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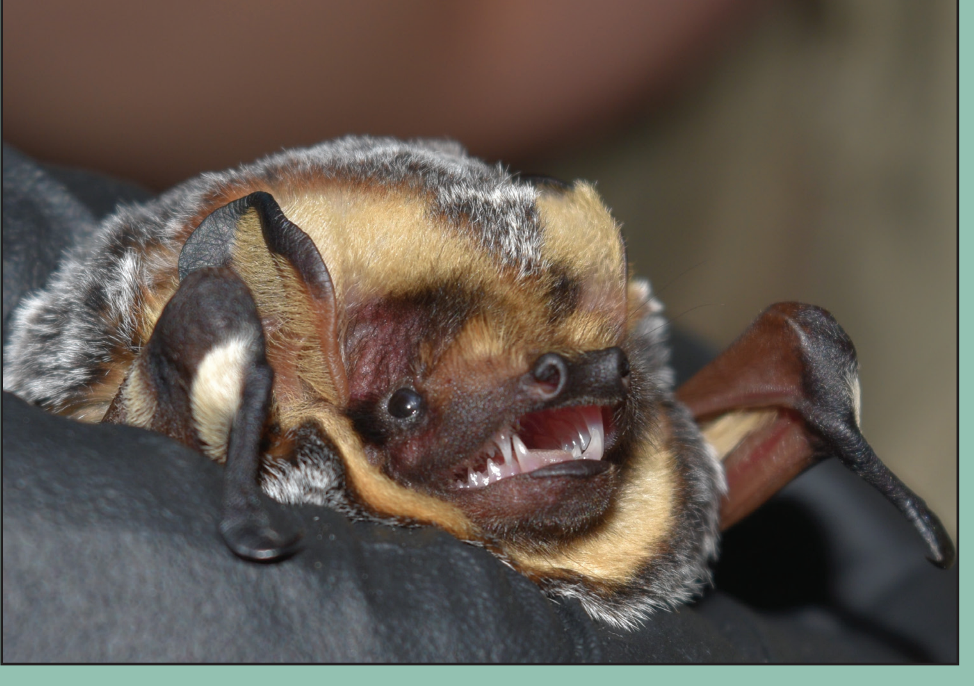

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Bats and Wind Turbines: Adding Ecological Context to the Olfaction Hypothesis

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Abstract - Several hypotheses attempt to explain why bats collide with wind turbines. One recent hypothesis is that collisions result from bats scent marking turbines and that scent-marked turbines produce odor plumes that attract bats. This olfaction hypothesis is intriguing, but currently lacks the ecological context required to assess its plausibility. To provide context, we review when we expect Northern Hoary Bats and Mexican Free-tailed Bats to scent mark under natural conditions, and determine if our findings align with observations of bats interacting with wind turbines. We then consider the plausibility of scent-marked turbines creating odor plumes that attract bats. We conclude that it is unlikely that bats scent mark turbines intentionally in mid-flight or are attracted to scent markings on turbines.

Wind is an important source of carbon-neutral energy production (Larson et al. 2021), but wind-energy facilities also are a source of bat fatalities (O'Shea et al. 2016). In North America alone, wind turbines account for hundreds of thousands of bat deaths per year (Allison and Butryn 2020, Arnett and Baerwald 2013). Migratory tree-roosting species, including *Lasiurus cinereus* (Palisot de Beauvois) (Northern Hoary Bat), *Lasiurus borealis* (Müller) (Eastern Red Bat), and *Lasionycteris noctivagans* (Le Conte) (Silver-haired Bat), as well as the migratory *Tadarida brasiliensis* (I. Geoffroy) (Mexican Free-tailed Bat) constitute >79% of bat fatalities (Allison and Butryn 2020). Collisions often occur following extended activity of bats near turbines, which has led researchers to investigate the potential drivers of bat activity at wind turbines (Cryan and Barclay 2009).

In a recent review, Guest et al. (2022) speculated that olfaction plays a role in bat-turbine interactions. This hypothesis stems from Weaver and Morton (2021), who while working in south Texas, used a video-processing technique to trace individual flight paths and observed several bats making contact with a meteorological tower, often multiple times in the same spot. The behavior was especially prevalent when 2 or more bats were in the video frame and engaged in presumed chase behaviors. During chases, the leading bat would contact the tower surface, and the pursuing individual(s) appeared to touch the same point. Furthermore, bats often approached the tower from downwind, which led to speculation that they were following a chemical gradient. These observations suggested that olfaction-driven turbine interactions consist of 2 mechanistic components. First, bats remained within the rotor-swept area for extended periods to engage in scent marking, and second, scent-marked turbines created odor plumes that attracted bats to tall structures via scent-seeking behavior. Tyler (2023) matched acoustic data to the video data used by Weaver and Morton (2021), to identify flight tracks to species. Using data obtained from September to November 2020

