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# CAUSES OF BAT FATALITIES AT WIND TURBINES: HYPOTHESES AND PREDICTIONS

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Thousands of industrial-scale wind turbines are being built across the world each year to meet the growing demand for sustainable energy. Bats of certain species are dying at wind turbines in unprecedented numbers. Species of bats consistently affected by turbines tend to be those that rely on trees as roosts and most migrate long distances. Although considerable progress has been made in recent years toward better understanding the problem, the causes of bat fatalities at turbines remain unclear. In this synthesis, we review hypothesized causes of bat fatalities at turbines. Hypotheses of cause fall into 2 general categories—proximate and ultimate. Proximate causes explain the direct means by which bats die at turbines and include collision with towers and rotating blades, and barotrauma. Ultimate causes explain why bats come close to turbines and include 3 general types: random collisions, coincidental collisions, and collisions that result from attraction of bats to turbines. The random collision hypothesis posits that interactions between bats and turbines are random events and that fatalities are representative of the bats present at a site. Coincidental hypotheses posit that certain aspects of bat distribution or behavior put them at risk of collision and include aggregation during migration and seasonal increases in flight activity associated with feeding or mating. A surprising number of attraction hypotheses suggest that bats might be attracted to turbines out of curiosity, misperception, or as potential feeding, roosting, flocking, and mating opportunities. Identifying, prioritizing, and testing hypothesized causes of bat collisions with wind turbines are vital steps toward developing practical solutions to the problem.

Key words: attraction, bats, causes, collision, migration, mitigation, mortality, wind energy

Industrial wind energy production is increasing throughout the world to meet growing demand for electricity generated without carbon emission (United States Energy Information Administration, www.eia.doe.gov, accessed 15 May 2009). Advances in wind turbine technology and the cost effectiveness of wind energy have led to a tremendous increase in the number of wind turbines deployed throughout the world during the past decade. As of May 2009, global industrial-scale development has resulted in a total installed energy capacity of about 121,000 megawatts (MW—World Wind Energy Association, www.wwindea.org, accessed 15 May 2009), with the average turbine now contributing between 1.5 and 2.5 MW. Typical wind turbines currently have tower heights of 60–100 m, blade lengths of 30–50 m, and maximum blade tip speeds of about 240–300 km/h. In the coming decades, the demand for electrical energy is expected to increase dramatically, and turbines will continue to be built in large numbers in windy areas around the world.

Bat fatalities at wind turbines were an unanticipated and unprecedented phenomenon. Beginning in the late 1990s, biologists began finding bat carcasses beneath turbines while studying bird mortality at wind energy sites (Johnson et al. 2003). This trend continued, and during 2003 high-profile events involving bats and wind turbines in the Appalachian Mountains of North America led to growing concern over the problem (Kunz et al. 2007b). Since then, multiple studies have consistently found bat fatalities at wind energy sites in North America, and unprecedented fatality rates of certain species at some facilities (Arnett et al. 2008; Johnson 2005). The cumulative impacts of such mortality on affected species of bats could have long-term population effects (Kunz et al. 2007b). Before this recent problem of bat fatalities at wind turbines, collision fatalities of bats at other tall anthropogenic structures were rarely reported, and the number of carcasses recovered after fatality events was consistently low (Anonymous 1961; Avery and Clement 1972; Crawford and Baker 1981; Elder and Hansen 1967; Ganier 1962; Overing 1936; Saunders 1930; Terres 1956; Timm 1989; Van Gelder 1956;

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Zinn and Baker 1979). Unlike the situation with birds and their collisions with tall structures (Avery et al. 1980; Kuvlesky et al. 2007), there is no evidence of human-induced mortality to any of the affected bat species that is of similar magnitude to mortality at wind turbines. Mortality of bats at wind turbines thus warrants additional study and explanation in an effort to determine the biological consequences and develop mitigation measures.

Several consistent patterns have emerged from the fatality data on bats at wind turbines. The species consistently affected, in terms of both overall numbers and geographic distribution, are those that rely heavily on trees as natural roosts throughout the year—tree bats (Griffin 1970). In North America, these species include hoary bats (*Lasiurus cinereus*), eastern red bats (*L. borealis*), and silver-haired bats (*Lasionycteris noctivagans*). A 4th North American species, the tricolored bat (*Perimyotis subflavus*), also might be characterized as a tree bat (Findley 1954; Veilleux et al. 2004), but its seasonal whereabouts during much of the year remain obscure (Barbour and Davis 1969; Fujita and Kunz 1984). In North America, tree bats comprise about 75% of documented fatalities to date, and hoary bats make up about half of all fatalities (Arnett et al. 2008). European species of bats most affected by wind turbines include the noctule bat (*Nyctalus noctula*), Leisler's bat (*N. leisleri*), Nathusius's pipistrelle (*Pipistrellus nathusii*), common pipistrelle (*P. pipistrellus*), soprano pipistrelle (*P. pygmaeus*), and particolored bat (*Vespertilio murinus*), all of which rely on trees as roosts, but also sometimes use human-made structures (Bach and Rahmel 2004; Dürr and Bach 2004; Rodrigues et al. 2008).

