (*Lasiurus cinereus*) on Southeast Farallon Island, California, from 1968 through 2005, including the year, number of days that ≥ 1 hoary bats were seen in roosts, and the dates on which bats were first and last seen

Year	No. days bats seen	First seen	Last seen
1968	1	29-Sep	29-Sep
1969	5	4-Sep	15-Sep
1970	4	28-Aug	22-Sep
1971	11	18-Aug	4-Oct
1972	6	2-Sep	25-Oct
1973	4	2-Sep	18-Oct
1974	3	9-Sep	28-Sep
1975	2	30-Sep	30-Sep
1976	3	5-Sep	1-Oct
1977	5	11-Aug	10-Sep
1978	0	–	–
1979	9	18-Aug	16-Oct
1980	15	24-Aug	10-Oct
1981	35	19-Aug	31-Oct
1982	8	13-Aug	15-Oct
1983	7	6-Sep	29-Sep
1984	6	30-Aug	2-Oct
1985	10	23-Aug	1-Oct
1986	10	13-Aug	28-Oct
1987	18	25-Aug	21-Oct
1988	17	10-Aug	24-Oct
1989	17	21-Aug	11-Oct
1990	4	18-Sep	28-Sep
1991	16	19-Aug	22-Sep
1992	10	25-Aug	5-Oct
1993	9	14-Sep	28-Sep
1994	4	14-Sep	25-Sep
1995	5	9-Sep	21-Sep
1996	4	11-Sep	1-Oct
1997	1	16-Oct	16-Oct
1998	6	14-Sep	11-Nov
1999	9	4-Sep	17-Oct
2000	0	–	–
2001	2	8-Sep	8-Sep
2002	5	19-Sep	17-Oct
2003	12	26-Aug	3-Oct
2004	2	22-Aug	22-Aug
2005	10	28-Aug	13-Sep
Total	295	10-Aug	11-Nov

L. borealis) at wind turbines from various published and unpublished sources (Gruver, 2002; Johnson et al., 2003; Fiedler, 2004; Johnson et al., 2004; Arnett, 2005; Johnson, 2005; E. Baerwald and R.M.R Barclay, pers. comm.).

3. Results

3.1. Observations of bats

Hoary bats were observed on SEFI during all but two of the 38 autumns that records were kept, for a total of 295 days of occurrence (Table 1). The average number of bats observed per day of occurrence was 5.0 ± 1.6 ($\bar{x} \pm$ SD of lognormal dist.; range 1–101) and bats were observed an average of 8.2 ± 6.7 ($\bar{x} \pm$ SD; range 1–35) days per autumn. Hoary bats were most often observed roosting in the trees and mallow plants, but on a few occasions (<12 days) individual bats used additional roosts such as rock outcrops, buildings, and a small cave. However, the latter sites were searched daily and there is no evidence that they were used on a regular basis. Bats were observed more frequently in September than any other month and usually visited the island between the last week of August and the end of October (Fig. 2). In addition to autumn records, hoary bats were observed using the island on 7 days during late April and early May of 1990.

3.2. Statistical analysis

Goodness-of-fit tests revealed that the global models for both the arrival ($p = 0.95$) and departure ($p = 0.99$) data sets were well fit. We found slight differences in the top-ranked models between arrivals and departures (Table 2), even though the same set of candidate models was used to separately analyze arrival and departure data. For arrivals, a model that included four variables (wind speed, barometric pressure, cloud cover, and moon illumination) ranked best, whereas the top-ranked model for describing departures included only three of these variables (wind speed, cloud cover, and moonlight). Parameter estimates and their 95% confidence intervals for both top models were similar in direction and magnitude (Table 3). No parameters in the two top-ranked models had confidence intervals that covered zero, but all competing models ($\Delta_i < 2$) in both the arrival and departure analyses had at least one variable with a confidence interval that included zero. Relatively low wind speeds, moon illumination, and relatively high degrees of cloud cover were important predictors of both bat arrivals and departures, whereas low barometric pressure was an additional condition that helped predict arrivals. Table 4 shows summary statistics for weather and moonlight conditions during arrival days, departure days, and absence days. Among variables included in the top-ranked models, Pearson