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and April to December 2021, Tyler (2023) identified 5 species by matching 31 video flight tracks to acoustic data. Species present included Northern Hoary Bats and Mexican Free-tailed Bats, 2 of the most wind-affected species (Allison and Butryn 2020). Tyler (2023) found that Mexican Free-tailed Bats accounted for 52% (n = 16) of flight tracks identified to species and further observed tracks of Mexican Free-tailed Bats in 7 of the 8 months during which data were collected. In at least 5 flight tracks (3 in May and 2 in August), Mexican Free-tailed Bats interacted with 2 or more conspecifics and, in some cases, heterospecifics. Tyler (2023) also matched flight tracks from April, May, June, and November (n = 5) to acoustic calls of Northern Hoary Bats.

To prioritize research activities effectively, biologists must assess which hypothesis best aligns with our current understanding of the natural world. To date, the olfaction hypothesis has not been thoroughly contextualized with what we know of bat natural history and ecology (but see Jonasson et al. 2024). Towards this process of contextualization, we first consider if bats are likely to scent mark wind turbines. We review and contrast the ecology and reproductive phenology of Mexican Free-tailed Bats and Northern Hoary Bats (though much of our review is applicable to other North American species affected by wind energy), to determine when and in what contexts we expect scent marking to occur and whether our expectations from the literature align with the purported scent-marking behavior at a meteorological tower (Tyler 2023). Second, we review the literature on the distance at which scent marks are likely perceivable by bats and consider the possibility that scent-marked turbine surfaces create odor plumes that could attract bats to tall structures via scent-seeking behavior.

Scents play a prominent role in the social lives of bats (Bloss et al. 2002, Flores and Page 2017, McCracken and Wilkinson 2000, Muñoz-Romo and Kunz 2009, Muñoz-Romo et al. 2021, Safi and Kerth 2003). Scent marking, during which an individual deposits an odoriferous substance on itself or a substrate, is a mechanism by which the animal distributes compounds that elicit behavioral or physiological responses from an intended target. These odors facilitate various social behaviors, including courtship and territorial displays or demarcation (Adams et al. 2018, Caspers et al. 2008, French and Lollar 1998). Scent marking may be stimulated internally (e.g., hormonally) or externally (e.g., proximity to conspecifics or presence of a scent mark made by another animal; Müller-Schwarze 2006). However, our understanding of scent marking in bats comes mostly from captive colonies, and the extent of scent marking and its role throughout the year remain largely unknown, particularly in temperate-zone bats.

Among bats, odor-producing glands are more common in males than females, and scent marking is most often associated with reproductive periods (Adams et al. 2018, Caspers et al. 2009, Dechmann and Safi 2005, French and Lollar 1998, Muñoz-Romo and Kunz 2009, Rodriguez et al. 2023). Given that glandular hypertrophy usually correlates with the reproductive season, bat interactions with wind turbines and meteorological towers, if driven by scent marking, should align with the reproductive period.

The ecology and reproductive phenology of Mexican Free-tailed Bats and Northern Hoary Bats are distinct, resulting in notable behavioral differences throughout the annual cycle. Male and female Mexican Free-tailed Bats, for example, have gregarious roosting habits throughout the year, with mating occurring over 2–4 weeks in spring (Keeley and Keeley 2004, Smotherman et al. 2016). Conversely, Northern Hoary Bats are typically solitary year-round (Shump and Shump 1982), and mating peaks during late summer and fall (Cryan et al. 2012, Drueker 1972).

Mexican Free-tailed Bats likely rely on odor cues to some extent throughout the year. At close range (<1 m), adult females distinguish roost mates via scent (Englert and Green

2009), and mothers also use odor to locate their pups in dense creches (Gustin and McCracken 1987, McCracken and Gustin 1991). Olfaction may further be important during the mating season when the gular gland hypertrophies. The gular gland is a conspicuous sebaceous gland located on the upper chest and is typical of adult males in the family Molossidae (Muñoz-Romo et al. 2021). Dominant individuals actively smear the secretions on surfaces, to mark territories and establish social hierarchies within bachelor roosts, as well as on themselves and females (French and Lollar 1998). Hypertrophy of the gular gland and associated marking behavior occur in synchrony with gametogenesis in males, suggesting a link to mating (Krutzch et al. 2002).

If scent marking is temporally restricted to the mating period (spring), it is unlikely that the Mexican Free-tailed Bats observed at a meteorological tower across 3 seasons (spring–fall) were engaged in scent marking (Tyler 2023). This disconnect leads to a few hypotheses. First, Mexican Free-tailed Bats engage in scent-marking for reasons not associated with reproduction. Second, they scent mark using alternative glandular or chemical sources, such as saliva or genital excretions. Third, the behaviors observed at meteorological towers are not associated with scent marking or chemical cues, but some other activity.