Another consistent characteristic of species of bats most affected by turbines is their propensity for long-distance, latitudinal migration (Cryan 2003; Hutterer et al. 2005; Steffens et al. 2007). However, 1 North American species affected by turbines currently is not considered a migrant (*P. subflavus*—Fujita and Kunz 1984, but see Jones and Pagels 1968; LaVal and LaVal 1988; Reynolds 2006), and certain consistently affected European species are not thought to migrate extensively in areas where they are often found beneath turbines (e.g., *P. pipistrellus* in Germany—Dürr and Bach 2004; Hutterer et al. 2005; Steffens et al. 2007). Another consistent pattern at wind turbines in both North America and Europe is that most fatalities occur during late summer through autumn each year, and tend to peak during the period that coincides with autumn migration (Arnett et al. 2008; Bach and Rahmel 2004; Cryan and Brown 2007; Dürr and Bach 2004; Johnson 2005). The latter trend has led many researchers to believe that migration plays a key role in the particular susceptibility of bats to wind turbines.

Considerable progress has been made during recent years in summarizing patterns of bat fatalities at wind turbines, estimating fatality rates, studying behavior of bats around turbines, describing physical condition of fatalities, and discussing the potential impacts of turbines on affected populations of bats. However, there have been fewer efforts to unambiguously establish the underlying causes of bat fatalities at wind turbines, although numerous hypotheses have been advanced (e.g., Arnett et al. 2008; Johnson 2005; Kunz et al. 2007b). In this synthesis, we review hypothesized causes of bat fatalities at wind turbines, make predictions regarding the evidence necessary to support the various hypotheses, and summarize existing information relevant to each prediction. We see the articulation, organization, and prioritization of such hypotheses and predictions as a necessary step in determining the underlying causes of bat mortality at wind turbines, and in stimulating appropriate research, including both observational and experimental studies.

We base our review on hypotheses of cause published in peer-reviewed scientific literature, but also include information from select unpublished sources. We consolidate and rename hypotheses to better characterize themes, as well as to highlight trends and major differences among explanations. We divide causal explanations for mortality into 2 broad categories—proximate and ultimate causes. Hypotheses of proximate cause are those that address the factors directly responsible for the deaths of individual bats. For example, the proximate cause of the bat's death at the wind turbine may be that its skull was crushed when it was hit by a moving blade. Hypotheses of ultimate cause are those that address why bats are in the vicinity of turbines in the 1st place. For example, the ultimate cause of the bat's death may be that it perceived the turbine as a potential place to roost. For most hypotheses, we propose 1 or more predictions intended to serve as examples of the type of supporting evidence needed. We assess the status of each prediction and provide relevant citation, again based on our review of published and unpublished papers. Status of predictions is based on the limited available information and our assessments should be considered preliminary in almost every case. Evidence pertinent to most predictions is weak, at best, and additional study is needed. We also believe that, at least for the present, hypotheses and predictions should be applied at the species level and that it is likely that causal explanations will vary among species. For example, the susceptibility of little brown bats (*Myotis lucifugus*) and hoary bats to wind turbines may be very different and driven by completely different causes, as may differences among tree bats. We encourage readers to take these hypotheses and predictions as starting points for consideration rather than a comprehensive list of possibilities.

## HYPOTHESES, PREDICTIONS, AND DATA

*Proximate causes of bat fatalities.*—We identified 3 hypotheses for explaining proximate causes of bat fatalities at wind turbines (Table 1). These involve bats colliding with turbine towers, colliding with moving blades, or suffering internal injuries (barotrauma) after being exposed to rapid pressure changes near the trailing edges and tips of moving blades (Baerwald et al. 2008). While flying at night, birds occasionally collide with tall structures such as buildings and communication towers (Avery et al. 1980; Gehring et al. 2009), and the same may be true for the towers of wind

**TABLE 1.**—Proposed hypotheses for explaining the proximate and ultimate causes of bat fatalities at wind turbines. Here we define proximate causes as those that address the mechanistic factors directly responsible for the deaths of individual bats. Ultimate causes are those that address why bats are in the vicinity of turbines before death. Hypotheses are not mutually exclusive and are intended to be applied at the species level. Italicized hypotheses of ultimate cause are those we consider 1st degree (Fig. 1), the disproval of which would eliminate associated 2nd-degree hypotheses (i.e., those not italicized; Fig. 1).