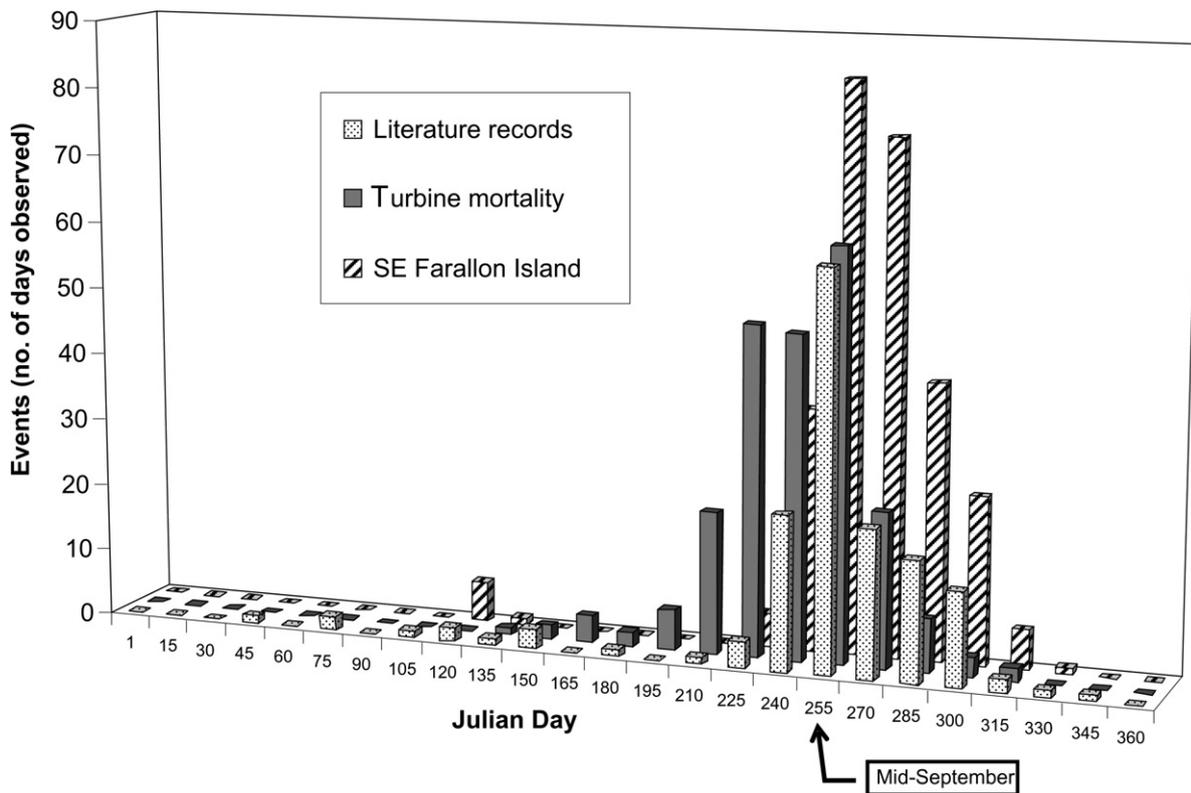


Fig. 2 – Timing of events, by Julian day, in which species of *Lasiurus* were observed in situations that suggested they were actively migrating. Horizontal stippled bars represent miscellaneous records found in the literature, solid gray bars represent mortality data from studies at wind turbine sites, and diagonally stippled bars represent the data reported herein showing the timing of occurrence of hoary bats on Southeast Farallon Island, California. See Section 2 for sources of literature and turbine records.

