Behavior of bats at wind turbines

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Wind turbines are causing unprecedented numbers of bat fatalities. Many fatalities involve tree-roosting bats, but reasons for this higher susceptibility remain unknown. To better understand behaviors associated with risk, we monitored bats at three experimentally manipulated wind turbines in Indiana, United States, from July 29 to October 1, 2012, using thermal cameras and other methods. We observed bats on 993 occasions and saw many behaviors, including close approaches, flight loops and dives, hovering, and chases. Most bats altered course toward turbines during observation. Based on these new observations, we tested the hypotheses that wind speed and blade rotation speed influenced the way that bats interacted with turbines. We found that bats were detected more frequently at lower wind speeds and typically approached turbines on the leeward (downwind) side. The proportion of leeward approaches increased with wind speed when blades were prevented from turning, yet decreased when blades could turn. Bats were observed more frequently at turbines on moonlit nights. Taken together, these observations suggest that bats may orient toward turbines by sensing air currents and using vision, and that air turbulence caused by fast-moving blades creates conditions that are less attractive to bats passing in close proximity. Tree bats may respond to streams of air flowing downwind from trees at night while searching for roosts, conspecifics, and nocturnal insect prey that could accumulate in such flows. Fatalities of tree bats at turbines may be the consequence of behaviors that evolved to provide selective advantages when elicited by tall trees, but are now maladaptive when elicited by wind turbines.

Bats are long-lived mammals with low reproductive potential and require high adult survivorship to maintain populations (1, 2). The recent phenomenon of widespread fatalities of bats at utility scale wind turbines represents a new hazard with the potential to detrimentally affect entire populations (3, 4). Bat fatalities have been found at wind turbines on several continents (3–6), with hypothesized estimates of fatalities in some regions ranging into the tens to hundreds of thousands of bats per year (4, 6). Before recent observations of dead bats beneath wind turbines, fatal collisions of bats with tall structures had been rarely recorded (7). Most fatalities reported from turbines in the United States, Canada, and Europe are of species that evolved to roost primarily in trees during much of the year (“tree bats”), some of which migrate long distances in spring and late summer to autumn (8). In North America, tree bats compose more than three-quarters of the reported bat fatalities found at wind-energy sites (6, 9), although there is a paucity of information from the southwestern United States and Mexico. Similar patterns occur in Europe (4). Another prominent pattern in bat fatality data from northern temperate zones is that most fatalities are found during late summer and autumn, sometimes with a much smaller peak of fatality in spring (4, 6). Concurrent involvement of species with shared behaviors suggests that behavior plays a key role in the susceptibility of bats to wind turbines, and that tree bats might somehow be attracted to wind turbines (8).

The causes of bat collisions with wind turbines are unknown, and many explanations for this phenomenon remain unexplored (8). Proposed causes of susceptibility range from bats randomly being struck by turbine blades while migrating past in large numbers to bats being attracted to wind turbines while searching for important resources, such as food, shelter, and social opportunities (8). Although causes of susceptibility remain unknown, altering turbine operations under certain conditions during periods of high risk can reduce bat deaths. Fatalities during late summer and autumn tend to occur when average wind speeds are lower than about 5–6 m/s (4, 9, 10), and studies in Canada (11), the United States (12), and Germany (4) demonstrated that bat fatalities can be substantially reduced by preventing turbine blades from turning until winds reach such speeds. Such operational modifications at wind facilities bring logistical and financial costs but may prove to be effective at reducing bat fatalities in many areas (11, 12). Discovering the underlying reasons why bats are susceptible to wind turbines could help improve the efficiency of existing strategies and potentially uncover new ways of further reducing fatalities while maximizing power production.

In late summer and autumn of 2012, we observed the behaviors of bats at a wind facility in northwest Indiana using thermal video-surveillance cameras, supplemented with near-infrared video, acoustic detectors, and radar. Our aim was to better understand how wind and turbine blade movement influence behaviors of energy development | sensory perception | video surveillance | wildlife | wind energy

Bats are dying in unprecedented numbers at wind turbines, but causes of their susceptibility are unknown. Fatalities peak during low-wind conditions in late summer and autumn and primarily involve species that evolved to roost in trees. Common behaviors of “tree bats” might put them at risk, yet the difficulty of observing high-flying nocturnal animals has limited our understanding of their behaviors around tall structures. We used thermal surveillance cameras for, to our knowledge, the first time to observe behaviors of bats at experimentally manipulated wind turbines over several months. We discovered previously undescribed patterns in the ways bats approach and interact with turbines, suggesting behaviors that evolved at tall trees might be the reason why many bats die at wind turbines.

Significance

Bats are dying in unprecedented numbers at wind turbines, but causes of their susceptibility are unknown. Fatalities peak during low-wind conditions in late summer and autumn and primarily involve species that evolved to roost in trees. Common behaviors of “tree bats” might put them at risk, yet the difficulty of observing high-flying nocturnal animals has limited our understanding of their behaviors around tall structures. We used thermal surveillance cameras for, to our knowledge, the first time to observe behaviors of bats at experimentally manipulated wind turbines over several months. We discovered previously undescribed patterns in the ways bats approach and interact with turbines, suggesting behaviors that evolved at tall trees might be the reason why many bats die at wind turbines.


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PNAS Early Edition | 1 of 6
bats around turbines, and thus fatality risk. Turbine operation was manipulated so that we could observe if bat behaviors and activity patterns differed around rotating versus stationary blades, and how bats interact with turbines under various operating and environmental conditions. Specifically, we tested the hypotheses that wind and blade rotation speed influenced the way that bats approached turbines.

Results

We recorded bat activity in the rotor-swept zones of three turbines on 163 camera-nights (one camera deployed for one night at a turbine) during July 29 to October 1, 2012, for a total of 1,304 h of thermal imagery. Video detections of bats were treated as the same event when detected within 1 min or less of other bat observations (Fig. 1). Bats were detected at turbines throughout the study period (Fig. S1) and throughout the night without any apparent trend toward later or earlier activity over the study period (Fig. S1).

Approximately 3-4 million animals were detected by radar flying through the monitored portions of the wind facility at or below about 200 m above ground level during this study (SI Results). Of this number, about a quarter were vertebrates occurring within the range of heights swept by turbine blades (<200 m) (SI Results). Among a total of 1,261 video detections of flying animals, a large proportion were identified as bats (79%), with fewer detections of bat-like targets (15%), birds (2%), likely insects (5%), and unidentified objects (1%); only the bat detections (n = 993) were included in this analysis. Adjusting for the number of thermal cameras operating per night, the average number of animal detections on video per turbine-night was 7.8 (min: 0; first quartile: 2; third quartile: 12; max: 31) and the average number of bat detections per turbine-night was 6.2 (min: 0; first quartile: 1; third quartile: 12; max: 26).