| | Hypotheses | Predictions |
|---|---|---|
| Proximate causes | Collision with turbine towers | Numerous fatalities at nonmoving turbines |
| | | Numerous fatalities at other tall structures |
| | Collision with moving blades | Traumatic external injuries |
| | | No fatalities at nonmoving turbines |
| | Barotrauma (decompression) near moving blades | Internal injuries |
| Ultimate causes | | |
| Random | *Fatalities proportional to bats present* | Fatalities reflect indices of activity or abundance |
| | | Demographics of fatalities reflective of the population present |
| Coincidental | *Susceptible while migrating* | Most fatalities involve migrants rather than residents |
| | | Nonmigratory species or populations least affected |
| | | Fatalities peak during migration periods |
| | | Fatalities peak earlier at higher latitudes |
| | Migrants clump in time and space | Distribution of bats more clumped during migration |
| | | More migrating bats occur in windy areas |
| | | More fatalities with passage of storm fronts |
| | | Most fatalities during migration periods |
| | Migrating bats fly higher than nonmigrants | More migrants at higher altitudes |
| | | More fatalities at taller turbines |
| | Migrating bats less likely to echolocate | No echolocation detected at nacelle height |
| | | More bats present than echolocation passes detected |
| | | Atypical echolocation calls (e.g., startle) |
| | *Susceptible when not migrating* | Most fatalities involve residents rather than migrants |
| | Greater feeding activity results in greater mortality | Coincidental seasonal increases in feeding buzzes of affected bats |
| | Greater mating activity results in greater mortality | Coincidental seasonal increases in captures of mating bats |
| | | Adult bias to fatalities |
| | Lack of flight experience results in greater mortality | More young, inexperienced bats among fatalities |
| | *Prey distribution influences fatality* | Fatality rate correlated with regional or altitudinal prey abundance |
| Attraction | *General attraction to turbines* | Bats more likely to fly toward than past turbines |
| | Attracted to lights | More fatalities at turbines with aviation lights |
| | Attracted to sound of moving blades or generator | More activity at moving than at nonmoving blades |
| | | Playback of sound attracts bats |
| | | Bats respond more to sound on low-wind nights |
| | | Turbines emitting particular noises kill more bats |
| | Attracted to blade motion | More activity at moving than at nonmoving blades |
| | | Devices simulating blade movement will attract bats |
| | Attracted to insect aggregations | Feeding buzzes more common around turbines |
| | | Insect abundance greater around turbines |
| | | Consistent patterns of insect activity around turbines |
| | | Dead bats have full stomachs |
| | | Consistent prey in bat stomachs |
| | | Dead bats have insects in mouth |
| | Attracted to modified landscape features | More fatalities near newly created edge habitats, roads, or wetlands |
| | Attracted to turbines as roosts | Highly visible turbines kill more bats |
| | | More fatalities on moonlit nights |
| | | More activity at tallest, treelike structures |
| | | Low activity of species that do not roost in trees |
| | | Most fatalities occur as nightly activity ends |
| | | Equal activity at moving and nonmoving turbines |
| | Attracted to turbines as mating or gathering sites | Most activity at tallest trees or treelike structures in landscape |
| | | Mating activity at moving and nonmoving turbines |
| | | Male territorial behavior at moving and nonmoving turbines |
| | | Group formation at moving and nonmoving turbines |
| | | Sperm in males and females |
| | | Male bias to fatalities that disappears over time |
| | | Social calls detected at nacelle height |
| | | More social interaction at turbines in low winds |
| | | Equal activity at moving and nonmoving turbines |

turbines (Kuvlesky et al. 2007). If bats also collide with turbine towers, this could explain at least some fatalities at wind turbines. If this were the case, then bat fatalities should occur when turbines are nonoperational, and at other tall structures such as the meteorological towers often associated with wind turbines. As noted above, bat fatalities are rare at stationary structures, and at wind energy facilities bat fatalities have not been reported at nonoperational turbines or meteorological towers (Arnett et al. 2008). In addition, reduction in turbine operation is associated with a reduction in bat fatalities (Baerwald et al. 2009; E. B. Arnett, Bat Conservation International, pers. comm.). There is little evidence that bats consistently collide with nonmoving turbine blades or towers.

If bat fatalities occur due to strikes from moving turbine blades, then carcasses should show traumatic injuries. Indeed, many carcasses have such injuries, including broken or amputated wings, crushed skulls, broken vertebral columns, and severe lacerations (e.g., Baerwald et al. 2008; Johnson et al. 2003). In addition, thermal imaging devices have been used to document bats being struck by moving turbine blades (Horn et al. 2008). Despite clear evidence that some bats are hit by moving blades, other bats found dead at wind turbines have no external injuries (Baerwald et al. 2008). These carcasses, as well as many of those with external trauma, have internal injuries to the thoracic and abdominal cavities that are consistent with rapid decompression, or barotrauma (Baerwald et al. 2008; Dürr and Bach 2004; von Hensen 2004). Like other airfoils, moving wind turbine blades have areas of high and low pressure around them. In particular, a relatively small vortex at the tip of each blade involves a drop in atmospheric pressure sufficient to cause internal injuries when the air in the lungs of bats flying through the vortex expands rapidly. Small blood vessels in the lungs are damaged causing bleeding into the thoracic cavity (Baerwald et al. 2008). This suggests that even if bats can avoid direct contact with moving turbine blades, they may suffer sufficient noncontact injuries to cause death.

*Ultimate causes of bat fatalities.*—Hypotheses of ultimate cause are numerous but tend to fall into 3 general categories (Table 1; see also Horn et al. 2008; Kunz et al. 2007b). These categories are random collisions, coincidental collisions, and collisions resulting from attraction of bats to turbines. We define random collisions as those that occur due to chance alone. This hypothesis involves no assumptions of circumstance or attraction. Under the random collision hypothesis, all individuals of a particular species are equally vulnerable when occurring near turbines, regardless of sex, age, reproductive condition, or time of year; turbines randomly sample bats flying in the airspace around them. Hypotheses of coincidental collision involve bats being victims of unfortunate behavioral circumstances—certain aspects of their behavior put them at greater risk of colliding with turbines. Hypotheses of attraction are just that; some attractor or combination of attractors draws bats to wind turbines. Although a few of the coincidental hypotheses involve a regional spatial scale (e.g., regional differences in distribution of migrants or prey), all others are intended to be applied at the scale of individual turbines. These various hypotheses need not be mutually exclusive. For example, specific behaviors may increase the chances of bats being near turbine facilities during particular times of year (coincidental), but then attractors could draw certain individuals closer or, alternatively, bats present could randomly collide with turbine blades.