Table 2 – Rankings by Akaike's information criterion of logistic regression models (Proc GENMOD in SAS-SAS Institute Inc., Cary, North Carolina, USA) comparing weather and moonlight conditions on days that bats were observed on Southeast Farallon Island, California, to conditions on days that bats were not observed

Candidate models	Arrival days			
	k	AIC	Δ_i	w_i
WIND BARO CLOU MOON	6	659.55	0.00	0.48
WIND VISI BARO CLOU MOON	7	661.24	1.68	0.21
WIND BARO CLOU	5	661.87	2.32	0.15
WIND VISI BARO CLOU	6	663.59	4.04	0.06
WIND CLOU MOON	5	663.98	4.43	0.05
WIND VISI CLOU MOON	6	665.84	6.29	0.02
WIND CLOU	4	666.00	6.45	0.02
WIND VISI CLOU	4	667.87	8.32	0.01
CLOU MOON	4	672.60	13.05	0.00
VISI CLOU MOON	5	674.25	14.70	0.00
Departure days				
WIND CLOU MOON	5	655.87	0.00	0.26
WIND BARO CLOU MOON	6	656.77	0.91	0.17
WIND VISI CLOU MOON	6	656.90	1.03	0.16
WIND VISI BARO CLOU MOON	7	657.57	1.70	0.11
WIND MOON	4	657.94	2.08	0.09
WIND BARO MOON	5	658.69	2.83	0.06
WIND VISI MOON	5	659.88	4.01	0.04
WIND CLOU	4	660.52	4.65	0.03
WIND VISI BARO MOON	6	660.68	4.81	0.02
WIND VISI CLOU	4	661.51	5.64	0.02

Δ_i is the difference in AIC value between the *i*th and top-ranked model and w_i is the Akaike weight (the weight of evidence in favor of model *i* as being the best model in the candidate set). Sets of up to five independent variables were used to separately model the arrival of bats to the island and departure of bats from the island. Independent variables were wind speed (m/s; WIND), visibility (km; VISI), barometric pressure (kPa; BARO), cloud cover (%; CLOU), and moon face illumination (%; MOON). See text for definition of arrival and departure days.

correlation coefficients revealed only a weak, negative association (−0.30) between cloud cover and wind speed.

3.3. Literature records

We compiled data from the literature concerning 147 separate days in history when species of *Lasiurus* were observed: landing on ships at sea ($n = 12$); flying over large bodies of water or appearing on remote islands ($n = 50$); colliding with buildings

or communication towers ($n = 79$); or flying in concentrated groups ($n = 6$). The majority of these events occurred on days between early September and late October, with a peak in mid-September (Fig. 2). We compiled data from 230 additional days when species of *Lasiurus* were killed by wind turbines. Thus far (i.e., since about 2002), fatalities of *Lasiurus* spp. at wind turbines have occurred mostly during mid-August through late September, with a peak in mid-September (Fig. 2).

4. Discussion

This is the first study to investigate factors influencing the migratory passage of hoary bats through a specific area and the first to show that environmental conditions might be used to predict the occurrence of migrating bats at such sites. Specifically, we found that the autumn arrivals and departures of hoary bats from the island were most likely to occur during dark phases of the moon, when wind speeds were relatively low, and when the sky is obscured by clouds. In addition, the arrival of bats to the island is also associated with low barometric pressures. These patterns reveal potentially important information about the perceptive abilities of migrating hoary bats and may lead us toward a better understanding of why this species regularly collides with wind turbines.

4.1. Factors influencing occurrence on the island

Our results show that bats were more likely to arrive and depart from the island on evenings when wind speeds were relatively low. Little is known about the influence of wind speed on migrating bats and we do not know if the observed pattern was the result of more bats traveling on nights with low winds or simply due to a greater probability of encounter under such conditions. Several studies have shown that bat activity, in general, is suppressed during strong winds, but much of this work focused on bats foraging near their roosts rather than while migrating (Erkert, 1982). Studies of bat fatalities at wind facilities in Tennessee (Fiedler, 2004), Pennsylvania, and West Virginia (Arnett, 2005; Horn et al., provisionally accepted) revealed higher levels of bat mortality at turbines on nights with light winds. Potential advantages of flying during light winds include a greater probability of encountering and capturing aerial insects, greater efficiency of echolocation for opportunistically feeding during travel, maintaining group cohesion, avoiding heat or water loss from increased convec-