Most (88%) video detections of bats involved flight trajectories indicating the individual was moving toward the turbine, hereafter referred to as “focal” behavior. We observed multiple focal behaviors of bats at turbines, several of which have not been previously reported (Table S1 and Movies S1–S9) (13). Behaviors included close approaches to the monopole and nacelle (enclosure of machinery on top of monopole to which rotor and blades are attached), close approaches to slowly moving blades, flight loops and dives centered on the turbine, distant hovering, and chasing other bats toward or near the turbines. Focal behaviors often involved bats closely (<2 m) approaching the turbine monopole (15%), nacelle (30%), and occasionally blades (6%); (Table S1).

Most bats exhibiting focal behavior made single approaches and then moved away (72%), but many (27%) approached turbines multiple times during a detection (Table S1) and such interactions at times lasted several minutes. Bat detections within a night at a turbine were found to be significantly clustered in time for 23 of the 163 camera-nights (14%), as measured by an index (14) applied to bat counts in sequential 10-min periods. Bats were more frequently detected during periods when the moon phase was more than half full and visible above the horizon (Kolmogorov-Smirnov test, D = 0.0822, P < 0.0001) (Fig. S2). Because the thermal cameras do not rely on reflected light, we assume this relationship with moonlight was attributable to biological causes rather than detection bias.

Twelve fresh bat fatalities were found under turbines after nights when video imagery was recorded (SI Results). Possible strikes or bats being moved by air around turbine blades were observed on video during two of the nights after which fatalities were found, and during only 18 of the 993 bat video detections (2%). Because of this low frequency of video-observed strikes and other rarely observed interactions and behaviors (<1% prevalence in Table S1), we were unable to adequately test the effects of wind and turbine blade speed on these phenomena. Based on the species composition of fatalities and acoustic calls recorded on the turbines (SI Results), it is likely that most of our video detections involved nonfatality interactions.

Bats were detected more frequently at lower relative to higher wind speeds, and this pattern was evident regardless of whether the turbine blades were spinning (Kolmogorov-Smirnov test, D = 0.2365, P < 0.0001) or not (D = 0.1937, P < 0.0001) (Fig. S3). When the wind was blowing >1 m/s (96% of the time), bats exhibiting focal behaviors were observed significantly more often (~80% of detections) on the leeward (downwind) compared with the windward side of the turbine (χ² test = 329.3, df = 1, P < 0.0001), regardless of turbine nacelle orientation. When the wind was blowing ≤1 m/s, observed activity between leeward and windward areas (gauged relative to nacelle orientation) was approximately equal and the strong prevalence of leeward bat activity was not evident (Fig. 2A). However, the propensity for leeward activity at higher wind speeds was also influenced by the rotation of turbine blades. Similar to the general trend observed in video detections, logistic regression revealed a significant interaction between wind speed and blade rotation that resulted in opposite patterns of leeward activity (P = 0.0196). For example, when turbine blades were prevented from rotating, the observed frequency of leeward approaches to the nacelle increased from 65% to >90% as wind speeds increased from 0 to >8 m/s, whereas the proportion of leeward activity declined from >85% to <70% with a similar increase in wind speed when the turbine blades were spinning (Fig. 2B).

Focal bat behaviors, including close approaches to the monopole, blades, and nacelle, were observed across a range of wind speeds (0–9.6 m/s), but were detected more frequently at low blade-rotation speeds and less frequently at intermediate and high speeds (classified as 0 to <1 rpm, 1–10 rpm, >10 rpm). For example, of the 55 detections that involved apparent investigations of turbine blades, 31% occurred when the blades were stationary; 69% occurred when blades were spinning very slowly (<1 rpm, a speed typical of near-windless conditions or when the blade edges were pointed into the wind), and none were detected when blades were spinning ≥1 rpm (χ² test = 27.5, df = 2, P < 0.0001). Similarly, about 41% of the 110 monopole approaches occurred when the blades were stationary, 51% occurred when blades were spinning very slowly, and only 8% of detections were noted at higher rotation speeds (χ² test = 31.6, df = 2, P < 0.0001). Nacelle approaches demonstrated a similar pattern, with 42%, 40%, and 18% of the 258 detections in the stationary, very slow, and higher rotation-speed categories, respectively (χ² test = 28.6, df = 2, P < 0.0001). These findings are all consistent...
with the hypotheses that wind speed and blade rotation speed influenced the way that bats approached turbines.

Most video detections of bats involved single individuals, although a small proportion (3%; \(n = 29\)) included pairs of bats. Bats were seen chasing or following each other during 48% (\(n = 14\)) of the observations involving pairs. On a few occasions, bats chasing each other near turbines appear to touch in flight. One video event revealed two hoary bats (Lasiurus cinereus; identified from concurrent acoustic recordings) hovering next to each other in the airspace near the turbine nacelle for over 10 s after a prior sequence in which they interacted in the lee of the turbine tower (Movie S10).

**Discussion**

Our video observations indicate that many bats passing close (<50 m) to wind turbines with stationary or slow-moving blades during late summer and autumn are attracted to and actively approach them using minimally turbulent air currents, vision, and to some degree echolocation for orientation. In contrast, radar observations indicate that nocturnally migrating vertebrates, presumed to be mostly birds, likely far outnumbered bats in the airspace, yet their near absence from video observations suggests that birds did not interact with turbines in the same way as bats, possibly avoiding them. Furthermore, acoustic detectors pointing upward from the tops of the turbine nacelles regularly detected the calls of bats not observed by video cameras, indicating that some bats passed high in the airspace above the turbines without closely approaching. It remains to be determined what proportion of passing bats approach turbines and whether they might respond to the presence of turbines over greater distances than those we observed with video cameras.