Northern Hoary Bats produce conspicuously musky odors (J. Clerc, National Renewable Energy laboratory, Golden, CO, and T.J. Weller, US Forest Service, Arcata, CA, 2022 pers. observ.). The source(s) of these odors is unknown, but they may originate from interaural glands located in the preorbital region of the face (Rehorek et al. 2010). These glands produce chemically complex secretions, containing >50 discrete compounds (J. Clerc, National Renewable Energy laboratory, Golden, CO, and T.J. Weller, US Forest Service, Arcata, CA, 2022 unpubl. data). Regardless of the origin of odors in Northern Hoary Bats, we expect scent marking, if it occurs, to be most prevalent during the mating season. Between August and October, males transition from being solitary to aggregating, possibly in the hundreds, to mate, and often aggressively interact with each other in mid-flight (Hall 1946). Although copulation in this species has not been observed, another lasiurine, the Eastern Red Bat, often initiates copulation in mid-flight (reviewed by Cryan and Brown 2007). If Northern Hoary Bats also begin to copulate while flying, it seems more likely that males would scent mark themselves, rather than structures, to advertise the animals' quality to potential mates (Herrera et al. 2023). Currently, there is no evidence that Northern Hoary Bats scent mark surfaces, as part of mating or any other behavior, whether the animal is in flight or roosting. Furthermore, Tyler's (2023) observations of purported scent marking by Northern Hoary Bats at a meteorological tower occurred in April, May, June, and November, but these months are outside the typical mating season of the species.

Can scent-marked surfaces create odor plumes that attract bats to wind turbines, as suggested by Guest et al. (2022)? Odor plumes occur when wind transports scent molecules farther from their source than molecular diffusion alone could (Reddy et al. 2022). To investigate requires us to consider whether bats track odor plumes at distances beyond the rotor-swept area of a wind turbine (>100 m), and whether bats can mark substrate with scent in concentrations sufficient to disperse beyond the footprint of a wind turbine.

To follow an odor to its source, an animal must detect the odor and then resolve concentration and timing gradients to determine directionality. Concentration gradients depend on environmental conditions, such as wind speed and turbulence (Kadakia et al. 2022). In turbulent flows typical of wind-turbine wakes, concentration gradients fluctuate rapidly (Celani et al. 2014), resulting in odor cues that do not reliably point toward the source (Murlis et al. 1992, Reddy et al. 2022). Even if the brief (<1 sec) time of contact with meteorological towers observed by Tyler (2023) was adequate to transfer glandular secretion in concentrations capable of generating an odor plume on wind turbines, tracking odors to their source within a wind-energy facility would be challenging because of rapid fluctuation in concentration gradients.

Though more research is needed to determine if bats are able to track odor plumes over long-distances (>100 m), there is currently no evidence that bats follow odor plumes. Although frugivorous and nectivorous bats use olfaction to localize and discriminate food at distances of <1 m (Acharya et al. 1998, Brokaw and Smotherman 2021, Korine and Kalko 2005), these bats rely more on spatial memory than odor to locate food at distances >5 m (Brokaw et al. 2021, Harten et al. 2020, Morrison 1978). Furthermore, Mexican Free-tailed Bats and Northern Hoary Bats are insectivorous (Shump and Shump 1982, Whitaker et al. 1996), and insect-eating species have reduced olfactory structures, suggesting even less reliance on olfactory cues during flight, compared to frugivores and nectarivores (Eiting et al. 2023, Hutcheon et al. 2002, Smith et al. 2024).

Based on the literature, we suggest that it is unlikely that scent markings on wind turbines could attract bats from more than a few meters away, although other turbine stimuli, such as visual cues, might attract bats to turbines for mating or territory-related scent-marking behavior. We outlined the existing state of knowledge on scent-marking in 2 species to explore the hypothesis of Guest et al. (2022) that bats interacting with wind turbines are engaged in scent marking. We do not expect Northern Hoary Bats or Mexican Free-tailed Bats, 2 of the species most commonly killed at wind facilities, to scent mark turbines. Our review suggests that scent marking under natural conditions for Northern Hoary Bats or Mexican Free-tailed Bats likely coincides with the mating season. However, the restricted mating season for both species contrasts with the much broader temporal period over which Tyler (2023) observed bats approaching meteorological towers. Moreover, there is no evidence that either species scent marks on surfaces in mid-flight, as Tyler (2023) indicated. If Northern Hoary Bats or Mexican Free-tailed Bats behave differently than we expect and do scent mark turbines, it is unlikely that the bats are capable of depositing glandular secretions in concentrations sufficient to produce odor plumes that would attract other bats, given the windy and turbulent flow at wind-energy facilities. Anthropogenic landscape features may elicit maladaptive behaviors in invertebrates and vertebrates alike (Robertson et al. 2017, Van Doren et al. 2017), and although bats may maladaptively express attraction toward turbines, our review suggests that these interactions are not mediated by scent marking.

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