Table 3 – Parameter estimates and associated 95% confidence intervals for variables in the best models for explaining the arrival and departure of hoary bats on Southeast Farallon Island, CA

Parameter	Arrivals			Departures		
	Estimate	Lower CI	Upper CI	Estimate	Lower CI	Upper CI
Intercept	70.6982	17.5949	123.8014	−2.1525	−2.8188	−1.4862
Wind speed	−0.1333	−0.2157	−0.0508	−0.1735	−0.2577	−0.0894
Barometric pressure	−0.7270	−1.2510	−0.2029	–	–	–
Cloud cover	0.1430	0.0829	0.2032	0.0548	0.0009	0.1087
Moon illumination	−0.0067	−0.0131	−0.0003	−0.0085	−0.0150	−0.0020

Table 4 – Summary statistics of weather and moonlight variables, by evening during autumn: before bats arrived on the island (Arrivals), left the island (Departures), and were not observed on the island (Absences)

Variable	Arrivals (n = 86)		Departures (82)		Absences (1932)	
	Mean (SD)	95% CI	Mean (SD)	95% CI	Mean (SD)	95% CI
Wind direction (°)	326 (40)	306–343	331 (48)	317–344	337 (50)	335–340
Wind speed (m/s)	4.4 (2.3)	3.9–4.4	4.3 (2.5)	3.8–4.9	6.2 (3.4)	6.0–6.3
Visibility (km)	14.2 (11.4)	11.8–16.7	17.4 (13.3)	14.5–20.4	18.6 (13.4)	18.0–19.2
Bar. pressure (kPa)	101.30 (0.30)	101.24–101.36	101.36 (0.33)	101.30–101.44	101.41 (0.36)	101.39–101.42
Cloud cover (%)	77 (36)	69–85	64 (44)	54–73	47 (46)	45–49
Moon illumination (%)	44.7 (35.3)	37.2–52.3	42.2 (33.1)	35.0–49.5	52.3 (34.9)	50.8–53.9

Data were collected between 1 August and 31 October during every year from 1971 to 2005.

tion, or simply maintaining control in flight. Alternatively, it could be that bats are more likely to migrate at lower altitudes or make more stops on nights with low wind speeds and are thus more likely to be encountered. Further research into the effect of wind speed on bat migration is needed. On SEFI, autumn winds tended to be more westerly during bat arrivals (Table 4). This trend may indicate that bats migrating along the coastline overcompensate for breezes originating over the ocean, or that bats migrating farther out to sea are blown in toward the coast.

Although the influence of moonlight on bat behavior and activity patterns is probably species-specific (Lang et al., 2006), researchers have observed a negative relationship between bat activity and amount of moonlight in tropical latitudes (Fenton et al., 1977; Morrison, 1978; Elangovan and Marimuthu, 2001; Fleming and Eby, 2003). However, such effects have not been clearly demonstrated among insectivorous bats at higher latitudes (Negraeff and Brigham, 1995; Kalcounis et al., 1999; Erickson and West, 2002; Karlsson et al., 2002). Several direct (e.g., predation) and indirect (e.g., prey availability) reasons for decreased levels of bat activity in bright moonlight have been proposed (Anthony et al., 1981; Erkert, 1982), but few targeted studies have been conducted. Thus, we can only speculate about whether hoary bats migrate less on moonlit nights. Despite the predominance of hoary bat arrivals and departures on SEFI during darker phases of the moon, migrants have occurred there during brighter phases of the moon, including nights when the moon was full. Moon illumination may influence the probability of bats detecting the island rather than the actual number of bats aloft on a given night, particularly when the role of cloud cover is considered.

