

COULD WHITE-NOSE SYNDROME MANIFEST DIFFERENTLY IN *MYOTIS LUCIFUGUS* IN WESTERN VERSUS EASTERN REGIONS OF NORTH AMERICA? A REVIEW OF FACTORS

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ABSTRACT: White-nose syndrome (WNS) has notably affected the abundance of *Myotis lucifugus* (little brown myotis) in North America. Thus far, substantial mortality has been restricted to the eastern part of the continent where the cause of WNS, the invasive fungus *Pseudogymnoascus destructans*, has infected bats since 2006. To date, the state of Washington is the only area in the Western US or Canada (the Rocky Mountains and further west in North America) with confirmed cases of WNS in bats, and there the disease has spread more slowly than it did in Eastern North America. Here, we review differences between *M. lucifugus* in western and eastern parts of the continent that may affect transmission, spread, and severity of WNS in the West and highlight important gaps in knowledge. We explore the hypothesis that western *M. lucifugus* may respond differently to WNS on the basis of different hibernation strategies, habitat use, and greater genetic structure. To document the effect of WNS on *M. lucifugus* in the West most effectively, we recommend focusing on maternity roosts for strategic disease surveillance and monitoring abundance. We further recommend continuing the challenging work of identifying hibernation and swarming sites to better understand the microclimates, microbial communities, and role in disease transmission of these sites, as well as the ecology and hibernation physiology of bats in noncavernous hibernacula.

Key words: Disease susceptibility, hibernacula microclimate, little brown myotis, *Myotis lucifugus*, noncavernous hibernacula, *Pseudogymnoascus destructans*, western North America, white-nose syndrome, WNS.

Myotis lucifugus, the little brown myotis, is a hibernating bat that uses a wide variety of landscapes, foraging habitats, and roost structures and was once abundant across North America. This species is perhaps the most well studied bat in North America, yet our knowledge base is heavily biased toward studies from eastern North America (east of the Rocky Mountains; hereafter the East). This imbalance is particularly true of its winter ecology; because eastern *M. lucifugus* occurs in large colonies in accessible caves and mines, it is relatively easy to study. Interest in the winter ecology and physiology of *M. lucifugus* has increased since 2006 because of the rapid spread of white-nose syndrome (WNS), a fungal disease of hiber-

nating bats that has substantially affected several of the 12 North American bat species in which the disease has been documented (Frick et al. 2010; Cheng et al. 2021). *Myotis lucifugus* is estimated to have declined by up to 90% across the WNS-affected portion of its eastern distribution (Cheng et al. 2021).

White-nose syndrome is caused by the psychrophilic fungus *Pseudogymnoascus destructans* (*Pd*). With its optimal growing conditions between 12.5 C and 15.8 C (Verant et al. 2012), *Pd* infects tissues during hibernation when bats have relatively low skin temperatures and immune response is suppressed (Bouma et al. 2010). Infections increase arousal frequency during hibernation, which depletes fat stores and leads to

starvation and death (Reeder et al. 2012; Warnecke et al. 2012; Verant et al. 2014). In the East, where bats hibernate in large numbers in caves and mines (Cheng et al. 2021), transmission occurs mostly within hibernacula (Langwig, Frick et al. 2015; Hoyt et al. 2018). Bats acquire infections by contacting other bats or *Pd*-contaminated surfaces within hibernacula, which serve as an environmental reservoir for the fungus (Lorch et al. 2013; Hoyt et al. 2015).

In North America, WNS was initially noted from a cave in New York in late 2006 (Blehart et al. 2009) and by 2022 had spread to 38 US states and eight Canadian provinces (USFWS 2022). In 2016, the disease was unexpectedly discovered in the state of Washington (Lorch et al. 2016). In most of the East, the spread of WNS was documented in samples taken from hibernating bats; where environmental samples were also taken, detection of *Pd* typically lagged behind the detection of WNS on bats by up to 1 yr (Langwig, Frick et al. 2015; Verant et al. 2018). Contrastingly, in the Great Plains and California, initial detections of *Pd* were from environmental samples (e.g., caves, bridges) or samples from active bats in the spring, rather than the disease being documented on hibernating bats (USFWS 2022). Although WNS has been documented in eastern portions of Montana and Wyoming and *Pd* has been detected in eastern Idaho (USFWS 2022), Washington remains the only US state or Canadian province where WNS has been confirmed in bats in the West (defined here as the Rocky Mountains and further west in North America). In Washington, WNS appears to be spreading more slowly than it did in the East, with limited evidence of mass mortality (see section on WNS in Washington).

Although WNS has devastated *M. lucifugus* in the East, it is still unclear whether the disease will have similar effects on this bat in the West. *Pseudogymnoascus destructans* is believed to have originated in Europe (Leopardi et al. 2015; Drees et al. 2017) and is found throughout Asia and the Middle East (Puechmaile et al. 2011; Hoyt et al. 2016). However, Eurasian bats do not experience

high mortality despite developing clinical signs of WNS (Wibbelt et al. 2010; Puechmaile et al. 2011; Hoyt et al. 2016). Eastern North America also has one large hibernaculum where WNS has not resulted in high mortality: Tippy Dam, a concrete spillway in Michigan with approximately 20,000 hibernating *M. lucifugus* (Kurta et al. 2020). That WNS does not always result in severe disease, combined with apparent slower spread and differences in patterns of initial detection moving westward, raises the possibility that WNS may manifest differently in western *M. lucifugus*.

Myotis lucifugus is broadly distributed across North America (Fenton and Barclay 1980). Within that vast distribution, it is associated with many types of forests, grasslands, and deserts. The occurrence of the species across this range of conditions, where localized adaptation of subpopulations exists within a metapopulation (Morrison et al. 2020), reflects a generalized and expanded species niche breadth (Sexton et al. 2017; Carscadden et al. 2020). Adaptations to myriad biotic and abiotic conditions among regions (e.g., Morales et al. 2016) suggests a high potential that the susceptibility of *M. lucifugus* to WNS could vary across North America.

This review seeks to summarize briefly what is currently known about the hibernation ecology and behavior, genetic structure, and physiology of western *M. lucifugus*; highlight differences from eastern *M. lucifugus*; and examine how these differences may influence the spread and severity of WNS in the West. We also explore alternatives to winter colony counts for monitoring changes in species' abundance and conducting disease surveillance and offer recommendations for future research needs.

Global differences in presentation of WNS

Although Eurasian bats develop clinical signs of WNS, infection does not result in high mortality (Puechmaile et al. 2011). Hoyt et al. (2020) found that differential mortality could be attributed to seasonal changes in *Pd*

TABLE 1. Numbers of white-nose syndrome (WNS) surveillance samples collected from live and dead bats and bat roost substrates in Washington, USA, between January 2016 and July 2021 by month of collection and disease status. The causative agent of WNS is a fungus, *Pseudogymnoascus destructans* (*Pd*), that infects hibernating bats. Samples were considered positive for WNS when both histologic lesions were present on bat tissue and *Pd* was detected by PCR or fungal culture; if lesions were not present or the sample was from the environment, it was considered positive for *Pd* only.

Month	WNS-positive	<i>Pd</i> -positive	Inconclusive	WNS-/ <i>Pd</i> -negative
December	0	0	0	10
January	4	0	1	25
February	64	0	0	28
March	25	5	0	14
April	33	1	0	80
May	10	5	2	73
June	6	4	1	163
July	4	1	0	17

levels in the environmental reservoir. In eastern North America, fungal levels within hibernacula remain high year-round, which means that bats become infected early in hibernation and develop high fungal loads by the end, resulting in high mortality (Hoyt et al. 2020). By contrast, *Pd* levels in Eurasian hibernacula decline dramatically over the summer, to approximately 1% of levels observed during hibernation (Hoyt et al. 2020). Returning bats acquire infections much later in the hibernation season, resulting in less severe disease effects (Hoyt et al. 2020). Why *Pd* levels in the environmental reservoir drop in Eurasia, but not in eastern North America, is unclear. Hoyt et al. (2020) compared winter and summer hibernacula temperatures among regions but found no differences. Natural soil microbes may out-compete *Pd* (e.g., Zhang et al. 2015), and Hoyt et al. (2020) hypothesized that microbial competition or predation reduced *Pd* in soil or sediment substrates of Eurasian caves over the summer. Lending support to this hypothesis, a large winter colony of *M. lucifugus* has persisted at Tippy Dam in Michigan, US, despite the presence of WNS since 2015, and microbial communities found on bats hibernating there differed from those hibernating at caves or mines in the region (Kurta et al. 2020). That WNS does not always result in severe disease where it occurs raises the possibility that differences in hibernation

conditions and ecology may mitigate the effects of disease on *M. lucifugus* in western North America.