Bats likely can sense and respond to air currents. We saw no preference in the directions from which they approached turbines when the wind was not blowing or was blowing very gently, but bats consistently approached from leeward at wind speeds >1 m/s. The downwind direction of activity only when air was moving suggests that bats know which way the wind blows and approach tall structures in a patterned way that is independent of cardinal direction. As do many animals that move through air (15), bats orient by sensing and responding to flows through which they fly. Bats sometimes commute and forage on the leeward sides of windbreaks, such as tree rows and cliffs, with the postulated benefits of leeward activity including lower risk of predation, favorable conditions for energy-efficient flight, and greater availability of insect prey, particularly during high winds (16, 17). Being able to follow flows can provide substantial selective advantages to animals, particularly when other sensory cues are limited and when important resources can be predictably found within flows (15). It was once believed that bats made their way through darkness with the help of highly sensitive touch receptors in their wings and ears (18), but this concept of landscape orientation received little subsequent attention after the discovery of echolocation (19). Highly evolved hair-cell receptors on the skin surfaces of bat wings recently have been studied in detail; hair receptors in bat wings are now known to play an important role in flight control by sensing minute changes in airflow across the wing surfaces (20). Whether wing receptors help bats to sense subtle patterns of airflow at larger spatial scales is unclear, but Brazilian free-tailed bats (Tadarida brasiliensis) show evidence of orienting through wind currents and exploiting migrating insects concentrated in airflows in the absence of other visual or acoustic cues at high altitudes [up to 3,000 m above ground level (21, 22)]. In light of previous general observations of bat activity in the lee of windbreaks and our observations of consistent leeward bat activity at turbines, we suspect that bats are well adapted for sensing and orienting by airflows at landscape scales and that going with the flow, or against in the case of bats at turbines, may be an underappreciated sensory modality that evolved in these night-flying mammals.

Our thermal video cameras detected bats at turbines more often during periods of night with bright moon illumination and less often during periods with lower levels of moonlight, suggesting that vision plays a role in bats perceiving and approaching wind turbines. Bats rely on vision for long-distance orientation (23–25), are known or suspected to orient through landscapes using light cues, such as stars and postsunset glow (26, 27), and use visual cues to help them find roosts in trees (28). The effects of moonlight on bat activity and fatality at turbines are not well understood, but a study in Alberta, Canada, reported higher fatality rates of silver-haired bats (Lasionycteris noctivagans) at wind turbines on nights when the moon was fully illuminated (29). There is no evidence that tree bat activity in the absence of, or distant from, turbines varies with lunar cycles or illumination (30). Acoustic data gathered on the turbines we monitored, which included many calls from bats passing higher in the airspace than our cameras could image, did not show a trend toward proportionally more activity under moonlit conditions (SI Results), further indicating that general activity levels are not influenced by moonlight.

The patterns we observed on autumn nights are suggestive of the visual conspicuousness of the wind turbines waxing and waning with the moon, affecting the probability of passing bats seeing and moving closer to them to investigate.

Despite our observations that suggest bats orient toward wind turbines using flow and visual cues, the reasons why they do so remain unknown. Although we could not determine why bats behaved the way they did around turbines, we suspect that such behaviors evolved in association with trees. At a fundamental level, tree bats may not be able to discriminate wind turbines from trees (3). Both trees and turbines have tall and cylindrical “trunks” (monopoles), visually conspicuous “crowns” (nacelles), and radially extending “limbs” (blades). Bats are rarely reported interacting or colliding with other tall structures (7), as might be expected if the behaviors we observed were a general response to structural stimuli. However, a recent study revealed higher activity of tree bats during late summer and autumn at tall communication towers compared with surrounding habitats (31). Bats may not have the cognitive ability to differentiate wind turbines or other tree-like structures from real trees either at a distance or at close range, particularly if visual cues, such as similar silhouettes against the night sky, are accompanied, reinforced, or overwhelmed by other perceptual cues, such as similar downwind airflow patterns. For example, the predatory beetle (Rhizophagus grandidis) responds to disturbance of airflow around a simulated tree more than the tree’s visual silhouette (32). We do not know if the patterns of behavior we observed apply to cave-roosting species of
bats that die at wind turbines [e.g., genera Myotis and Tadarida (6)], but even cave-roosting bats may occasionally visit trees for the reasons discussed below.

Key findings of our study were that wind speed and blade rotation speed influenced the way that bats approached turbines. Bats approached turbines less frequently when their blades were spinning fast and the prevalence of leeward approaches to the nacelle increased with wind speed at turbines with slow-moving or stationary blades. A plausible explanation for these patterns (see SI Discussion for others) is that airflow profiles around tall trees and turbines with stationary blades may be very similar to each other (e.g., oscillating swirling patterns, called a Kármán vortex street), whereas the spinning blades of turbines cause chaotic downwind turbulence (33) that is unlikely to resemble any natural airflow patterns that bats might associate with trees. If tree bats find and orient toward trees by sensing and moving into upstream airflows, turbines may resemble trees only when the blades are moving slowly or are stationary. In other words, airflow paths that bats potentially follow may not be present downwind of turbines with fast-spinning blades. Nighttime flight behaviors of bats around tall trees during late summer and autumn have not been reported, but finding and observing such behaviors if they exist might help explain why tree bats are susceptible to wind turbines.

Compounding the potential for bats to mistake wind turbines for trees is the possibility that they expect important resources when they arrive at the “trees.” Such possible expectations may not apply to concurrently migrating birds, which radar detected in apparently high abundance in the surrounding airspace yet were infrequently observed on video near turbines. Bats may exploit streams of air flowing downwind from trees, turbines, and perhaps other tree-like structures [e.g., communication towers (31)] at night while searching for roosts, conspecifics, and possibly feeding on nocturnal insects that could accumulate in such flows. Many of the hypothesized causes of tree bat susceptibility to turbines involve attraction (8). Our observations are consistent with the possibility that bats are attracted at close distances (<50 m) to turbines with stationary or slow-moving blades, but the potential source of attraction remains unknown. We did not see evidence of close-scale attraction based solely on physical phenomena, such as heat, electromagnetic fields, or sounds generated by specific parts of the turbines, because focal behaviors were dispersed across many different parts of the turbine structure, often involving motionless blades and inert monopoles. A prior study also reported bats focusing attention on monopoles, nacelles, and blades of wind turbines, but no part stood out as attracting disproportionately more bats than others (13). The variety of turbine parts toward which bats focus their attention suggests a general close-range attraction, but the strong leeward component to these varied focal behaviors may offer clues to what bats might be trying to find.