Migratory passerine birds are most likely to arrive on SEFI following overcast nights (Pyle et al., 1993) and our results indicate that hoary bats arrive under similar conditions. These similarities between the migration behaviors of birds and bats on SEFI suggest that birds and bats are either migrating together or that they evolved similar migration strategies (*sensu* Alerstam, 2006). Migratory bats are occasionally found among groups of migratory birds killed at anthropogenic structures (Anonymous, 1961; Ganier, 1962; Elder and Hansen, 1967; Avery and Clement, 1972), but there is too little information in those reports to adequately address the question of whether they were traveling together. Van Gelder (1956) summarized the common factors under which migratory bats struck buildings or communication towers during autumn,

which included coincidence with bird collisions, the presence of fog or a low cloud ceiling, and the occurrence at structures that projected high above the natural skyline. Crawford and Baker, 1981 observed several bat kills during autumn at a communication tower in Florida and noted that about 58% of bat collisions occurred on nights with cloud cover greater than 40% and only about 21% occurred on nights with no clouds. However, there is limited evidence that bird and bat collisions at tall structures occur independently of each other (Terres, 1956; Crawford and Baker, 1981). Cloudy conditions during collision events may somehow alter the perception of both migrating birds and bats in a similar, yet independent, way. On SEFI, it has been hypothesized that migratory birds traveling above the clouds during the night are unable to keep track of the coastline and thus more likely wander out to sea and subsequently encounter the island when they descend through the clouds in the morning hours (Pyle et al., 1993). Is this scenario plausible for explaining bat arrivals to the island as well? The importance of cloud cover as a predictor in models of bat occurrence on SEFI suggests that it is. However, unlike birds, our observations of roosting bats from the island indicate that they arrive during the dark hours of the night. Taken together, the nighttime arrival of hoary bats on overcast nights during darker phases of the moon suggests that their occurrence on the island is influenced by conditions of nighttime visibility. We believe that this pattern is due to the increased probability of bats seeing and moving toward the artificial light on top of the island under such conditions. Laboratory experiments demonstrated that the insectivorous bat *Eptesicus fuscus* was capable of detecting visible light at intensities similar to those produced by bright stars (Childs and Buchler, 1981) and it is plausible that hoary bats can see the lighthouse on top of the island for several kilometers on dark nights. Several entries in the island journals describe individuals or groups of bats (as many as 30) circling the light during the nighttime hours, lending support to this supposition.

We found that low barometric pressure was also an important predictor of bat arrival to the island. Low barometric pressures often coincide with the passage of cold fronts that are exploited by migrating birds (Alerstam, 1990) and have been shown to influence the movement of birds past SEFI (Pyle et al., 1993). It is possible that the trend toward low barometric pressures with the arrival of hoary bats on the island is associated with migrating bats exploiting weather fronts and thus higher overall rates of passage through the area.

Additionally, low barometric pressure is often associated with westerly winds and high cloud cover, therefore creating a suite of conditions that might influence the movement of bats to the island.

4.2. Relevance to turbine kills

There are several reasons why the results of our study are relevant to the problem of bat fatalities at wind turbines: (1) they illustrate that arrivals of migrating tree bats at particular sites may be predictable events; (2) they provide conclusive evidence that tree bats migrate over offshore waters where future construction of wind turbines has been proposed; (3) they suggest that migrating hoary bats use vision to navigate during migration and are drawn toward visual stimuli; (4) they show a clear relationship between the timing of autumn migration by species of *Lasiurus* and collisions with anthropogenic structures; and (5) they point to a possible behavioral explanation for collisions with wind turbines.