Bat fatalities at wind turbines may be the result of random collisions. It is possible that the spatial, temporal, and demographic variation observed in fatality rates of bats at different wind energy sites (Arnett et al. 2008; Baerwald and Barclay 2009) merely reflects the relative abundance of bats in the vicinity of wind turbines. If this is true, then the composition of fatalities in terms of timing, sex, age, and reproductive condition should match the composition of bats in the area (Table 1). Such measures are difficult to obtain for bats (O'Shea and Bogan 2003), but a distinct lack of correspondence between regional species composition and fatalities has been observed at several sites; resident species tend to be killed at wind turbines less frequently than migratory species, even in areas where the resident species are common throughout the summer (Arnett et al. 2008; Johnson et al. 2003; Kunz et al. 2007b). Most fatalities usually occur during the late summer and autumn, although activity levels of species not regularly killed by turbines can be high throughout the summer (Arnett et al. 2008; Johnson et al. 2003). Examination of some fatality data also suggests biases between sexes, with adult males dominating samples for several affected species in North America (Arnett et al. 2008). Such trends suggest nonrandom interactions between bats and wind turbines.

Several hypotheses of ultimate cause involve collisions occurring under coincidental circumstances. Bat fatalities observed at wind turbines thus far have involved many species that migrate long distances ($>$250 km), and because most fatalities occur during a period that coincides with their autumn movements, migration has been invoked as a primary explanation for the particular susceptibility of bats to wind turbines. Hypotheses that involve the coincidental susceptibility of migrating bats seem well justified; however, we caution that even the most basic among them, such as that most fatalities involve individuals that are migrating rather than those that are resident in the area of the turbines, need to be tested and not taken for granted. Stable isotope analysis and other techniques for assessing the geographical origins of bats killed at wind turbines may prove useful in testing the migrant hypothesis (Hobson and Wassenaar 2008). Studying the phenology of fatalities at continental scales also may help us better understand the role of migration (Cryan and Diehl 2009). As detailed below and in Table 1, there are several possible behaviors associated with migration that could result in fatalities, but that do not necessarily require the act of migration. Certain risky behaviors might have evolved with a migratory lifestyle, yet not be dependent on migration. Is it that migrating bats are particularly susceptible, or simply that other aspects of these species' behavior change in autumn (e.g., mating or feeding) and make them susceptible, whether they are migrating or not?

Some of the coincidental migration hypotheses pertain to a regional spatial scale and involve migrants being clustered near turbines in time and space. Foremost among predictions here is that bats concentrate in certain regions during migration, such as in ''corridors'' or at ''stopover'' habitats, or in areas where topography or prevailing winds, or both, force them into close proximity as they travel. Such landscape features might include windy places such as mountain ridges, passes, coastal areas, and river valleys (Cryan and Diehl 2009; Furmankiewicz and Kucharska 2009). Little is known about the temporal and spatial distribution or density of bats during migration, particularly the species most affected by wind turbines. In Alberta, Canada, autumn activity and fatality of migrating species is concentrated near the foothills of the Rocky Mountains, suggesting that migrating bats follow particular routes on their way south (Baerwald and Barclay 2009).

Certain weather conditions may further influence migrants to cluster in time. Fatality rates of bats at turbines often increase with the passage of storm fronts (Arnett et al. 2008). These observations, combined with the fact that most fatalities occur during a few weeks in late summer and autumn, suggest that migrating bats exploit certain weather conditions during late summer and autumn that put them at risk. Very little is known about the effects of weather on the behavior of migrating bats (Cryan and Brown 2007) and this seems like a rich area for cooperation between biologists and atmospheric scientists interested in forming collaborations within the emerging field of aeroecology (Kunz et al. 2008).

Other coincidental explanations for the role of migration in fatalities apply at the spatial scale of individual turbines and postulate that migrating bats behave in distinctive ways that put them at greater risk. These hypotheses include migrants flying higher above the ground than other bats and high-flying migrants being less likely to echolocate and detect spinning turbine blades (Table 1; Kunz et al. 2007b). Predictions associated with these explanations include more fatalities at taller turbines, detection of more migrants high above the ground, and no echolocation detected around the blades of turbines. Fatality rates of bats are greater at taller turbines in North America (Barclay et al. 2007), and studies have revealed greater echolocation activity of migratory species higher above the ground compared with other species (Baerwald and Barclay 2009; E. B. Arnett, in litt.). Such activity may be indicative of high-flying migrants, but also could reflect species differences in flight and foraging style (e.g., Norberg 1994). Certain atmospheric conditions, such as temperature inversions or overcast skies, also may cause high-flying migrants to drop to lower altitudes where they are more likely to encounter turbines (Kunz et al. 2007b). If flight altitude alone is a primary cause of bat fatalities, detection of species killed by turbines should be greater at the height of turbine blades during the late summer and autumn, but not during other seasons when fatalities are less frequent. Few data exist for assessing whether migrating bats are less likely to echolocate, but it may be possible to test this hypothesis by comparing the number of bats detected with thermal imaging devices to the number of echolocation passes picked up by echolocation detectors (Horn et al. 2008; Hristov et al. 2008). It is clear that at least some high-flying migrants echolocate, because they are regularly detected well above the ground (e.g., Baerwald and Barclay 2009). However, some recordings involve abrupt sequences of calls suggestive of nonecholocating individuals being startled by the presence of turbine blades and echolocating in response (J. Reimer, University of Calgary, pers. comm.).