Resource-based hypotheses of attraction include bats seeking shelter, social opportunities, or food at turbines (3, 8, 9, 13), all of which may occur more often on the leeward sides of tall, tree-like structures. The simplest explanation for bats closely approaching turbines may be that they are seeking places to roost in what they perceive as trees while migrating. We regularly observed hoary bats and eastern red bats (Lasiusus borealis) flying in under the bottom of the leeward nacelle and making close approaches to the recessed exhaust port (Movie S4). Although we did not see clear evidence of bats consistently trying to land on turbines, we frequently observed bats approaching the monopoles very closely, as previously reported (4, 13, 34). The high proportions of close approaches focused on nacelles and monopoles (Table S1) are consistent with bats trying to find places to land. After not finding suitable places to alight upon (e.g., close investigations reveal turbine surfaces too smooth), bats may simply move on.

Bats might also closely approach turbines while looking for social opportunities. Similarities in the social behaviors of tree bats in North America and Europe led to speculation that bats might use the tallest trees in landscapes as flocking or gathering places (35). Tree bats tend to begin mating during the time when most mortality is documented at turbines (36), and bats seeking mates at trees may be drawn toward turbines (37) and other tall structures (31). We observed pairs of bats in 3% of our observations, and in about half of those cases they appeared to be following or chasing each other. In one case we observed two hoary bats in the lee and recorded social calls (Movie S10), but did not see evidence of larger social aggregations that were hypothesized for this species (37). Many species of tree bats in Europe exhibit mating flight displays centered on trees during late summer and autumn, but such flight behaviors have not been reported for any temperate North American bats (37). We speculate that some of the sustained leeward focal behaviors that we observed at turbines in our study, such as repeated looping returns and dives (Movie S2), might be associated with mating displays that could occur at trees. The “upstream orientation” we frequently observed is common in other types of flying and swimming organisms during foraging and mate-searching movements (15).

Bats may be drawn in by insects whose distribution is concentrated around wind turbines. Empirical data demonstrating the consistent presence and aggregation of insects at turbines during the night are lacking, but insects are known to foul turbine blades (38), be attracted to certain turbine paint colors (39), and migrate in large numbers during periods of bat fatality at turbines (40). In addition, bats have been observed foraging near turbines (4, 34) or found dead beneath them with full stomachs (41, 42), highlighting the plausibility of the feeding hypothesis. Although we regularly observed insects in the video imagery, we did not observe the frequent presence of insects with bat detections or record any unambiguous feeding calls of bats at turbines (SI Results), nor did we regularly observe what we would consider typical foraging behaviors of bats during our study. However, this observed lack of insects and typical foraging patterns does not preclude the possibility that bats expected to find insects at the turbines they approached.

There are several general patterns of insect behavior and distribution that give us reason to suspect the leeward behaviors we observed at turbines might be associated with bats expecting insects. The structure and orientation of the structures are consistent with the presence of the actual presence of insects. Insects often accumulate on the leeward sides of artificial and natural structures, and behind windbreaks insects tend to increase in number and density with wind speed (43, 44). Many diurnal and crepuscular insects swarm above prominent high points in landscapes during calm conditions and such aggregations often blow leeward in windy conditions (45, 46). Certain nocturnal insects, such as gypsy (Lymantria dispar) and spruce-budworm (Choristoneura spp.) moths, lay eggs in and disperse from the tops of tall trees during late summer and autumn (47, 48). Bats sometimes feed on insects dispersing from trees. For example, Lloyd et al. (49) reported bats feeding on emerging spruce-budworm moths, and Lewis (50) reported eastern red bats feeding on moths in the airflows leeward of human-made structures: “When a moderate, steady wind is blowing over a moth-infested [corn] crib I have seen bats strung out in a narrow belt to a distance of 200 yards or more, catching moths that were carried by the wind.” Given the likelihood of insects accumulating at night above and in the lee of tall trees in natural environments, the leeward focus of bat behaviors at tree-like structures may not be coincidental.

Resource-based attraction hypotheses involving shelter, social opportunities, and food all seem plausible in the light of our results, but gathering direct evidence of such resource use by bats may not be possible at wind turbines or other anthropogenic structures. The roosts, conspecifics, and insect prey that bats might expect at turbines or other tree-like artificial structures would not necessarily have to occur there to draw them in and put them at
risk. Bats may be acting upon the expectation of resources rather than the actual presence of resources. Fatalities of bats at turbines may be the consequence of behaviors that evolved to provide selective advantages when elicited by tall trees, but are now maladaptive when elicited by wind turbines. Paradoxically, direct evidence of the causes of tree bat susceptibility to wind turbines may not be observable at wind turbines, but instead at the trees and their associated resources where potentially causative behaviors evolved.

Our observations have practical implications. Although our scope of inference is limited to certain tree bats (L. borealis, L. cinereus, and L. noctivagans), areas of turbines from the rotor-swept zone around the nacelle to near the ground (different behaviors may occur higher in the airspace), and are based on observations from just three turbines in midwestern North America, efforts to monitor bat activity near turbines (e.g., acoustic detectors and video cameras), or deter bats from turbines [e.g., devices producing startling sounds (51)] may benefit by aiming instruments from the back of the nacelle into the leeward airspace, an area where we consistently observed higher bat activity regardless of changing wind directions. Strategies for minimizing fatalities of bats at turbines currently focus on preventing blades from spinning during low wind periods (4, 11, 12). Our observations that tree bats show a tendency to closely investigate inert turbines and sometimes linger for minutes to perhaps hours (in the cases of clustered observations) highlight the plausibility of a scenario in which bats are drawn toward turbines in low winds, but sometimes remain long enough to be put at risk when wind picks up and blades reach higher speeds. Therefore, the frequency of intermittent, blade-spinning wing gusts within such low-wind periods might be an important predictor of fatality risk; fatalities may occur more often when turbine blades are transitioning from potentially attractive (stationary or slow) to lethal (fast) speeds. Efforts to minimize bat fatalities at wind facilities might benefit by averaging wind-speed curtailment thresholds over longer periods of time (e.g., >10 min) to prevent gusts from intermittently pushing blades to lethal speed during low-wind periods. Finally, fatalities may be reducible by altering the appearance of the turbine. Fewer fatalities of eastern red bats were found under turbines with flashing red aviation lights at a large wind facility in Texas (52), hinting at the possibility that supplemental lighting of turbines might make some bats less likely to mistake them for trees.