Our results show a clear relationship between the occurrence of migratory tree bats on SEFI and certain weather and moonlight conditions during autumn. Although, we do not suggest that these data are adequate for predicting fatalities of hoary bats at wind turbines, we believe that they serve as a valuable model for attempting to quantify fatalities at wind energy facilities. Most wind energy facilities have automated systems for recording climate data and, although cloud and moonlight data are not regularly recorded, such information would be relatively easy to gather and incorporate. Weather data from wind turbine facilities would provide high quality information with which to model factors leading up to bat fatalities. As with our data from SEFI, it is important not to confuse occurrence (or fatalities) at a particular site with activity levels (i.e., “waves”) of migrating animals. We currently do not know if we are measuring the effects of weather on trends in overall migration activity or simply the conditions under which bats are more likely to be detected, or in the case of wind turbines, killed. For example, if hoary bats are visually attracted to turbines on nights when the turbines are more likely to be seen, the conditions leading to that level of visibility may have little to do with numbers of bats moving through the area. Regardless, building robust predictive models of environmental conditions preceding bat mortality events at wind facilities may be the most efficacious way of trying to improve understanding and avoid the problem in the coming years.

The regular occurrence of hoary bats on SEFI provides clear evidence that this species is capable of making long distance flights over water. Previous analysis of occurrence records also revealed evidence that hoary bats and other closely related species (e.g., *L. borealis*) occur more frequently along coastlines during autumn than in other seasons (Cryan, 2003). With the growing trend toward installation of wind power facilities in offshore waters, it is likely that turbines will have an impact on bats in marine habitats as well as on land.

4.2.1. Orientation during migration

Birds orient and navigate using a suite of sensory modes, including celestial cues, magnetic compasses, and visual

landmarks (Alerstam, 2006; Holland et al., 2006). Compared to birds our understanding of how bats orient and navigate during migration is limited (Griffin, 1970; Cryan and Diehl, in press). The high frequency sound used by echolocating bats attenuates quickly in air (Griffin, 1971), thus bats are not capable of perceiving their surroundings through echolocation at distances > about 30 m, and typically operate within a range of about 20 m (Neuweiler, 2000). Several lines of evidence suggest that bats navigate across large landscapes using vision, and that their eyes are probably most important for orientation during long-distance migration (>500 km; Griffin, 1970). Although circumstantial, evidence from our study suggests that a visual cue (the rotating beams of light coming from the lighthouse on top of SEFI on dark nights) influences the presence of migrating hoary bats at this site. This information is important in the context of wind turbines because it suggests that hoary bats move toward visible landscape features during autumn migration. The presence of aviation lighting on wind turbines has not been shown to influence bat fatalities (Arnett et al., in press). However, the greater intensity and motion of the light on SEFI likely provides a much larger visual image to migrating bats. The majority of bats killed at wind turbines thus far in North America are species that roost in trees throughout the year (Johnson, 2005; Kunz et al., in press). Kunz et al. (in press) postulated that bats might visually perceive turbines as roost trees and are thus attracted to them as places to rest, but there are currently too few data to adequately address this hypothesis. In a study of bird and bat fatalities at a wind turbine facility in Wyoming, Young et al. (2002) found 0.72 hoary bats killed ($n = 52$) per turbine in an array treated with paint that reflected 60% of ultraviolet (UV) light, but only 0.32 hoary bats per turbine ($n = 11$) at an array with paint that reflected only 10% of UV light. Unfortunately, there were differences in the number and coverage of turbines in the two groups and the array with highly reflective paint covered a broader geographic area. However, might these results hint at the possibility that migrating bats are attracted to tall landscape structures that are highly visible? Recent studies indicate that the eyes of bats may be particularly sensitive to UV light (Winter et al., 2003; J. Ryan, pers. comm.) and the perception of such a high-energy spectral component of moonlight may confer benefits to animals that visually orient in the dark. Fiedler (2004) did not find an effect of moonlight on bat fatalities at a wind energy facility in Tennessee, but did not include information on cloud cover in her models, and suggested that omission of those data might have obscured potential relationships. We recommend that measures of nighttime visibility (e.g., moon illumination, cloud cover, and visibility) be recorded in future studies of the environmental effects leading to bat fatalities at wind facilities. Moreover, researchers should consider that if hoary bats are visually attracted to turbines, site pre-assessment surveys that rely on detecting bats in the absence of turbines may provide misleading results.