WNS in Washington, US

White-nose syndrome was first documented in King County, Washington, US, in 2016, although models based on the symbiotic virus associated with *Pd* suggest the fungus was probably introduced to Washington in 2014 (Thapa et al. 2021). As of July 2021, 7 yr later, 163 additional confirmed cases of *Pd* or WNS had been documented in 7/39 Washington counties (Fig. 1A). Positive WNS and *Pd* samples have been found between January and July, with 40% detected in February (Table 1). The proportion of positive WNS or *Pd* samples collected in Washington increased from 2% (of 173 samples) in 2015–2016 to 53% (of 134 samples) in 2019–2020, suggesting that WNS had become more prevalent (Washington Department of Fish and Wildlife 2021; A. Tobin pers. comm.).

Disease surveillance efforts in Washington suggest a greatly reduced rate of spread compared with the rate observed in the East (Fig. 1B). Within 6 yr of first detection in the East (i.e., by 2011), WNS was confirmed or suspected in 14 states in the US and three Canadian provinces (USFWS 2022), encompassing an area approximately 315,000 km². By contrast, the documented area of fungal

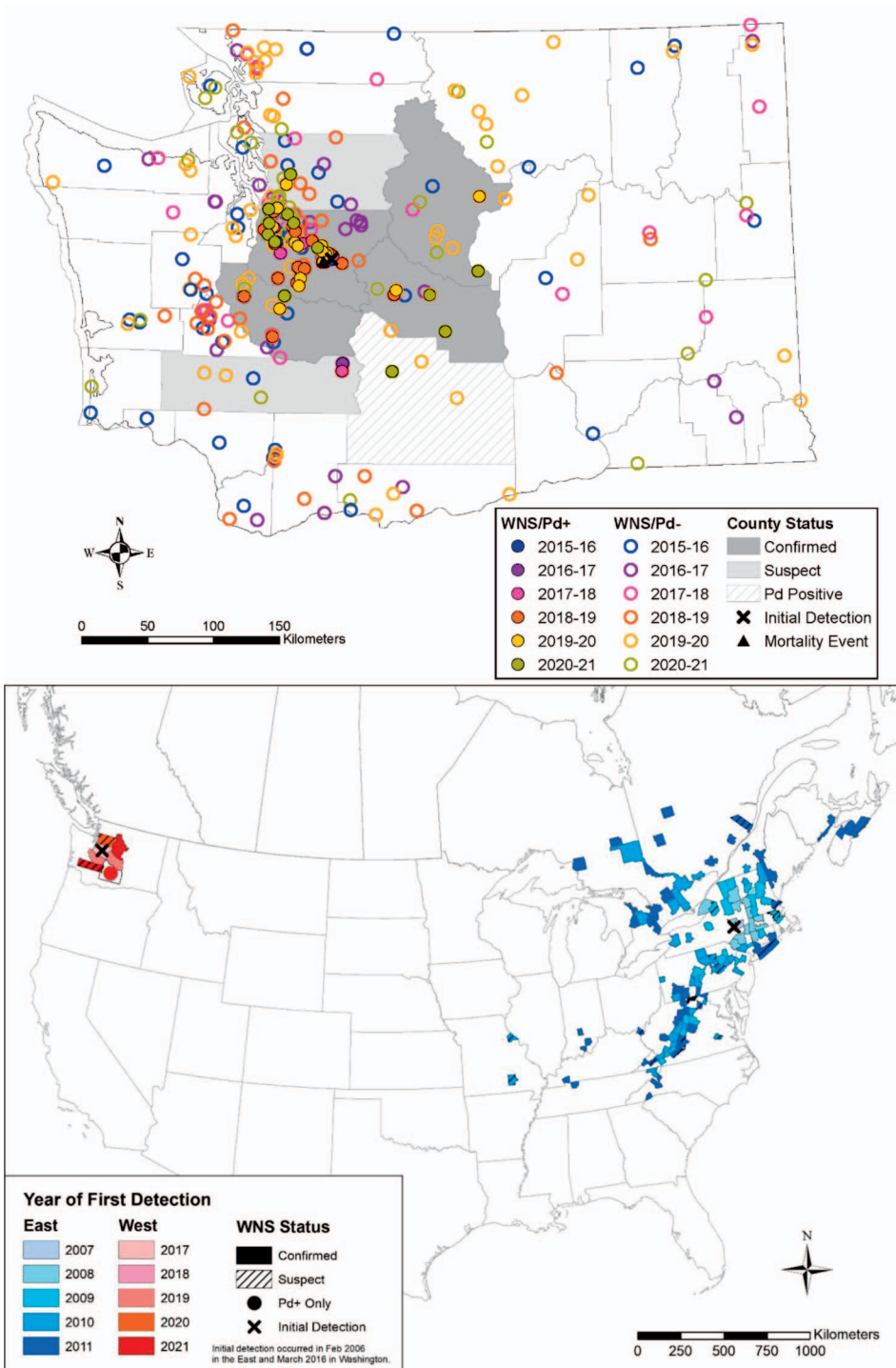


FIGURE 1. (A) Locations of samples collected for white-nose syndrome (WNS) surveillance efforts (passive and active combined) in Washington, USA, from 2016 to 2021. Each circle represents an individual sample: solid circles indicate a sample was positive for either WNS or *Pseudogymnoascus destructans* (*Pd*), and hollow circles indicate negative results, with color indicating the year that sample was collected. Shading of counties in Washington indicates WNS status: confirmed WNS-positive (dark gray shading), suspect for WNS (light gray

spread within Washington in the 6 yr following initial detection (i.e., by 2021), was approximately 38,000 km², calculated as the area of the counties within which WNS had been confirmed or suspected (Fig. 1B). Despite the proximity of *Pd* to southwestern British Columbia, all 277 samples collected within 400 km of the US-Canada border in British Columbia between 2016 and 2021 tested negative (M. Kellner pers. comm.). Surveillance efforts in Oregon also failed to detect either WNS or *Pd* (USFWS 2022), suggesting that by 2021 the fungus had not spread from Washington. Because of the lack of known and accessible hibernacula, sample collection is reliant on dead bat submissions from the public and bat rehabilitators and from actively sampling for fungus at summer roosts. These circumstances may partially explain the observed lower rates of WNS spread in the West relative to the East.

Mortality from WNS in Washington remains well below the mortality reported in eastern hibernacula as WNS spread in that region (Frick et al. 2010; Cheng et al. 2021). In early spring of 2020, >40 dead bats with clinical signs of WNS (UV fluorescence; Turner et al. 2014) were found below a mixed *M. lucifugus* and *Myotis yumanensis* (Yuma myotis) roost in a bat box in King County (Fig. 1A). This mortality event accounts for ≥23% of bats confirmed with WNS in Washington and is the largest observed in the West to date. However, because of the lack of known hibernacula, WNS mortality in Washington cannot be observed directly, and monitoring has focused on maternity colony emergence counts instead. Counts at three mixed *M. lucifugus* and *M. yumanensis* maternity colonies that are within 40 km of the first known detection of WNS in King County have declined 54–97% in the 3–5 yr after first detection of WNS or *Pd* at those sites. It is not

possible to determine whether WNS is the sole cause of the observed declines; however, colonies that have tested negative for WNS or *Pd* have not shown comparable declines over the last several years, even when located in similar habitat (C. Anderson pers. comm.).