Establishing migration as a coincidental causal explanation for bat deaths at turbines will require explaining the apparent lack of fatalities associated with spring migration, or the high numbers of fatalities of species or subpopulations that are not known to migrate (Arnett et al. 2008; Dürr and Bach 2004). Almost nothing is known about the specific behaviors of bats during migration (Cryan and Diehl 2009). If migration is a primary driver of fatalities at turbines, it is possible that behaviors of bats during migration differ enough between spring and autumn to explain the autumnal bias to fatalities, but we do not yet know enough to assess that possibility. Investigating differences in general migration behavior of bats between spring and autumn may be a useful way of narrowing down the possible causes of bat fatalities at turbines.

Given that bird migration has been studied for much longer than bat migration, we suggest that much may be learned from data regarding birds (Larkin 2006). For example, many migratory passerine birds fly at night (Alerstam 1990), yet they appear less affected by wind turbines than bats (Barclay et al. 2007 and references therein). The timing of bird fatalities at turbines also frequently differs from that of bats, and bird fatalities are not as consistent in terms of their seasonality (Kuvlesky et al. 2007). Does this suggest that behaviors, other than simply migrating, differ between bats and birds and result in different susceptibility? There is a wealth of information in the scientific literature regarding the migratory behavior of birds (e.g., Alerstam 1990; Berthold et al. 2003) and these methods need to be incorporated into studies of bat migration (McGuire and Guglielmo 2009).

Bats may be vulnerable to wind turbines for coincidental reasons that are not associated with migration. The fact that most fatalities involve species that migrate may not be due to migratory behavior, but to some other behavior common to these species when they are sedentary. Hypotheses in this category include the possibilities that seasonal changes in the behavior of bats lead to coincidental increases in their susceptibility to turbines.

Energy requirements of bats change throughout the year, and seasonal increases in energy demand associated with producing young, mating, or preparing for hibernation could lead to seasonal increases in foraging time or feeding areas (Kurta et al. 1989; Lacki et al. 2007; Speakman and Thomas 2003). Late-summer increases in fatalities at turbines might be attributable to an increase in foraging activity to allow bats to meet the challenges of overwintering, migrating, or mating. If this was the case, coincidental seasonal increases in echolocation calls associated with feeding (''buzzes''—Griffin 1958) should be detectable around turbines during periods of high fatality. Such data likely exist but have not been reported in this context. The potential influence of seasonal changes in foraging dispersal and timing on susceptibility of bats to turbines also could be investigated by radiotracking affected species across seasons.

Species of temperate-zone insectivorous bats usually begin mating in autumn (Racey and Entwistle 2000). Increased flight activity associated with finding mates also could lead to coincidental increases in the probability of bats coming into contact with turbines. Many of the species affected by wind turbines engage in mating activity during the same period when their carcasses are found in the greatest numbers beneath turbines (Cryan 2008). This synchronicity between mating activity and fatalities could reflect a cause that is independent of migration or attraction. Bats in search of mates may simply fly in places where they do not regularly fly at other times of year. A prediction under this hypothesis would be an increase in captures or other observations of reproductively active bats, with a bias toward adults, coinciding with fatality peaks at wind turbines. Existing data for assessing this hypothesis are few and anecdotal (Cryan 2008). During an 8-year study of bats in the Ouachita Mountains of Arkansas, R. Perry (Southern Research Station, United States Forest Service, pers. comm.) observed large increases in capture rates of male *L. borealis* each year in August and September, and regularly observed pursuit, aggression, and copulation behavior of eastern red bats around nets that suggested that mating activity led to greater susceptibility of capture. Although long-term sperm storage in male and female bats makes the precise timing of mating events difficult to discern based on anatomy alone, quantifying levels of circulating hormones associated with male libido (e.g., androgens) may be a useful technique (Gustafson 1979; Martin and Bernard 2000). Seasonal changes in nighttime flight activity of demographic groups and species most affected by turbines also could be assessed using radiotelemetry.

Another coincidental hypothesis is that the late-summer and autumn peak in fatalities is attributable to introduction of inexperienced young into bat populations, and that juveniles lack the flight skills to avoid turbine blades. However, existing data on the age composition of fatalities do not support this hypothesis (Arnett et al. 2008; Baerwald 2008).

Regardless of whether bats are migrating or sedentary, differences in distribution of their insect prey also may be a coincidental cause of fatalities (Kunz et al. 2007b). For example, if insects upon which bats feed are more likely to occur in regions, habitats, or air layers where turbines are built, the bats that exploit them may be at greater risk. A prediction associated with this hypothesis is that fatality rate would be correlated with regional, habitat-specific, or altitudinal prey abundance—a possibility that remains untested.

There are a remarkably large number of plausible hypotheses involving attraction of bats to wind turbines (Table 1). These hypotheses generally involve bats being attracted to turbines out of curiosity or misperception, or as potential feeding, roosting, flocking, and mating opportunities. Thus far, the only attraction hypothesis with sufficient evidence to reject may be the attraction of bats to aviation warning lights on top of turbines. Numerous studies have found no difference in the number of fatalities recovered under turbines lit and unlit in this way (Arnett et al. 2008; Baerwald 2008). Although other studies indicate that bats are able to perceive and respond to cues from artificial lights (Childs and Buchler 1981; Cryan and Brown 2007), we are not aware of any evidence to suggest that lights on tall structures increase the probability of bat collisions, as is known to occur with birds at communication towers and buildings (Avery et al. 1980; Gehring et al. 2009). However, it is still plausible that lights illuminating large parts of turbine towers and blades may influence fatalities in other ways, as discussed below.