4.2.2. Seasonal bias in fatalities

One of the most puzzling aspects of bat fatalities at wind turbines is that most kills occur during autumn migration, with fewer incidents happening during spring migration. The arrival of hoary bats on Southeast Farallon Island closely coin-

cides with the time of year when species of *Lasiurus* collided with wind turbines, buildings, communication towers, and were encountered in other situations indicative of long-distance migration (Fig. 2). Why do we observe such a seasonal bias? There are currently too few data to adequately answer this question. Species of *Lasiurus* have never been followed during migration, so it is unknown whether there are differences in flight behaviors between spring and autumn. Seasonal differences in weather patterns between migration seasons probably influence the preponderance of autumn incidents with species of *Lasiurus*. However, we believe that observations from SEFI offer another possible explanation. We hypothesize that the preponderance of migratory tree bats during autumn at wind turbines and other anthropogenic structures is the result of flocking behavior, and possibly mating activity. Hoary bats exhibit marked seasonal differences in behavior, which may help explain their occurrence in unusual situations during autumn. Female hoary bats, already pregnant, typically leave the wintering grounds about a month earlier than males during spring (Findley and Jones, 1964; Bogan, 1972; Cryan, 2003) and use a different thermoregulatory strategy during their journey north (Cryan and Wolf, 2003). In spring and summer months, adult male and female hoary bats tend to be geographically separated, sometimes by hundreds of kilometers (Findley and Jones, 1964; Cryan, 2003), and live mostly solitary lives during those seasons (Shump and Shump, 1982). During the late summer and early autumn, the previously disparate distributions of male and female hoary bats begin to overlap as the bats begin returning to wintering grounds (Cryan, 2003).

Species of bats that are solitary during the summer often form groups to migrate (Fleming and Eby, 2003). Observations of flocking hoary bats were made during late summer and early autumn (Merriam, 1884; Hall, 1946) and similar observations of concentrated groups of *L. borealis* occurred during those periods as well (Mearns, 1898; Seton, 1909; Baker and Ward, 1967; Mumford, 1973; LaVal and LaVal, 1979; Saugey et al., 1989). Several benefits of flocking by bats during migration were proposed by Fleming and Eby (2003), one of which is the increased probability of finding mates. We believe that this is a plausible hypothesis for explaining autumn flocking behavior by hoary bats and possibly their occurrence at wind turbines during autumn. In both historical accounts of flocking hoary bats, the observers noted behavior suggestive of mating activity (e.g., males fighting and “rushing wildly about”; Merriam, 1884; Hall, 1946). Physiological and anatomical information (e.g., peak of spermiogenesis in males and presence of sperm in reproductive tracts of females) indicates that copulation in hoary bats begins during autumn, and that both males and females are sexually mature by the end of their first summer (Druecker, 1972). We are not aware of any previously published observations of copulation by hoary bats, but on two occasions this species was observed copulating in the trees on SEFI during the day (island journal entries 8/26/87 and 8/31/03). Furthermore, most observations of mating by eastern red bats (93%; $n = 14$) were made during the period of late summer and autumn (Allen, 1869; Murphy and Nichols, 1913; Dearborn, 1946; Stuewer, 1948; Glass, 1966; Saugey et al., 1989, 1998; A. Hicks, pers. comm., S. McConnell, pers. comm.). Curiously, in nearly every account, observers

of copulation by eastern red bats noted that coupling occurred in flight. The synchronous timing of flocking and possible mating behavior by species of *Lasiurus* with observed fatalities at tall anthropogenic structures may not be coincidental. How do such flocks and mating groups form, particularly in a species such as the hoary bat that is solitary during summer and in which the sexes segregate by hundreds of kilometers across the continent? We hypothesize that migrating hoary bats, and perhaps other species of tree bats, meet at rendezvous points along their migration routes and that, barring memory of such sites, simply orient toward and loiter around the tallest structures they perceive while passing through a landscape. Perhaps the high fatalities experienced by migratory tree bats stem from behaviors that evolved around aggregating at tall and highly-visible landscape structures, which until recent times only consisted of the crowns of trees.

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