How hibernacula type and microclimate may affect the spread and severity of WNS

In stark contrast to the East, where winter cave colonies may contain tens of thousands of bats (Cheng et al. 2021), the paucity of *Myotis* hibernating in caves and mines in the West has long been recognized (Twente 1960; Perkins et al. 1990). A comprehensive review of winter bat surveys of 2,888 caves and mines in 11 western states found only seven caves in Idaho and Montana, most located east of the Rocky Mountains, that contained ≥100 *Myotis* bats (excluding *Myotis velifer*, the cave myotis; Weller et al. 2018). Furthermore, 95% of 502 aggregations were composed of 10 or fewer bats, with single bats accounting for 45% of nonzero counts of *Myotis* bats in caves and 51% in mines (Weller et al. 2018). Recent surveys in western Canada produced similar results. The largest hibernaculum for *M. lucifugus* was a limestone erosion tube east of the Rocky Mountains in the Northwest Territories that contained nearly 3,000 individuals (Wilson 2014). In Alberta, midwinter counts at nine cave or mine hibernacula were smaller, ranging from 3 to 1,830 individuals (L. Wilkinson pers. comm.); most of those sites are on or near the eastern slopes of the Rocky Mountains, with two in the northern Boreal Canadian Shield. In contrast, no *M. lucifugus* cave or mine hibernacula have been confirmed west of the Rocky Mountain Continental Divide in British Columbia, despite hundreds of underground acoustic deployments and some internal inspections (Lausen et al. 2022). These results indicate

← shading), and positive for *Pd* only (hatching). A county was considered suspect for WNS when a sample from a bat tested positive for *Pd* and field signs of WNS were present, but the disease was not confirmed by histology. The initial detection of WNS in Washington is denoted by a black triangle and a mortality event by a black X. (B) Rate of spread by county, district, or rural municipality for WNS and the causative pathogen, *Pd*, in the 6-yr period after the first detections in New York and Washington, USA.

that western *M. lucifugus* relies on non-cavernous structures for hibernation.

Most bat species in the West appear to use rock features rather than caves and mines for hibernation (Neubaum et al. 2006; Johnson et al. 2017; Klüg-Baerwald et al. 2017; Neubaum 2018; Blejwas et al. 2021). To date, only a handful of noncavernous hibernacula have been identified for western *M. lucifugus*. In Colorado, US, Neubaum (2018) found *M. lucifugus* individuals made short elevational movements up to large talus fields, where they presumably hibernated. In coastal Alaska, US, *M. lucifugus* hibernated on steep, forested talus slopes, as well as in holes in the soil beneath the root systems of trees or stumps (Blejwas et al. 2021). The irregular network of underground voids between rocks in talus deposits, known as the Milieu Souterrain Superficiel (MSS), provides roosting habitat and is abundant in mountainous areas of the West (Theobald et al. 2015). Acoustic (Hammesfahr and Ohms 2018) and radiotelemetry studies (Neubaum et al. 2006; Michaelsen et al. 2013; Johnson et al. 2017) indicate other bat species also probably hibernate in the MSS. Both Neubaum (2018) and Blejwas et al. (2021) noted the availability of unused caves and mines within 90–100 km of their study sites, indicating a preference for non-cavernous hibernacula. These observations suggest that management of bats in the West could benefit from thinking beyond the conventional wisdom that “bats hibernate in caves,” because alternative resources for hibernation are plentiful.

Hibernacula in the MSS exhibit different microclimates and microbial communities than those found in caves (Mammola et al. 2016). These factors have the potential to influence not only the growth of *Pd*, but also the hibernation physiology and survival of bats infected with WNS. Higher temperatures in hibernacula correlate positively with fungal growth rates, fungal loads, and WNS effects (Langwig et al. 2016). Cold hibernaculum microclimates, where growth of *Pd* is constrained (Verant et al. 2012), have been associated with higher survival of bats in both laboratory (Johnson et al. 2014; Grieneisen et

al. 2015) and field studies (Langwig et al. 2012; Grimaudo et al. 2022; Loeb and Winters 2022; Turner et al. 2022), including sites where airflow was manipulated to reduce winter temperatures (Turner et al. 2022). Mean temperatures in rock hibernacula across the West ranged from -4.7 C to 1.9 C (see Supplementary Material Table S1; Neubaum et al. 2006; Klüg-Baerwald et al. 2017; Blejwas et al. 2021). These temperatures are all colder than those reported for cave and mine hibernacula of *M. lucifugus* in the East, which commonly range from 4.9 C to 12.4 C (Perry 2013; Verant et al. 2018). These results suggest that in the West, where cold temperatures and periodic bouts of below-freezing temperatures are characteristic of all non-cavernous hibernacula identified to date, the effects of WNS on *M. lucifugus* may be lower.

The effects of humidity on fungal growth and survival of WNS-infected bats have received less attention. Growth of *Pd* at 13 C in the laboratory increased with higher humidity until relative humidity reached 81.5% (Marroquin et al. 2017), and fungal growth was higher in cold and wet hibernacula than in cold and dry hibernacula (Grimaudo et al. 2022). However, Grimaudo et al. (2022) found that *Pd* tissue invasion was more extensive in dry environments, probably because of the fungus seeking moisture from the tissue itself (Grimaudo et al. 2022). Disease severity was further exacerbated by higher evaporative water loss in the dry conditions and resulted in lower survival in cold and dry sites (12/30 bats) than in cold and wet sites (29/30 bats), leading Grimaudo et al. (2022) to conclude that higher humidity reduced WNS severity at cold sites. Hibernacula in the MSS may differ from bounded crevices in a cliff or rock face because they are open to both the surface above and the subsurface below. This openness may account for the high relative humidity observed during winter, which approaches 100% where it has been recorded in Alaska (Blejwas et al. 2021) and Colorado (see Supplementary Material Table S1). Because *M. lucifugus* has relatively high rates of evaporative water loss compared with other bat species (McGuire, Fuller, Dzal,

Haase, Klüg-Baerwald et al. 2021), MSS hibernacula may be favored for hibernation in moist ecoregions. In Alaska and Colorado, where MSS hibernacula are both cold and wet, survival of WNS-infected bats may be higher than in eastern caves and mines. However, because MSS hibernacula are shallower and more sensitive to surface conditions than caves and mines (Mammola et al. 2016), microclimates in western hibernacula probably vary by ecoregion, which may result in varying levels of WNS effects across the West.

Although most attention has focused on hibernaculum microclimates in winter, Hoyt et al. (2020) found that high survival of Eurasian bats resulted from a dramatic decrease in *Pd* levels in caves over the summer, suggesting that summer conditions may also play a role in mediating WNS effects. Hoyt et al. (2020) concluded that summer temperatures in cave hibernacula, which remained relatively cool (3–9 C) in both Eurasia and North America, did not affect persistence of *Pd* and hypothesized that microbial competition or predation was responsible for reducing *Pd* in soil or sediment substrates. However, the only large winter colony in North America to survive despite the presence of WNS hibernates in a concrete spillway, not a cave, and summer temperatures exceed 20 C (Kurta et al. 2020). In Colorado, mean summer (June–August) temperatures at four hibernacula in the MSS were also higher than in caves or mines, ranging from 11 C to 19 C, with corresponding average relative humidity ranging from 42% to 76% (see Supplementary Material Table S1). The possibility that high summer temperatures may affect the persistence of *Pd* over the summer, perhaps by altering the species composition or competitive interactions of the microbial community of sites, merits further investigation, particularly because it may vary between natural and anthropogenic sites (Kurta et al. 2020).