Methods

Study Area and Experimental Design. We conducted this study at a wind turbines facility (Fowler Ridge Wind Farm, BP Alternative Energy, Oakland, CA and Dominion Resources Inc., Richmond, VA) in Benton County, IN, which consisted of 355 wind turbines with a total nameplate capacity of 600 megawatts (MW). The 20,234-ha site is dominated by agricultural lands (mostly soybean and corn fields) with buildings and forested areas composing <5% of the total area. The topography is mostly flat with elevations ranging from about 210-225 m. The three turbines monitored (Model VB2, Vestas Wind Systems) each had a nameplate capacity of 1.65 MW, 82 m rotor diameter, and 80-100 m high monopole.

To observe bat interactions with turbines across a range of weather and operating conditions, turbines were run under three different scenarios: (i) blades never rotating, (ii) blades not rotating (curtailed) until wind speeds reached 6.5 m/s, and (iii) blades rotating under normal operating conditions (begin rotating at about 2 m/s wind speed). We randomly assigned operation treatments each night so that on any given night, one of the three turbines was randomly assigned to be never rotating, curtailed, or fully operational.

Recording Video Imagery. We monitored the three turbines using video surveillance cameras with sensors that operate in the “thermal” spectrum of infrared light (<9,000-14,000 nm; Model Q1921-E with a 19-mm lens, Axis Communications) and which require no supplemental illumination. The effective sensor-array size of the cameras was 384 × 288 pixels, and we recorded digital video at a rate of 30 frames per second using netbook computers (Model 110A A7K67UT, Hewlett-Packard) equipped with external hard drives. We positioned these cameras 12 m from the base of each turbine so that they imaged about two-thirds of the rotor-swept zone. Video recording began within 1 h of sunset and continued until ~1 h after sunrise. In addition to the thermal cameras, we simultaneously recorded supplemental near-infrared (NIR) video imagery (SI Method).

Review of Video Imagery. We manually reviewed video imagery at high speed (scan speed ~1 min/h of recorded imagery) with viewing software (VirtualDub, www.virtualdub.org; VLC, www.videolan.org) and then a second time using custom-written code (Dataset S1) and matrix-based statistical software (Matlab with Image Processing Toolbox, Mathworks) that automatically detected events in which animals flew through the thermal video scenes. Automatic processing algorithms identified frames with motion of small objects not associated with the moving turbine blades. Although video was recorded at 30 frames per second, only every 30th video frame was analyzed because of time constraints on automated processing, resulting in detection of events mostly lasting <1 s. However, because bats usually took several seconds to traverse the tens of meters of airspace around the turbine, we saw no evidence that this sampling rate consistently missed bats when they were present. Species of bats we observed likely fly at speeds <7 m/s (53). The size of the field of view was about 55 × 40 m given the ~110-m resolution range of the cameras. We estimate that a bat at that height would require at least 5–6 s to traverse the imaged area and would be detected in as many video frames. Therefore, any bias associated with missing bats passing through the video scenes in <1 s would involve those passing relatively close to the camera and affect the detection rate at the turbine site.

All potential flying objects detected by high-speed scanning or software algorithms were visually reviewed and characterized by at least two observers (P.M.C. and P.M.G.). These detections included insects flying close to the cameras (which were ignored and not tabulated), as well as bats and small birds flying around the turbines up to the airspace above the nacelle, larger birds flying higher above the rotor-swept zone, and airplanes and clouds much higher. Based on the pixel resolution of the thermal cameras and the distance at which a bat could be resolved with more than 1 pixel, we estimate our range of detecting bats with the cameras was upwards of 110 m. With the thermal cameras situated 12 m from the base of the turbine and the nacelles sitting atop 80-m towers, the distance from camera to nacelle was 81 m. Our video observations from the thermal cameras and supplementary imaging from the NIR cameras (SI Method) revealed that, for example, eastern red bats, identified acoustically (SI Method) were easily detectable up to nacelle height but tended to become much less detectable as they moved higher than the nacelle, whereas larger bats (for example, hoary bats, identified acoustically) were detectable in the airspace 20-40 m above the nacelle. Although spatial positions of objects are sometimes difficult to determine in 2D video imagery, we were typically able to judge locations of bats in the airspace using reflections in the thermal imagery (e.g., during close approaches thermal reflections of bats could be seen on the turbine tower, shadows in the corresponding NIR imagery (e.g., bat passing close under bottom of nacelle), and by visually observing the parallax of the bat from the different view angles of the thermal and NIR cameras.

For each detection of a bat in the thermal imagery we recorded the following information: number of individuals present, orientation of the nighttime horizon as the turbine nameplate frame of reference. The direction the turbine nose was pointing (leeward, windward), rotor speed (rpm), whether the bat altered course in response to the presence of the turbine (focal behavior), whether the bat made close (<2 m) approaches to the turbine monopole, nacelle, or blades during the event, whether the bat appeared to be struck or displaced by a moving turbine blade, as well as descriptive comments about the event. Turbine orientation was characterized from video, but we also analyzed meteorological and operational data gathered at the turbine nacelle. These data included wind speed (m/s) and rotor speed. Moon illumination was recorded as the proportion of lunar disk illuminated given that it was visible above the horizon. Moon illumination data were obtained from the Astronomical Applications Department of the US Naval Observatory (aa.usno.navy.mil/index.php).

Analysis of Bat Behavior from Video Detections. Patterns of bat detection in relation to behavior, wind speed, and turbine operation were examined with Kolmogorov-Smirnov and χ2 tests and logistic regression. Kolmogorov-Smirnov tests of bat behavior compared conditions (e.g., moon illumination) during bat detections relative to that recorded throughout the study period for all nighttime 10-min intervals. All statistical analyses were performed in program R (v2.15.1; R Development Core Team, R: A Language and Environment for Statistical Computing, 2011). The temporal clustering of bat detections within a night at each turbine was evaluated with an index developed for use with temporal sequences where the data are grouped into equally-spaced intervals (14). Detections were grouped by 10-min intervals,
Supplemental Monitoring with Other Techniques. In addition to monitoring the three wind turbines with thermal and near-infrared video surveillance cameras, we concurrently monitored them with acoustic detectors mounted on the turbine nacelles and radar, as described in S1 Methods. See Movies S11 and S12 for examples of bats flying close to turbines with fast-moving blades.