Bats may be attracted to the sights, sounds, or movements of wind turbines. Accounts of bats possibly being attracted to the ‘‘swishing sound’’ of sticks waved through the air (Barbour and Davis 1969:153), or unknown cues at roosts previously used by congeners (Constantine 1958; Downes 1964), as well as thermal images of bats apparently chasing moving turbine blades (Horn et al. 2008), highlight the plausibility of such attraction. Predictions associated with these hypotheses include more activity around moving than nonmoving blades, variation in fatality rate associated with variation in emission of sounds by turbines, and attraction of bats to playback of turbine sounds or devices that simulate blade movement. To our knowledge, these predictions and hypotheses remain untested, although they seem especially well suited to experimental studies.

It is possible that hunger brings tree bats into close proximity of turbines because they are attracted to insects that gather around turbines. The tallest structures in a landscape are used as gathering points during the daytime by some flying insects (‘‘hilltopping’’ behavior reviewed by Thornhill and Alcock [1983]) and insects may be attracted to aviation lights or the warmth or color of turbines, in turn drawing in hungry bats (Kunz et al. 2007b). Aggregations of insects around turbines could serve as easily learned and consistent food sources for bats, particularly for hungry migrants traveling through unfamiliar areas. Migrating bats were observed feeding on insects around offshore turbines in Scandinavia (Ahlén et al. 2009). Predictions associated with the feeding-attraction hypothesis include detection of more feeding buzzes around turbines than elsewhere, consistent presence and activity of insects around turbines, and consistent presence of insects that occur around turbines in the gastrointestinal tracts of bats killed at turbines. In Alberta, Canada, bats killed at turbines had full stomachs, indicating that they had fed the night they were killed, but many of the insects detected in the stomachs, such as aquatic hemipterans, were unlikely to have come from around turbines (J. Reimer, pers. comm.). In addition, few feeding buzzes were recorded at blade height. There is currently no evidence that nocturnal insects upon which bats feed engage in hilltopping behavior, and the benefits to the insects of such behavior in the dark are not obvious. Considering the many different regions and types of habitats in which bat fatalities at turbines have been found, a feeding explanation would require evidence that some type of prey consistently occurs around turbines, that affected bats regularly feed on that type of prey, and that such a relationship occurs across a wide variety of locations and situations, especially during autumn.

Land cleared during the construction of access roads, turbine foundations, and power transmission lines might attract bats by mimicking natural linear landscape features, such as natural forest edges, along which foraging and commuting bats may regularly travel (Kunz et al. 2007b; Verboom and Huitema 1997). A prediction associated with the linear-element hypothesis is that more fatalities should occur at turbines nearer forest edges, newly created clearings, and other linear landscape features. However, published studies in North America reveal a surprising lack of correlation between local landscape features and fatalities at wind energy sites (Arnett et al. 2008). Also, relatively high fatality rates of bats at sites in open, treeless, scarcely modified landscapes (e.g., Alberta, Canada—Baerwald 2008) suggest that this explanation may be of limited application at best.

Hypotheses involving attraction of bats to turbines as roosts seem plausible considering that the species of bats killed most often by wind turbines tend to rely on trees as their primary natural roost structures. Bats visually orient across landscapes (Griffin 1970) and the silhouettes of turbines might attract them from considerable distances (>1 km). If this is the case, visibility of turbines to bats should influence fatality rates. However, such differences likely involve visibility of large areas of the turbine structure, rather than small parts of it, such as aviation lights. Predictions under this hypothesis include equal activity at moving and nonmoving turbines, more activity and fatalities at higher-visibility turbines, higher fatality rates on moonlit nights, higher fatality rates at experimentally illuminated turbines, and activity around turbines peaking at dawn when bats are likely to investigate potential daytime roosts. Contrary to the last prediction, bat activity at turbines in southern Alberta occurred throughout the night with no peak near dawn (Baerwald 2008). However, Cryan and Brown (2007) presented evidence that responses of migrating hoary bats to visible landscape cues (a lighthouse) varied with cloud cover and moonlight. Baerwald (2008) found that moonlight had an effect on fatality rates of bats at turbines, with higher fatality rates on moonlit nights. These results suggest a connection between the visibility of turbine structures and bat fatalities—a possibility that warrants additional research.

Many species of bats favor taller trees as roosts (Kalcounis-Rüppell et al. 2005) and fatalities at turbines appear to be correlated with turbine height (Barclay et al. 2007). Turbines far exceed the height of most trees and are approaching the heights of the tallest trees on Earth (about 112 m). If bats simply investigate the tallest trees they encounter for possible roosting opportunities, then such behavior should be observable at the tallest trees and other tall landscape structures (e.g., cellular phone towers and water towers), as well as at experimental structures that can be manipulated to assess relationships between structural height, visibility, and bat activity (Cryan 2008; Cryan and Brown 2007). To our knowledge, the tallest-tree hypothesis has not been tested.