The effects of WNS may vary throughout the West according to site microclimate and duration of winter. In many parts of the West, particularly along the coast, winters are

warming rapidly (McClure et al. 2022), and shorter winters may increase survival of bats hibernating in caves, with or without WNS (Hranac et al. 2021). However, hibernacula in the MSS are closer to the surface and more sensitive to external conditions, and temperatures in the MSS in Alaska were less stable in warm than in cold winters (Blejwas et al. 2021). Loss of insulating snow cover and increasingly extreme temperature fluctuations during winter may render shallower hibernacula unsuitable for hibernation in some areas, although bats may be able to find more stable temperatures by moving deeper into the MSS (Blejwas et al. 2021). The ability for bats to modulate hibernation temperatures with movements to colder areas within the hibernaculum may allow them to moderate disease effects (Blejwas et al. 2021; Loeb and Winters 2022).

How aggregation size, movement distances, and swarming may affect transmission and spread of *Pd*

Transmission of WNS in the East occurs primarily within hibernacula during winter (Langwig, Frick et al. 2015; Hoyt et al. 2018), where the development of an environmental reservoir of *Pd* within 1–3 yr of its arrival was found to result in an infection prevalence of almost 100% early in the hibernation season, regardless of colony size (Langwig, Hoyt et al. 2015; Frick et al. 2017). Before the arrival of WNS, 59% of 255 winter colonies in the East had >100 *M. lucifugus*, with some numbering more than 10,000 individuals (Cheng et al. 2021). The combination of large aggregations, high site fidelity to hibernacula, and high infection prevalence meant that the spread of *Pd* to a relatively small number of hibernacula resulted in large and rapid WNS effects (Cheng et al. 2021). This observation is consistent with modeling results reported by Laughlin et al. (2019) for communally roosting species: they found that pathogen spread and mortality were high when hosts were distributed among a small number of large roosts, even with low levels of host movement among sites. By contrast, hosts that exhibit high site fidelity but are distributed among many small

roosts may be buffered from both the spread of pathogens and mortality (Laughlin et al. 2019). In the East, the effects of WNS were lower on *Myotis leibii* (eastern small-footed bats), which tend to roost solitarily or in small aggregations during winter; populations did not decline significantly after the introduction of WNS (Langwig et al. 2016; Moosman et al. 2017; O’Keefe et al. 2019), and probability of presence actually increased in one study (Johnson et al. 2021). The absence of large hibernacula in caves and mines in the West also suggests the latter scenario. Although hibernating bats in Colorado and Alaska were not visible from the surface because of the jumbled nature of rocks within the MSS, the small size of the interstitial spaces precludes the large aggregations found in caves or mines (Neubaum 2018; Blejwas et al. 2021). No bats were radio-tracked to a location used by another bat in either study, but trail cameras used by Blejwas et al. (2021) did document use of some of the same hibernacula in the MSS in multiple years.

Shorter seasonal movement distances may also slow the rate of *Pd* spread in the West. In areas where rock resources are limited, *M. lucifugus* relies on caves and mines for hibernation, and movements between summer ranges and hibernacula can be substantial: 16–251 km in the eastern US (Griffin 1945), 10–647 km in eastern Canada (Norquay et al. 2013), and 178–236 km in Alberta, Canada (D. Hobson pers. comm.). In the West, which is more topographically diverse, greater availability of structures suitable for hibernation yields shorter movement distances. Autumn movements in the Rocky Mountains averaged 3.0 km (range 0–21.4 km) in Colorado, US (Neubaum 2018), and 5.9 km (range 1.2–19.6 km) in Wyoming, US (Johnson et al. 2017). In coastal Alaska, US, distances between autumn tagging locations and hibernacula ranged from 1.4 to 24.2 km (Blejwas et al. 2021). Shorter movements to hibernacula used by fewer bats in the West should reduce the rate of *Pd* spread compared with longer commutes of larger aggregations of bats moving to and among infected caves in the East.

Bats may spread *Pd* to new hibernacula either by winter movements of bats between hibernacula or during fall swarming. Humans can also spread the fungus to new caves or mines from their equipment or clothing (Ballmann et al. 2017), but poor accessibility of hibernacula in the West should limit this mode of transmission. Although our knowledge of winter movements by bats in any system is scant, Langwig et al. (2021) found evidence for winter movements of eastern bats from larger to smaller colonies in caves before the arrival of WNS. Such movements proved critical for the spread of *Pd* in the Midwest, where 68% of introductions of WNS to new hibernacula occurred later in the hibernation season (Langwig et al. 2021). In the West, *Eptesicus fuscus* (big brown bat) and *Lasionycteris noctivagans* (silver-haired bat) movements between hibernacula during winter have been detected acoustically, although movements typically have been <1 km (Lausen and Barclay 2006; Klüg-Baerwald et al. 2017; Lausen et al. 2022; Neubaum et al. 2022). However, *M. lucifugus* is rarely detected acoustically during winter in the West (Lausen and Barclay 2006; Burles et al. 2014; Neubaum et al. 2022), including at hibernaculum entrances (Blejwas et al. 2021), suggesting infrequent winter movements outside of hibernation sites. Furthermore, where MSS hibernacula are covered by deep snow, movements may not be possible (Neubaum 2018; Blejwas et al. 2021).

Studies of swarming behavior have largely been conducted in the East, where in late summer and early autumn, bats circle at cave and mine entrances for mating and to find suitable hibernacula (Fenton 1969; Thomas et al. 1979). Evidence of autumn swarming behaviors and the geographic features used during this time by *M. lucifugus* in the West is limited but includes cave entrances in Colorado, US (Navo et al. 2002; Neubaum and Siemers 2021), and Vancouver Island, British Columbia, Canada (Davis et al. 2000), and at a cliff face (Shively and Barboza 2017) and MSS hibernacula (Blejwas et al. 2021) in Alaska, US. Cave-hibernating bats often swarm at the same caves where they hibernate (van Schaik

et al. 2015). Given that most western *M. lucifugus* has been found hibernating in smaller numbers at dispersed hibernacula (Neubaum 2018; Blejwas et al. 2021), it may also swarm at other types of sites, such as prominent geographic features, maternity roosts, bridges, or water features that are frequented by larger numbers of bats. Bats in Colorado have been documented swarming at caves where they do not hibernate (Navo et al. 2002; Neubaum and Siemers 2021), which lends support to this hypothesis, as does the appearance of reproductive males with stored sperm at maternity roosts in late summer (Lausen et al. 2022).

Conditions at swarming sites or other sites frequented by bats during this period that are suitable for *Pd* persistence might facilitate intra- and interspecific transmission of *Pd* to a larger number of bats before hibernation, as well as introduce *Pd* to new environments, potentially creating new pathogen reservoirs (Neubaum and Siemers 2021). However, environmental reservoirs are unlikely to develop at maternity roosts, where high summer temperatures limit viability of fungal spores (Hoyt et al. 2021), or in locations open to UV rays during the day (Palmer et al. 2018). Understanding more about autumn swarming behavior, the geographic features used, the suitability of these features as environmental reservoirs for *Pd*, and bat fidelity to these sites may help elucidate the role swarming has in *Pd* transmission and the severity of WNS in the West.

Genetics and physiology of western *M. lucifugus*

Genetic sequencing has confirmed substantial differences in mitochondrial DNA haplotypes among western *M. lucifugus* (Lausen et al. 2008; Morales and Carstens 2018), although an examination of breeding patterns by population genetics suggests widespread breeding among haplotypes (Lausen et al. 2008). Whether differences exist in WNS susceptibility among the different mitochondrial DNA haplotypes remains unexplored. Three studies using both mitochondrial and nuclear markers have found that western *M.*

lucifugus exhibits greater genetic structure than eastern *M. lucifugus*, with bats in the far northwestern portion of the *M. lucifugus* distribution (Alaska in the US, Yukon and northwestern British Columbia in Canada) being the most genetically distinct (Vanhof et al. 2015; Wilder et al. 2015; Davy et al. 2017). This observation suggests a smaller scale of geneflow among western *M. lucifugus* during breeding, which probably results from western bats mating and hibernating closer to their summer ranges than their eastern conspecifics (Moussy et al. 2013; Wilder et al. 2015; Davy et al. 2017). The previously described short movement distances (<25 km) observed in radiotelemetry studies of western *M. lucifugus* (Johnson et al. 2017; Neubaum 2018; Blejwas et al. 2021) support this hypothesis.