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Cryan et al.
Supporting Information

Cryan et al. 10.1073/pnas.1406672111

SI Methods

Recording Supplemental Near-Infrared Video Imagery. In addition to thermal imagery, we used near-infrared (NIR) video cameras (Model KP-E500, Hitachi; Model GX1920, Allied Vision Technologies) and NIR illuminators (Model T90A42, Axis Communications; Model Mark 40, Luma Scientific; Model ALS-40, Sofradir EC) to gather concurrent, supplemental imagery of bats at turbines. It is difficult to see visual details or judge depth of field from thermal imagery alone (1), and NIR imagery helped us identify targets detected, judge spatial relationships between flying targets and the turbines, and gather additional details about behaviors of bats interacting with the turbine towers, nacelles, and blades. These NIR cameras and illuminators operate at wavelengths of light ranging from 700 to 1,000 nm, which fall outside the visible spectrum of bats (2–5). NIR cameras were positioned at 30 m from the base of each turbine and NIR illuminators were positioned at 12 m and 60 m from the turbine and aimed at the nacelle.

Acoustic Monitoring for Bat Echolocation Calls on Top of Turbines. We used frequency division acoustic detectors (Model Anabat II; Titley Electronics) to monitor the airspace around turbines for bat echolocation calls. These detectors were mounted on top of each nacelle at the back, with their microphones pointed into the airspace directly behind the nacelle and away from the turbine blades. Detector microphones were housed in a 50-mm-diameter curved PVC tubes that faced upward at an angle of 45°. Detectors were programmed to record calls each night from 1 h before sunset to 1 h after sunrise for the duration of the study.

We analyzed bat-call data with sound analysis software (Analook, www.hoarybat.com) as described previously (6). All extraneous noise was visually filtered from the data before summary and analysis. We divided echolocation passes into two phonic groups based on minimum frequency of the call, in part because bats using different ranges of frequencies to echolocate may differ in their behaviors around turbines and in their responses to environmental factors. We manually classified bat passes as being produced by either high-frequency bats (≥33 kHz average minimum frequency) or low-frequency bats (<30 kHz average minimum frequency). High-frequency species of bats included Myotis spp., tricolored bats (Perimyotis subflavus), evening bats (Nycticeius humeralis), and eastern red bats (Lasiurus borealis). Low-frequency species include big brown bats (Eptesicus fuscus), silver-haired bats (Lasiemyotis noctivagans), and hoary bats (Lasiurus cinereus). We also identified passes of hoary bats as a third phonic subgroup (a subset of low-frequency bats) using a customized filter in Analook derived from those developed by Britzke and Murray (7) with a “Smoothness” setting of 12, a “Bodyover” setting of 110, a “MinFmin” setting of 14, a “MaxFmin” setting of 21, and a “CallNum” setting of 1. We specifically categorized the passes of hoary bats, because this species is particularly vulnerable to wind turbines (8) and because, unlike most other species present at the study site, their echolocation sequences are relatively easy to distinguish from those made by other bats. To assess whether or not bats were interacting with the turbines and potentially feeding, we examined calls with sound analysis software (Songscape 3.4, Wildlife Acoustics) and classified them as approach phase or terminal phase (“feeding buzz” [9]). We defined the approach phase as frequency modulated call sequences with intervals between pulses lasting from 0.01 to 0.05 ms and the terminal phase as frequency modulated call sequences with <0.01 ms between pulses.

Radar Monitoring of Airspace Surrounding Wind Turbines. We used an all-weather, 25-kW, x-band (3.19-cm wavelength) vehicle-mounted portable radar unit (Furuno 2127BB, Furuno Electric) to collect data on flying animals at the wind facility. The radar runs on 120-V alternating current supplied by a low-noise, regulated generator, and the radar was refitted with a 1.2-m-diameter, high-gain parabolic antenna with a greater range of detection and some height estimating capability not available with the original equipment manufacturer’s open-array antenna. The radar’s beam is shaped by the antenna’s electronics (pulse, 38.8-dB gain), the radar cross-section of targets, wavelength, and other factors (see, for example, ref. 10) that resulted in a ~3.3° wide beam for this study. The antenna was continuously rotated in azimuth through 360° every 2.5 s, updating animal locations with each rotation. The elevation angles used in this study, between 2.75° and 3.50° above the horizon, were not changed during operation and were as low as possible to avoid clutter while simultaneously monitoring as much of the rotor-swept areas of turbines as possible. However, it was not possible to detect flying animals within the immediate vicinity (area monitored by video cameras) of the wind turbines monitored because of electronic clutter created by the radar beam reflecting off the monopoles, nacelles, and blades. The resulting 2D circular display showed radar tracks of animal detections. Maximum range of detection in this study was capped at 3 km. We positioned the radar unit such that the detection area overlapped as much as possible the rotor-swept areas of the three turbines simultaneously monitored by video. The radar was moved among these three turbines according to a schedule such that all turbines were monitored regularly: one turbine was monitored continuously at the original position, one was monitored for 15 min, and one was monitored for 30 min. We estimated the radar data were recorded for ~11.5 h each night, beginning 30 min before local civil sunset. The radar recorded animal movement data as raster imagery during each update of the radar display using a programmable frame-capture card (Accustream 170 Express, Foresight Imaging). The locations from which focal turbines were monitored varied somewhat in response to changes in vegetation as seasonal harvest of crops progressed in this highly agricultural landscape. Despite these changes, effort was made to maintain the 2-km distance to focal turbines.

Radar-determined locations of flying animals within carefully chosen subsets of radar coverage areas were extracted manually to ensure data were as free as possible of noise and other unwanted artifacts. Observations were drawn uniformly across all ranges (i.e., heights) within the radar coverage area out to 3 km. These observations were then processed using R statistical software to estimate flight parameters and perform statistical analyses. Data from invertebrates can corrupt analyses, so we attempted to remove these by setting a threshold based on target airspeed. We estimated target airspeed using radar-determined ground velocities and local wind data, and these airspeeds were used to classify targets as either “vertebrate” (≥2 m·s⁻¹) or “invertebrate” (11). Currently, no method exists to distinguish bird from bat targets detected on portable radar (12). We computed metrics on each extracted radar target, including speed, direction, height, and location with respect to the radar. Knowing the antenna elevation and radar coverage area allowed us to compute height distributions of vertebrate and invertebrate targets.
**Fatality Monitoring on Ground Beneath Turbines.** We searched beneath all three turbines daily during the study period, weather permitting. We established 80-m-radius plots cleared of vegetation and centered on each turbine with parallel transect lines within each circular plot spaced 4 m apart. We searched 2 m on each side of the transect line to increase the potential of finding fresh carcasses (i.e., bat fatalities from the previous night). Searches were paired at each turbine, and each searcher walked half of a plot. To minimize potential searcher bias, searchers switched sides and walking direction each time a turbine was searched. Searchers walked at a rate of ~40 m/min along each transect. We began searches within 15 min of sunrise and searches ended before sunset. When a dead bat was found, we recorded the species, sex, age (where possible), condition of carcass (entire, partial, or scavenged), and estimated time of death (for example, <1 d, >2 d). In this analysis we only included data on fresh (determined by round, fluid-filled eyes and smell) fatalities estimated to have died the night before when thermal cameras recorded imagery.