Bats also might use the tallest trees in a landscape as gathering points during the breeding season and visually mistake turbines for the tallest trees, particularly during or before migration (Cryan 2008; Cryan and Brown 2007). If this hypothesis is correct, group formation and mating activity should be observable at nonmoving turbines and surrogate structures, and evidence of reproductive activity should be apparent in carcasses. Predictions under this hypothesis include equal activity at moving and nonmoving turbines, most activity occurring at the tallest trees or treelike structures in the landscape, mating activity (e.g., aerial copulation or male territorial behavior) or group formation occurring at nonmoving turbines, more social interaction at turbines in low winds, sperm in the reproductive tracts of both males and females or hormone levels indicative of active mating, social calls detected at the heights of turbine blades, and adult male bias to fatalities (associated with the early establishment of leks and mating territories) that disappears as autumn progresses. No studies directly assessing the mating hypothesis have been published, but several of the predictions may be testable using existing carcasses found at turbines, by analyzing bat calls recorded around turbines and other tall landscape structures, or by meta-analysis of demographic and temporal patterns in existing fatality data (Table 1). In a study conducted in Canada, no social calls were recorded from hoary or silver-haired bats flying at rotor height around turbines where fatalities were subsequently recovered (J. Reimer, pers. comm.). Calls associated with mating have not been characterized for North American species affected by wind turbines, although the prevalence and distinctness of mating calls among European species with similar life-history characteristics (Pfalzer and Kusch 2003) lead us to believe that North American species likely produce such calls. Although evidence suggests that some juvenile males of genera affected by turbines are reproductively active in their 1st autumn (e.g., *Lasiurus*, *Lasionycteris*, and *Nyctalus*—Druecker 1972; Myers 1977; Racey and Entwistle 2000), support for the mating hypothesis also must include establishing that juvenile bats killed by turbines are involved in mating activities.

## PRIORITIZING HYPOTHESES FOR FUTURE RESEARCH

Identifying, prioritizing, and testing the hypothesized causes of bat fatalities at wind turbines are vital steps toward developing practical solutions to the problem. There are major implications if the ultimate causes of turbine collisions are random, coincidental, or the result of attraction. Foremost, if there is an attractant, it might be possible to either eliminate the attraction or exploit it to draw bats away from wind energy facilities. Despite a few years of study into the problem of bat fatalities at wind turbines, it is surprising that so few of the

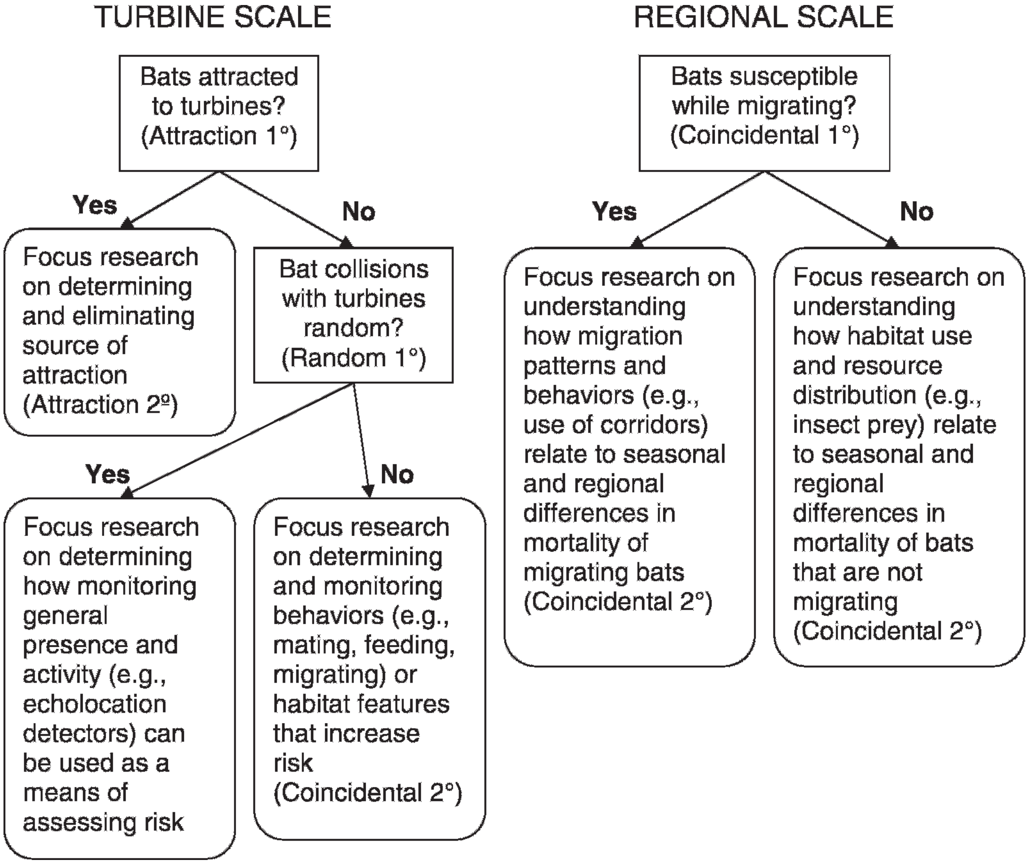

Fig. 1.—Decision trees suggested for testing hypothesized causes of bat fatalities at wind turbines and for focusing on areas of research. Decisions trees address questions at the spatial scales of individual turbines and larger regions. Each rectangle represents a disprovable 1st-degree (1°) hypothesis, with bifurcating outcomes to the next 1st-degree hypothesis, group of 2nd-degree (2°) hypotheses, or recommended focus areas for research. Detailed hypotheses are categorized and listed in Table 1.