Although the western mountain ranges do not entirely restrict gene flow, *M. lucifugus* in the Boreal zone and plains east of the Continental Divide is more closely related to eastern individuals than to more geographically proximate western individuals in the Rocky Mountains and adjacent foothills (Vanhof et al. 2015; Wilder et al. 2015). The foothills area on the eastern edge of the Continental Divide offers a mix of hibernaculum types, and the westernmost large cave hibernacula for *M. lucifugus* are found in this region, which is also the area of greatest genetic admixture between eastern and western groups (Vanhof et al. 2015; Wilder et al. 2015; Davy et al. 2017). Neubaum et al. (2007) noted similar genetic findings for *E. fuscus* along this same interface. The influence of genetic diversity on WNS susceptibility should be explored, given that genetics might influence skin and gut microbiomes (Avena et al. 2016; Nichols and Davenport 2021), immune system function (Moore et al. 2013), hibernal arousal rates (Lilley et al. 2016), and skin properties (Vanderwolf, Campbell et al. 2021; Vanderwolf, Kyle et al. 2021), all of which may play roles in determining susceptibility (Auteri and Knowles 2020; Lemieux-Labonté et al. 2020; Gignoux-Wolfsohn et al. 2021).

Greater genetic differentiation in western *M. lucifugus* may lead to variation in physiol-

ogy, including immune responses to WNS. For example, physiologic differences among bats hibernating in different environments may moderate the effects of differences in hibernation conditions. In Alberta, Canada, Klüg-Baerwald and Brigham (2017) concluded that *E. fuscus* adapted to dry crevice hibernacula in the prairies had lower rates of evaporative water loss than those hibernating in moist cave hibernacula in a forested area. This difference suggests other bat species may also exhibit intraspecific variation in hibernation physiology across ecoregions and hibernaculum types. By contrast, McGuire, Fuller, Dzal, Haase, Silas et al. (2021) found no differences in torpid metabolic rate from three cave hibernacula that spanned a 1,500-km latitudinal gradient. They concluded that although macroclimate varied widely among sites, bats chose hibernacula with preferred microclimates (~2–8 C), resulting in similar selection pressures. However, studies are needed to determine whether hibernating in noncavernous hibernacula, where microclimate options may be fewer within small underground spaces, might result in differences in hibernation physiology that in turn influence WNS susceptibility.

Mapping of the US by Theobald et al. (2015) indicates that the West exhibits more physiographic diversity than the East, and resulting differences in habitat availability may influence *M. lucifugus* in many ways. For example, a greater range of habitat diversity may equate to a wider range of microbiomes and possible differences in *Pd* resistance (Avena et al. 2016). Western topography may also play a driving role in genetic structure by creating more diverse summer foraging habitats and reducing movement distances through a combination of geographic barriers and the greater availability and variety of structures suitable for summer roosts and hibernation. In the northern reaches of the Rocky Mountains, the Continental Divide is a high-elevation division of drainages and climate, with montane forests west of the Continental Divide and Boreal zone and prairie grasslands to the east. These starkly contrasting ecotypes have

undoubtedly placed different selective pressures on bats, resulting in differing phenotypes (Morales et al. 2018).

Methods for monitoring western M. lucifugus: As WNS spreads in the West, important questions remain: where and how fast is spread occurring, how are colonies being affected, and where might disease mitigation be most effectively applied? Most western *M. lucifugus* hibernacula remain unknown; locating additional winter sites would improve our understanding of *M. lucifugus* ecology in the region, including their response to WNS. Development of predictive models to prioritize searches for hibernacula would be helpful, but the limited ability of land cover layers to capture features such as talus and rock crevices, because of issues of scale and resolution, currently limits such models (Theobald et al. 2015; Neubaum and Aagaard 2022). However, as remote sensing techniques such as light detection and ranging (LiDAR), ground-truthing (direct observation) of land cover for forestry practices, and development of soil mapping throughout the West are refined and expanded, the ability to target these habitats will improve. Nevertheless, accessing sites during winter, especially at high elevations, on steep slopes, or in snow-prone areas, will present challenges. Although it may not be widely effective to conduct disease surveillance or monitor colony sizes of *M. lucifugus* at hibernacula in the West, we encourage additional efforts to locate potential hibernation areas to improve understanding of their winter ecology.

Acoustic monitoring in summer is a viable option for documenting changes in the status of *M. lucifugus* and other species, as demonstrated by the North American Bat Monitoring Program (NABat; Loeb et al. 2015; Reichert et al. 2021). In the East, multiple studies documented dramatic declines in *M. lucifugus* activity in the first 1–4 yr after the initial detection of WNS (e.g., Brooks 2011; Dzal et al. 2011; Ford et al. 2011), which generally correlated well with changes in bat counts at hibernacula. However, acoustic monitoring, especially for occupancy trends (Udell et al. 2022), may not be sensitive

enough to track the subtler effects of WNS that could unfold in the West, and a general lack of NABat mobile transects in the West reduces the likelihood of documenting changes in relative abundance across the range of western *M. lucifugus*. Data from stationary acoustic detectors in the Pacific Northwest during 2003–2018 (Rodhouse et al. 2019) did not detect a decline in *M. lucifugus*, although little sampling occurred within *Pd*-positive areas, and the effects of WNS in the 2 yr after initial detection were probably limited. Hicks et al. (2020) proposed developing site-specific models of predicted activity from pre-WNS acoustic data that could be used to monitor for increases in winter activity or decreases in summer activity associated with WNS. Although increases in winter activity of *M. lucifugus* may suggest WNS is present, acoustic monitoring in summer cannot distinguish whether declines in activity would be due to WNS or to other factors such as loss of roosts, foraging habitat, or both. The difficulty of distinguishing *M. lucifugus* calls from those of *Myotis volans* (long-legged myotis) or *Myotis ciliolabrum* (western small-footed bat) in some areas further complicates efforts to monitor *M. lucifugus* in the West with acoustics. Long-term capture surveys at select sites provide important demographic information and have been used in many areas in the East to quantify changes in relative abundance of species over time, including in response to WNS (O’Keefe et al. 2019; Johnson et al. 2021; Reynolds et al. 2021). Capture surveys should be conducted wherever resources permit; however, implementing such a strategy extensively enough to generate statistically robust inferences across the West may be infeasible because of costs, training, travel logistics, and safety considerations.

Counting bats at maternity roosts provides a direct method of tracking colony sizes of *M. lucifugus* in the West and was successfully used to monitor the decline and persistence of a maternity colony at Fort Drum, New York, after the arrival of WNS (Dobony and Johnson 2019). *Myotis lucifugus* is a habitat generalist during summer, often using anthro-

pogenic structures that are easily accessible. Maternity roosts represent many of the largest known aggregations of *M. lucifugus* in the West (Schorr and Siemers 2021). We envision a network of sentinel maternity roost sites where counts of bats could be made annually to track changes in numbers at both local and regional scales. This method of monitoring is likely to be most effective in areas where a colony regularly uses one or few known maternity roosts. The NABat program is already compiling results of emergence counts at maternity roosts to be fed into NABat analyses, and a working group is documenting common survey protocols to provide technical guidance (B. Straw pers. comm.). Additionally, mark-recapture methods could be employed to better understand finer grained components of demographic parameters such as lifespan, annual survival rates, reproductive success, and changes in body condition over time (Schorr and Siemers 2021). Cumulatively, maternity roost monitoring might provide a deeper understanding of colony dynamics across the West.

Maternity roosts may also provide the most reasonable location for disease surveillance, specifically when bats first arrive in the spring. Although it would be preferable to conduct surveillance immediately after hibernation emergence—before bats can reduce fungal loads by homeothermy, increased immune function, and grooming activity (Hoyt et al. 2021)—locating bats at this time is challenging in the absence of known hibernacula. Many western states and provinces have already initiated WNS surveillance at maternity roosts through submission of guano samples. Encouraging the public to report precise return dates of bats at their summer maternity roosts could facilitate mobilization of disease surveillance teams to screen bats or collect guano samples. Additionally, bridges are effective sites for *Pd* surveillance (Olson 2021), largely because of accessibility to locations where bats aggregate and night-roost.