**SI Results**

**Acoustic Monitoring for Bat Echolocation Calls on Top of Turbines.** We recorded 695 bat call sequences on nacelle-mounted acoustic detectors during nights the thermal cameras were deployed and the majority of calls were consistent with the parameters of those made by species of migratory tree bats: 19% (n = 131) of the recorded calls were identified as those of hoary bats; 39% (n = 271) were low-frequency calls similar to those of hoary bats and silver-haired bats, although a small proportion were likely made by big brown bats; and 42% (n = 293) were high-frequency calls characteristic of eastern red bats, tricolored bats, and evening bats. Calls unambiguously characteristic of species of *Myotis* were not detected.

Bat calls were detected during only 218 (22%) of the 993 events in which bats were observed on video, likely because incomplete overlap in the detection areas of acoustic detectors (mostly above the nacelle) and video cameras (mostly below the nacelle). Of the 258 video detections of bats active around the nacelle near the acoustic detectors where they might have been recorded had they been echolocating and within the zone of reception of the acoustic detector (45° upward angle from top and back of nacelle), only 49% had associated acoustic detections, suggesting that bats might sometimes forego echolocation while flying close to wind turbines.

Acoustic calls did not indicate that bats were frequently capturing prey on or near the turbines monitored. Of 883 call sequences recorded from the top of the three turbines between July 13 and October 4, 2012 (about 2 wk longer than video monitoring period), only 8.8% were characteristic of bats closely approaching prey or structures, and none were terminal phase calls (“feeding buzz” [9]) characteristic of bats homing in on insect prey. We observed concurrent insect activity in only 7% of the video detections of bats, suggesting a lack of correlation between obvious insect abundance and bat activity at the turbines monitored. There were only a few video observations of bats feeding around turbines in typical ways known to be associated with the pursuit and capture of insects, and those events, confirmed with wider-view NIR imagery, mostly occurred nearer to the ground and were not centered on the turbine.

**Radar Monitoring of Airspace Surrounding Wind Turbines.** We recorded nearly 642 h of radar data during 56 nights of data collection. The final dataset comprised over 920,000 raster images. We estimate that the radar recorded the tracks of 3–4 million flying animals during the course of the study. This was far more information than could be analyzed, so a subset of data (n = 3,458 radar tracks) was selected for further examination in relation to height distribution, which ranged from 0 to 207 m above ground level (AGL). Of those results, further screening based on airspeed eliminated 42.3% of tracks as likely to be of invertebrates, leaving 1,995 vertebrate tracks. These were strongly skewed in favor of low flight heights, with a modal height of ~20 m AGL. Although radar was unable to detect animals flying within the areas close to turbines imaged by video cameras, 42.4% of vertebrate radar targets moving past the turbines flew at heights within the range swept by turbine blades (~50–120 m AGL).

**Fatality Monitoring on Ground Beneath Turbines.** We completed daily fatality searches after all but 5 (3%) of the 163 camera nights during which thermal imagery was gathered. We found a total of 12 fresh bat carcasses under the three turbines during fatality searches after camera nights. Tree bats composed 92% (n = 11) of fatalities, represented by eight eastern red bats (six adult female, two adult male), two silver-haired bats (both adult female), and one adult-female Seminole bat (*Lasiusius seminolus*), whereas one juvenile male big brown bat (*E. fuscus*) represented a species not considered a tree bat.

**SI Discussion**

We do not believe the lower observed activity at high rotation speeds represents detection bias caused by the fast-moving blades; the process for detecting bats in video imagery analyzed single video frames in which detection-area differences among frames with moving and nonmoving turbine blades were negligible (Fig. 1). It may be that tree bats have trouble flying upward into the strong turbulence of turbines with fast-moving blades. However, our occasional observation of windward and upwind flight at high wind speeds (Movie S1) suggests that, like other animals exhibiting rheotaxis (persistent upstream orientation for the purpose of maintaining a position within a flow) (13), tree bats are capable of flying upward against considerable airflow. It is also possible that bats visually or acoustically perceive and avoid fast-moving blades, yet we observed multiple instances in which bats flew on direct flight paths through blades rotating at full speed (from both upwind, downwind, and sometimes both) and in most cases they did not seem to alter course or respond to the blades until after they had passed through the plane of the moving blades (Movie S12). After such events, bats at times repeatedly returned to the areas of close encounters with blades, sometimes to be struck or displaced in the airspace again. We would not expect such returns if bats were visually or acoustically perceiving and actively avoiding the fast-moving blades, which can have tip speeds >55 m/s (200 kph). Similarly, if bats were visually perceiving and avoiding the moving blades we might expect fewer bats to occur near turbines when blades are turning on brightly moonlit nights than on dark nights, which was not the pattern we observed. Considered together, our evidence indicates that tree bats sometimes approach turbines in high winds when the blades are turning rapidly, but that they are less likely to do so than when the blades are not turning or are moving slowly, and that they may be unable to perceive fast-spinning blades.

Fig. S1. Video detections of bats relative to time since sunset and survey night (night 1 = July 29, 2012) for all three wind turbines monitored. For comparability over the survey period, time since sunset is standardized as fraction of time of night to account for the seasonal change in night duration. Hollow points on the x axis indicate nights with no thermal camera recordings.

Fig. S2. Cumulative distribution functions of moon illumination during bat detections relative to that recorded throughout the study period for both visual (video) and acoustic detectors. Illumination was recorded as the proportion of lunar disk lit while visible above the horizon. Increasing values of distance (the absolute difference at any interval between the pair of functions for each of the two samples) indicate illumination levels at which bats were detected less frequently than expected; decreasing values indicate more frequent observations than expected. For visual and acoustic detections, the Kolmogorov–Smirnov test statistics were $D = 0.0822$ ($P < 0.0001$) and $D = 0.0341$ ($P = 0.9466$), respectively.
Fig. S3. Cumulative distribution functions of wind speed during bat detections relative to that recorded at night throughout the study period for both nonrotating and rotating turbine blades. Increasing values of distance (the absolute difference at any interval between the pair of functions for each of the two samples) indicate wind speeds at which bats were detected more frequently than expected; decreasing values indicate fewer than expected observations. For nonrotating and rotating turbine blades, the Kolmogorov–Smirnov test statistics were $D = 0.1444 (P < 0.0001)$ and $D = 0.2365 (P < 0.0001)$, respectively.