attraction hypotheses have been tested. Because the conservation implications of bat attraction to wind turbines are by far the most serious, we suggest that testing the general hypothesis of attraction be a top priority (Fig. 1). Existing methods for following the flight paths of individual bats, such as radar and radiotelemetry (Cryan and Diehl 2009), could be used to determine whether bats are more likely to fly toward rather than past turbines (Table 1). Evidence of general attraction would warrant additional testing of secondary hypotheses addressing specific cause(s) of attraction. We also recommend prioritizing the general hypothesis that bats are more susceptible to turbines while migrating (Fig. 1). Populations of migratory bats may be particularly vulnerable to the detrimental impacts of human activities, because they rely on widely dispersed habitats and large proportions of their populations cluster into restricted spaces during migration. In addition, conservation strategies directed toward migratory bats must be integrated across huge spatial scales (Fleming and Eby 2003). If it is determined that bat fatalities at turbines mostly involve active migrants, research could be focused on understanding how migration patterns relate to mortality and avoiding high-use areas when building new turbines, or curtailing operations of existing turbines during migration events (Fig. 1). It is currently assumed that the endangered Hawaiian hoary bat (*L. cinereus semotus*) is less vulnerable to turbines on the Hawaiian Islands because it does not migrate long distances, even though the species (*L. cinereus*) makes up about one-half of all fatalities in continental North America where it is known to migrate long distances (Arnett et al. 2008; Cryan 2003). Proportionally high fatality rates of purportedly sedentary species and populations elsewhere stress the need to test the migration connection.

If it is determined that bats are not attracted to turbines, then we suggest testing the general hypothesis that fatalities are a random sample of bats present around turbines (Fig. 1). If collisions are determined to be the result of random processes, then research could focus on monitoring general activity of bats as a means of assessing risk, because activity and fatality should be correlated. We are aware of no published studies showing a correlation between activity of bats at a site before turbines are built and fatalities there after turbines are operational. However, the increasingly common practice of preconstruction acoustic monitoring for bats at proposed wind energy facilities as a method of risk assessment seems to rely in large part on an assumption that collisions of bats with wind turbines are random processes (e.g., they do not account for differences in sex, age, or reproductive status, or attraction). Considering evidence that fatalities at turbines are sex-biased, the assumption of random collisions is questionable. If it is determined that fatalities are not the result of attraction and are not random processes, then research could focus on determining and monitoring specific behaviors that increase risk (Fig. 1), such as seasonal changes in feeding or mating activities.

Determining whether the causes of bat fatalities are the result of attraction, coincidence, or random processes may not influence the effectiveness of current techniques for monitoring existing turbine sites for fatalities (Kunz et al. 2007a), but it will certainly have implications for assessment of risk and population impacts. For example, if mating individuals are disproportionately attracted to turbines in places where their species passes through geographic bottlenecks during migration, the chances of rapid and irreversible population decline will be greater than if collisions involve turbines randomly killing bats that are not migrating. If collisions are random or linked to coincidental phenomena such as migration or increased seasonal activity, then the prospects for preconstruction risk assessment and site selection are good, because such events are predictable at a site. However, if bats are attracted to turbines, particularly from the long distances over which they are capable of seeing at night, existing preconstruction techniques of risk assessment may be less useful, because bats might not be active at the site, and thus detectable, until turbines that attract them are built.

Testing hypotheses of cause will be a tremendous challenge. Bat researchers are now faced with the difficult situation of studying nighttime phenomena occurring as high as 40-story buildings and potentially across kilometers of airspace. For example, it will be important to measure random and coincidental hypotheses at spatial scales beyond the possible influence of attractors. The difficulty will be in determining what the range of attraction might be, and such distances likely differ for different attractive cues and potentially for different species and landscapes. Techniques exist for monitoring the movements of bats across large areas of airspace, as well as their interactions with turbines, but some may not be suited for investigating hypotheses of cause, and additional experimental methods are needed (Kunz et al. 2007a, 2008). Turbine facilities are well suited for both observational and manipulative experimental studies into hypotheses of cause, so industry cooperation seems essential.

A particularly promising avenue of research into hypotheses of cause is the analysis of carcasses recovered beneath turbines. There is much to be learned from analyzing fresh carcasses recovered in the vicinity of wind turbines (e.g., Baerwald et al. 2008) but proportionally few are collected or saved for such purposes. Analysis of stomach contents, reproductive status, injuries, and geochemical signatures of body tissues are just a few examples of how analysis of carcasses has and will continue to reveal important clues about why bats die at turbines, but also about the basic biology of bats. Additional insight also may come from closer study of affected species with life-history characteristics that differ from trends discussed above, particularly tree roosting and long-distance migration. For example, *P. subflavus* and *Pipistrellus pipistrellus* roost in trees but are not considered to be migratory in areas where they collide with turbines, and the caverniculous species *Tadarida brasiliensis* might account for most fatalities at some sites in southern North America (Arnett et al. 2008; Kunz et al. 2007b; Miller 2008). These examples emphasize that the same ultimate cause or causes of fatality may not apply to all species, or subspecies in the case of the *L. cinereus semotus*, and researchers conducting observational and experimental studies need to keep this in mind.

If the ultimate cause or causes of bat fatalities at wind turbines are not established, it may never be possible to accurately assess risk to bats before turbines are built, measure the true impacts of turbines on affected populations, or come up with the most efficient ways to avoid or minimize fatalities. Although mitigation techniques such as operational curtailment are likely to be an effective way of minimizing fatalities at existing turbines (Baerwald et al. 2009; E. B. Arnett, pers. comm.), land managers, conservationists, and wind energy developers also want to know in advance, *before* turbines are built, how they can avoid bat fatalities. Establishing the underlying causes of bat fatalities at turbines may be the most likely way of preventing them, starting at the earliest planning stages of wind energy development.

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