One potential challenge in monitoring *M. lucifugus* across much of the West is its tendency to share maternity roosts with *M. yumanensis*, a morphologically and ecologi-

cally similar species that can be differentiated acoustically and genetically (Weller et al. 2007). To date, mortalities from WNS in Washington are roughly equal for each species (Washington Department of Fish and Wildlife 2021), suggesting that both species will be affected by WNS in the West. Given the differential effects of WNS among *Myotis* spp. in the East (even those within the same hibernaculum; Langwig et al. 2012; Frank et al. 2014; Langwig, Frick et al. 2015), it will be important to quantify differential effects, risk factors, and responses between *M. lucifugus* and *M. yumanensis*. Mixed roosts should be monitored by acoustics, individual marking, genetics from guano or capture, or a combination of techniques to confirm species identity. At a minimum, infected individuals should be identified to species.

Research and management recommendations

We have summarized here that eastern and western *M. lucifugus* differ markedly in behavior, ecology, and genetic structure, and such differences are likely to influence the consequences of WNS for western *M. lucifugus*. We encourage researchers and managers to consider such ecoregional differences for broad-ranging bat species and account for this variation as they conduct analyses and recommend management actions. Such species, including *M. lucifugus*, may represent a metapopulation consisting of subpopulations. A metapopulation structure should result in subpopulations that engage in higher levels of internal interactions compared with the level of interaction among subpopulations (Millstein 2010), which would imply the potential for differing levels of effects from WNS. It will be important to understand whether western *M. lucifugus* possesses traits that may result in lower mortality from WNS, and a better understanding of the winter ecology and physiology of western *M. lucifugus* is important for forecasting and managing the transmission, spread, and effects of WNS in the West. New research approaches will be required to study bats occupying inaccessible, noncavernous hibernacula, such as the MSS,

which are difficult to identify and even more difficult to survey. Additionally, understanding behaviors during swarming, the geographic features used, and whether such sites serve as environmental reservoirs for *Pd* will help predict the rate and mode of transmission and severity of WNS in the West. A thorough study of gene flow across the West would be helpful for informing models of WNS spread, as well as disease mitigation and recovery strategies.

In the West, colony size monitoring and disease surveillance efforts focusing on maternity roosts in buildings, bridges, and bat boxes may be most valuable, given the opportunity to observe and capture bats reliably in those locations. Maternity roosts can be the focal sites for conducting *Pd* surveillance in early spring, monitoring numbers of bats by exit counts and mark-recapture in the summer, and radio-tagging in the autumn and for deploying disease mitigation tools (e.g., Forsythe et al. 2022) as they develop. Focusing monitoring efforts on maternity colonies will help researchers and managers both track the spread of the disease and evaluate its effect on *M. lucifugus* across the West.

SUPPLEMENTARY MATERIAL

Supplementary material for this article is online at <http://dx.doi.org/10.7589/JWD-D-22-00050>.

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LITERATURE CITED

- Auteri GG, Knowles LL. 2020. Decimated little brown bats show potential for adaptive change. *Sci Rep*10: 3023.
- Avena CV, Parfrey LW, Leff JW, Archer HM, Frick WF, Langwig KE, Kilpatrick AM, Powers KE, Foster JT, McKenzie VJ. 2016. Deconstructing the bat skin microbiome: Influences of the host and the environment. *Front Microbiol* 7:1753.
- Ballmann AE, Torkelson MR, Bohuski EA, Russell RE, Blehert DS. 2017. Dispersal hazards of *Pseudogym-*

- noascus destructans* by bats and human activity at hibernacula in summer. *J Wildl Dis* 53:725–735.
- Bleher DS, Hicks AC, Behr M, Meteyer CU, Berlowski-Zier BM, Buckles EL, Coleman JT, Darling SR, Gargas A, et al. 2009. Bat white-nose syndrome: An emerging fungal pathogen? *Science* 323:227.
- Blejwas KM, Pendleton GW, Kohan ML, Beard LO. 2021. The Milieu Souterrain Superficiel as hibernation habitat for bats: Implications for white-nose syndrome. *J Mammal* 102:1110–1127.
- Bouma HR, Carey HV, Kroese FGM. 2010. Hibernation: The immune system at rest? *J Leukoc Biol* 88:619–624.
- Brooks RT. 2011. Declines in summer bat activity in central New England 4 years following the initial detection of white-nose syndrome. *Biodivers Conserv* 20:2537–2541.
- Burles DW, Fenton MB, Barclay RMR, Brigham RM, Volkens D. 2014. Aspects of the winter ecology of bats on Haida Gwaii, British Columbia. *Northwest Nat* 95: 289–299.
- Carscadden KA, Emery NC, Arnillas CA, Cadotte MW, Afkhani ME, Gravel D, Livingstone SW, Wiens JJ. 2020. Niche breadth: Causes and consequences for ecology, evolution, and conservation. *Quart Rev Biol* 95:179–214.
- Cheng TL, Reichard JD, Coleman JTH, Weller TJ, Thogmartin WE, Reichert BE, Bennett AB, Broders HG, Campbell J, et al. 2021. The scope and severity of white-nose syndrome on hibernating bats in North America. *Conserv Biol* 35:1586–1597.
- Davis MJ, Vanderberg AD, Chatwin TA, Mather MH. 2000. Bat usage of the Weymer Creek cave systems on northern Vancouver Island. In: *Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk*. Vol. 1, Darling LM, editor. Kamloops, British Columbia 15–19 February 1999; Ministry of Environment, Lands and Parks, Victoria, British Columbia, Canada, University College of the Cariboo, Kamloops, British Columbia, Canada, pp. 305–312.
- Davy CM, Donaldson ME, Rico Y, Lausen CL, Dogantzis K, Ritchie K, Willis CKR, Burles DW, Jung TS, et al. 2017. Prelude to a panzootic: Gene flow and immunogenetic variation in northern little brown myotis vulnerable to bat white-nose syndrome. *Facets* 2:690–714.
- Dobony CA, Johnson JB. 2019. Observed resiliency of little brown myotis to long-term white-nose syndrome exposure. *J Fish Wildl Manage* 9:168–179.
- Drees KP, Lorch JM, Puechmaille SJ, Parise KL, Wibbelt G, Hoyt JR, Sun K, Jargalsaikhan A, Dalannast M, et al. 2017. Phylogenetics of a fungal invasion: Origins and widespread dispersal of white-nose syndrome. *mBio* 8:e01941–17.
- Dzal Y, McGuire LP, Veselka N, Fenton MB. 2011. Going, going, gone: The impact of white-nose syndrome on the summer activity of the little brown bat (*Myotis lucifugus*). *Biol Lett* 7:392–394.
- Fenton MB. 1969. Summer activity of *Myotis lucifugus* (Chiroptera: Vespertilionidae) at hibernacula in Ontario and Quebec. *Can J Zool* 47:597–602.
- Fenton MB, Barclay RMR. 1980. *Myotis lucifugus*. *Mamm Species* 142:1–8.
- Ford WM, Britzke ER, Dobony CA, Rodrigue JL, Johnson JB. 2011. Patterns of acoustical activity of bats prior to and following white-nose syndrome occurrence. *J Fish Wildl Manage* 2:125–134.
- Forsythe A, Fontaine N, Bissonnette J, Hayashi B, Insuk C, Ghosh S, Kam G, Wong A, Lausen C, et al. 2022. Microbial isolates with anti-*Pseudogymnoascus destructans* activities from western Canadian bat wings. *Sci Rep* 12:9895.
- Frank CL, Michalski A, McDonough AA, Rahimian M, Rudd RJ, Herzog C. 2014. The resistance of a North American bat species (*Eptesicus fuscus*) to white-nose syndrome (WNS). *PLoS One* 9:e113958.
- Frick WF, Cheng TL, Langwig KE, Hoyt JR, Janicki AF, Parise KL, Foster JT, Kilpatrick AM. 2017. Pathogen dynamics during invasion and establishment of white-nose syndrome explain mechanisms of host persistence. *Ecology* 98:624–631.
- Frick WF, Pollock JF, Hicks AC, Langwig KE, Reynolds DS, Turner GG, Butchkoski CM, Kunz TH. 2010. An emerging disease causes regional population collapse of a common North American bat species. *Science* 329:679–682.
- Gignoux-Wolfssohn SA, Pinsky ML, Kerwin K, Herzog C, Hall M, Bennett AB, Fefferman NH, Maslo B. 2021. Genomic signatures of selection in bats surviving white-nose syndrome. *Mol Ecol* 30:5643–5657.
- Grieneisen LE, Brownlee-Bouboulis SA, Johnson JS, Reeder DM. 2015. Sex and hibernaculum temperature predict survivorship in white-nose syndrome affected little brown myotis (*Myotis lucifugus*). *R Soc Open Sci* 2:140470.
- Griffin DR. 1945. Travels of banded cave bats. *J Mammal* 26:15–23.
- Grimaudo AT, Hoyt JR, Yamada SA, Herzog CJ, Bennett AB, Langwig KE. 2022. Host traits and environment interact to determine persistence of bat populations impacted by white-nose syndrome. *Ecol Lett* 25:483–497.
- Hammesfahr AM, Ohms RE. 2018. Winter bat activity in a landscape without traditional hibernacula. *Natural Resource Report NPS/DETO/NRR—2018/1654*. National Park Service. Fort Collins, Colorado, 30 pp.
- Hicks LL, Schwab NA, Homyack JA, Jones JE, Maxell BA, Burkholder BO. 2020. A statistical approach to white-nose syndrome surveillance monitoring using acoustic data. *PLoS One* 15:e0241052.
- Hoyt JR, Kilpatrick AM, Langwig KE. 2021. Ecology and impacts of white-nose syndrome on bats. *Nat Rev Microbiol* 19:196–210.
- Hoyt JR, Langwig KE, Okoniewski J, Frick WF, Stone WB, Kilpatrick AM. 2015. Long-term persistence of *Pseudogymnoascus destructans*, the causative agent of white-nose syndrome, in the absence of bats. *Ecohealth* 12:330–333.