Table S1. Behaviors of bats seen altering course toward wind turbines during video monitoring, from 872 detections of “focal” behaviors

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Single approach*</td>
<td>Alters course and approaches turbine only once before moving on (Movie S1)</td>
</tr>
<tr>
<td>$(n = 630; 72%)$</td>
<td></td>
</tr>
<tr>
<td>Multiple looping approaches</td>
<td>Approaches then loops outward in airspace away from turbine before returning</td>
</tr>
<tr>
<td>(239; 27%)</td>
<td>one or more times toward monopole, nacelle, or blades (Movie S2)</td>
</tr>
<tr>
<td>Close approaches: nacelle*</td>
<td>Flying very close ($&lt;2$ m) to turbine nacelle (Movies S3 and S4)</td>
</tr>
<tr>
<td>(258; 30%)</td>
<td></td>
</tr>
<tr>
<td>Close approaches: monopole*</td>
<td>Flying very close ($&lt;2$ m) to turbine monopole (Movie S5)</td>
</tr>
<tr>
<td>(110; 13%)</td>
<td></td>
</tr>
<tr>
<td>Close approaches: blades*</td>
<td>Closely approaches or follows turbine blade (Movie S6)</td>
</tr>
<tr>
<td>(55; 6%)</td>
<td></td>
</tr>
<tr>
<td>Chasing/following</td>
<td>Chasing or following other individuals in airspace close to turbine (Movie S7)</td>
</tr>
<tr>
<td>(14; 2%)</td>
<td></td>
</tr>
<tr>
<td>Hovering flight (7; &lt;1%)</td>
<td>Flapping flight that does not involve a clear directional component for $\geq 1$ s (Movie S3)</td>
</tr>
<tr>
<td>Air-braking (5; &lt;1%)</td>
<td>Abruptly stops forward motion of flight in midair (Movie S3)</td>
</tr>
<tr>
<td>Displacement returns (3; &lt;1%)</td>
<td>Returns to turbine after being moved through airspace by blade turbulence (Movie S8)</td>
</tr>
<tr>
<td>Serpentine flight (2; &lt;1%)</td>
<td>Flying on a serpentine (winding) course (Movie S9)</td>
</tr>
</tbody>
</table>

Values in parentheses indicate the number of times each behavior was noted, as well its proportional occurrence (%) among focal behaviors. Categories of behavior are not mutually exclusive. Those marked with an asterisk had been previously reported (13).
Movie S1. Bat making a single directed approach toward a turbine before changing course and flying away at ~0530 hours on September 9, 2012. Blade rotation 14 rpm, wind out of the southwest (225°) at 4.4 m/s, and 44% moon illumination.

Movie S2. Bat making repeated looping approaches to leeward side of wind turbine at ~0109 hours on August 29, 2012. Blade rotation <1 rpm, wind out of the east-northeast (58°) at 5.4 m/s, and 93% moon illumination.
Movie S3. A hoary bat (Lasiurus cinereus; identified acoustically) air-brakes, hovers, and then makes repeated approaches after flying downwind past a wind turbine with curtailed blades at ~0100 hours on August 25, 2012. Blade rotation <1 rpm, wind out of the southeast (131°) at 7.2 m/s, and no moon illumination.

Movie S4. Near-infrared, close-up video of a bat closely approaching and investigating the upper parts of a turbine at ~0430 hours on September 19, 2013. Blade rotation <1 rpm, wind out of the west-southwest (257°) at 2.7 m/s, and no moon illumination.
Movie S5. Bat making repeated close approaches to a turbine monopole at ~2150 hours on August 19, 2012. No blade rotation, wind out of the north-northwest (330°) at 0.4 m/s, and no moon illumination.

Movie S5

Movie S6. Near-infrared, close-up video of a bat closely following a slow moving turbine blade (shadowed on far side of monopole) at ~0240 hours on July 19, 2013 (before monitoring with thermal cameras began). Blade rotation <1 rpm, wind out of the east-northeast (70°) at 7.5 m/s, and no moon illumination.

Movie S6
**Movie S7.** Two bats chasing each other near wind turbine at ~2320 hours on August 5, 2012. No blade rotation, wind out of the north-northwest (321°) at 4.6 m/s, and no moon illumination.

**Movie S8.** Bat repeatedly returning to turbine after close encounters with spinning blades at ~0150 hours on August 22, 2012. Blade rotation 14 rpm, wind out of the east (93°) at 8.0 m/s, and no moon illumination.
Movie S9. Bat exhibiting serpentine flight in lee of wind turbine monopole and blades at ~0500 hours on September 29, 2012. No blade rotation, wind out of the northeast (315°) at 5.8 m/s, and 96% moon illumination.

Movie S9

Movie S10. Two hoary bats (Lasiurus cinereus) interacting in midair on the leeward side of a wind turbine at ~0200 hours on August 25, 2012. The species identification was made from concurrent acoustic calls recorded from the turbine nacelle, in which navigation and social calls characteristic of this species were heard during the close midair approaches. No blade rotation, wind out of the south-southeast (157°) at 8.3 m/s, and no moon illumination.

Movie S10
Movie S11. Bat flying upwind to investigate leeward areas of a wind turbine with blades rotating at full speed at ~0350 hours on July 31, 2012. Bat makes several upwind passes through the moving blades of the turbine without clear indication that it perceives and avoids the fast-moving blades before moving through their plane of motion. Blade rotation speed 14 rpm, wind out of the southwest (228°) at 7.2 m/s, and 95% moon illumination.

Movie S11

Movie S12. Bat flying upwind toward moving turbine blades at ~0600 hours on August 17, 2012 and repeatedly returning to investigate after close encounters with blades. Blade rotation speed 14 rpm, wind out of the north-northwest (324°) at 7.6 m/s, and no moon illumination.

Movie S12

Dataset S1. MATLAB code used for finding bats and other targets in thermal surveillance camera video imagery

Dataset S1