- Hoyt JR, Langwig KE, Sun K, Parise KL, Li A, Wang Y, Huang X, Worledge L, Miller H, et al. 2020. Environmental reservoir dynamics predict global infection patterns and population impacts for the fungal disease white-nose syndrome. *Proc Natl Acad Sci U S A* 117:7255–7262.
- Hoyt JR, Langwig KE, White JP, Kaarakka HM, Redell JA, Kurta A, DePue JE, Scullon WH, Parise KL, et al. 2018. Cryptic connections illuminate pathogen transmission within community networks. *Nature* 563: 710–713.
- Hoyt JR, Sun K, Parise KL, Lu G, Langwig KE, Jiang T, Yang S, Frick WF, Kilpatrick AM, et al. 2016. Widespread bat white-nose syndrome fungus, north-eastern China. *Emerging Infect Dis* 22:140–142.
- Hranac CR, Haase CG, Fuller NW, McClure ML, Marshall JC, Lausen CL, McGuire LP, Olson SH, Hayman DTS. 2021. What is winter? Modeling spatial variation in bat host traits and hibernation and their implications for overwintering energetics. *Ecol Evol* 11:11604–11614.
- Johnson C, Brown DJ, Sanders C, Stihler CW. 2021. Long-term changes in occurrence, relative abundance, and reproductive fitness of bat species in relation to arrival of white-nose syndrome in West Virginia, USA. *Ecol Evol* 11:12453–12467.
- Johnson JS, Reeder DM, McMichael JW 3rd, Meierhofer MB, Stern DWF, Lumadue SS, Sigler LE, Winters HD, Vodzak ME, et al. 2014. Host, pathogen, and environmental characteristics predict white-nose syndrome mortality in captive little brown myotis (*Myotis lucifugus*). *PLoS One* 9:e112502.
- Johnson JS, Treanor JJ, Lacki MJ, Baker MD, Falxa GA, Dodd LE, Waag AG, Lee EH. 2017. Migratory and winter activity of bats in Yellowstone National Park. *J Mammal* 98:211–221.
- Klüg-Baerwald BJ, Brigham RM. 2017. Hung out to dry? Intraspecific variation in water loss in a hibernating bat. *Oecologia* 183:977–985.
- Klüg-Baerwald BJ, Lausen CL, Willis CKR, Brigham RM. 2017. Home is where you hang your bat: Winter roost selection by prairie-living big brown bats. *J Mammal* 98:752–760.
- Kurta A, Foster RW, Daly BA, Wilson AK, Slider RM, Rockey CD, Rockey JM, Long BL, Auteri GG, et al. 2020. Exceptional longevity in little brown bats still occurs, despite presence of white-nose syndrome. *J Fish Wildl Manage* 11:583–587.
- Langwig KE, Frick WF, Bried JT, Hicks AC, Kunz TH, Kilpatrick AM. 2012. Sociality, density-dependence and microclimates determine the persistence of populations suffering from a novel fungal disease, white-nose syndrome. *Ecol Lett* 15:1050–1057.
- Langwig KE, Frick WF, Hoyt JR, Parise KL, Drees KP, Kunz TH, Foster JT, Kilpatrick AM. 2016. Drivers of variation in species impacts for a multi-host fungal disease of bats. *Philos Trans R Soc Lond B Biol Sci* 371:20150456.
- Langwig KE, Frick WF, Reynolds R, Parise KL, Drees KP, Hoyt JR, Cheng TL, Kunz TH, Foster JT, Kilpatrick AM. 2015a. Host and pathogen ecology drive the seasonal dynamics of a fungal disease, white-nose syndrome. *Proc R Soc B* 282:20142335.
- Langwig KE, Hoyt JR, Parise KL, Kath J, Kirk D, Frick WF, Foster JT, Kilpatrick AM. 2015b. Invasion dynamics of white-nose syndrome fungus, midwestern United States, 2012–2014. *Emerg Infect Dis* 21: 1023–1026.
- Langwig KE, White JP, Parise KL, Kaarakka HM, Redell JA, DePue JE, Scullon WH, Foster JT, Kilpatrick AM, Hoyt JR. 2021. Mobility and infectiousness in the spatial spread of an emerging fungal pathogen. *J Anim Ecol* 90:1134–1141.
- Laughlin AJ, Hall RJ, Taylor CM. 2019. Ecological determinants of pathogen transmission in communally roosting species. *Theor Ecol* 12:225–235.
- Lausen CL, Barclay RMR. 2006. Winter bat activity in the Canadian prairies. *Can J Zool* 84:1079–1086.
- Lausen CL, Delisle I, Barclay RMR, Strobeck C. 2008. Beyond mtDNA: Nuclear gene flow suggests taxonomic oversplitting in the little brown bat (*Myotis lucifugus*). *Can J Zool* 86:700–713.
- Lausen CL, Nagorsen DW, Brigham RM, Hobbs J. 2022. *Bats of British Columbia*. 2nd Ed. Royal British Columbia Museum, Victoria, British Columbia, Canada.
- Lemieux-Labonté V, Dorville NAS, Willis CKR, Lapointe FJ. 2020. Antifungal potential of the skin microbiota of hibernating big brown bats (*Eptesicus fuscus*) infected with the causal agent of white-nose syndrome. *Front Microbiol* 11:1776.
- Leopardi S, Blake D, Puechmaille SJ. 2015. White-nose syndrome fungus introduced from Europe to North America. *Curr Biol* 25:R217–R219.
- Lilley TM, Johnson JS, Ruokolainen L, Rogers EJ, Wilson CA, Schell SM, Field KA, Reeder DM. 2016. White-nose syndrome survivors do not exhibit frequent arousals associated with *Pseudogymnoascus destructans* infection. *Front Zool* 13:12.
- Loeb SC, Rodhouse TJ, Ellison LE, Lausen CL, Reichard JD, Irvine KM, Ingersoll TE, Coleman JTH, Thogmartin WE, et al. 2015. A plan for the North American Bat Monitoring Program (NABat). *Southern Research Station General Technical Report SRS-208*. US Department of Agriculture Forest Service, Asheville, North Carolina, 100 pp.
- Loeb SC, Winters EA. 2022. Changes in hibernating tricolored bat (*Perimyotis subflavus*) roosting behavior in response to white-nose syndrome. *Ecol Evol* 12: e9045.
- Lorch JM, Muller LK, Russell RE, O'Connor M, Lindner DL, Blehert DS. 2013. Distribution and environmental persistence of the causative agent of white-nose syndrome, *Geomyces destructans*, in bat hibernacula of the eastern United States. *Appl Environ Microbiol* 79:1293–1301.
- Lorch JM, Palmer JM, Lindner DL, Ballmann AE, George KG, Griffin K, Knowles S, Huckabee JR, Haman KH, et al. 2016. First detection of bat white-

- nose syndrome in western North America. *mSphere* 1:e00148–16.
- Mammola S, Giachino PM, Piano E, Jones A, Barberis M, Badino G, Isaia M. 2016. Ecology and sampling techniques of an understudied subterranean habitat: The Milieu Souterrain Superficiel (MSS). *Sci Nat* 103:88.
- Marroquin CM, Lavine JO, Windstam ST. 2017. Effect of humidity on development of *Pseudogymnoascus destructans*, the causal agent of bat white-nose syndrome. *Northeast Nat* 24:54–64.
- McClure ML, Hranac CR, Haase CG, McGinnis S, Dickson BG, Hayman DTS, McGuire LP, Lausen CL, Plowright RK, et al. 2022. Projecting the compound effects of climate change and white-nose syndrome on North American bat species. *Clim Chang Ecol* 3:100047.
- McGuire LP, Fuller NW, Dzal YA, Haase CG, Klüg-Baerwald BJ, Silas KA, Plowright RK, Lausen CL, Willis CK, Olson SH. 2021a. Interspecific variation in evaporative water loss and temperature response, but not metabolic rate, among hibernating bats. *Sci Rep* 11:20759.
- McGuire LP, Fuller NW, Dzal YA, Haase CG, Silas KA, Willis CK, Olson SH, Lausen CL. 2021b. Similar hibernation physiology in bats across broad geographic ranges. *J Comp Physiol B* 192:171–181.
- Michaelsen TC, Olsen O, Grimstad, KJ. 2013. Roosts used by bats in late autumn and winter at northern latitudes in Norway. *Folia Zool* 62:297–303.
- Millstein RL. 2010. The concepts of ‘population’ and ‘metapopulation’ in evolutionary biology and ecology. In: *Evolution since Darwin: The first 150 years*, Bell MA, Futuyma DJ, Eanes WF, Levinton JS, editors. Sinauer Associates, Sunderland, Massachusetts, pp. 61–86.
- Moore MS, Reichard JD, Murtha TD, Nabhan ML, Pian RE, Ferreira JS, Kunz TH. 2013. Hibernating little brown myotis (*Myotis lucifugus*) show variable immunological responses to white-nose syndrome. *PLoS One* 8:e58976.
- Moosman PR Jr, Anderson PR, Frasier MG. 2017. Use of rock-crevices in winter by big brown bats and eastern small-footed bats in the Appalachian Ridge and Valley of Virginia. *Banisteria* 48:9–13.
- Morales A, Villalobos F, Velazco PM, Simmons NB, Piñero D. 2016. Environmental niche drives genetic and morphometric structure in a widespread bat. *J Biogeogr* 43:1057–1068.
- Morales AE, Carstens BC. 2018. Evidence that *Myotis lucifugus* “subspecies” are five non-sister species, despite gene flow. *Syst Biol* 67:756–769.
- Morales AE, De-la-Mora M, Piñero D. 2018. Spatial and environmental factors predict skull variation and genetic structure in the cosmopolitan bat *Tadarida brasiliensis*. *J Biogeogr* 45:1529–1540.
- Morrison ML, Brennan LA, Marcot BG, Block WM, McKelvey KS. 2020. *Foundations for advancing animal ecology*. Johns Hopkins University Press, Baltimore, Maryland.
- Moussy C, Hosken DJ, Mathews F, Smith GC, Aegerter JN, Bearhop S. 2013. Migration and dispersal patterns of bats and their influence on genetic structure. *Mamm Rev* 43:183–195.
- Navo KW, Henry SG, Ingersoll TE. 2002. Observations of swarming by bats and band recoveries in Colorado. *West N Am Nat* 62:124–126.
- Neubaum DJ. 2018. Unsuspected retreats: Autumn transitional roosts and presumed winter hibernacula of little brown myotis in Colorado. *J Mammal* 99:1294–1306.
- Neubaum DJ, Aagaard K. 2022. Use of predictive distribution models to describe habitat selection by bats in Colorado, USA. *J Wildl Manage* 86:e22178.
- Neubaum DJ, Metza M, Jackson TJ. 2022. Use of acoustic monitoring to determine baseline bat activity at known cave and mine hibernacula in Colorado: 2011–2016. *Colorado Parks and Wildlife Internal Report*. Denver, Colorado.
- Neubaum DJ, O’Shea TJ, Wilson KR. 2006. Autumn migration and selection of rock crevices as hibernacula by big brown bats in Colorado. *J Mammal* 87:470–479.
- Neubaum DJ, Siemers JL. 2021. Bat swarming behavior among sites and its potential for spreading white-nose syndrome. *Ecology* 102:e03325.
- Neubaum MA, Douglas MR, Douglas ME, O’Shea TJ. 2007. Molecular ecology of the big brown bat (*Eptesicus fuscus*): Genetic and natural history variation in a hybrid zone. *J Mammal* 88:1230–1238.
- Nichols RG, Davenport ER. 2021. The relationship between the gut microbiome and host gene expression: A review. *Hum Genet* 140:747–760.
- Norquay KJO, Martinez-Nunez F, Dubois JE, Monson KM, Willis CKR. 2013. Long-distance movements of little brown bats (*Myotis lucifugus*). *J Mammal* 94:506–515.
- O’Keefe JM, Pettit JL, Loeb SC, Stiver WH. 2019. White-nose syndrome dramatically altered the summer bat assemblage in a temperate southern Appalachian forest. *Mamm Biol* 98:146–153.
- Olson C. 2021. Bats and bridges: Using guano sampling for species inventories and Pd surveillance. Webinar. Canadian Wildlife Health Cooperative, Saskatoon, Saskatchewan, Canada. <https://www.youtube.com/watch?v=eMN9TEVWdyM>. Accessed February 2022.
- Palmer JM, Drees KP, Foster JT, Lindner, DL. 2018. Extreme sensitivity to ultraviolet light in the fungal pathogen causing white-nose syndrome of bats. *Nat Commun* 9:35.
- Perkins JM, Barss JM, Peterson J. 1990. Winter records of bats in Oregon and Washington. *Northwest Nat* 71:59–62.
- Perry RW. 2013. A review of factors affecting cave climates for hibernating bats in temperate North America. *Environ Rev* 21:28–39.
- Puechmille SJ, Wibbelt G, Korn V, Fuller H, Forget F, Mühldorfer K, Kurth A, Bogdanowicz W, Borel C, et al. 2011. Pan-European distribution of white-nose

- syndrome fungus (*Geomyces destructans*) not associated with mass mortality. *PLoS One* 6:e19167.
- Reeder DM, Frank CL, Turner GG, Meteyer CU, Kurta A, Britzke ER, Vodzak ME, Darling SR, Stihler CW, et al. 2012. Frequent arousal from hibernation linked to severity of infection and mortality in bats with white-nose syndrome. *PLoS One* 7:e38920.
- Reichert BE, Bayless M, Cheng TL, Coleman JTH., Francis CM, Frick WF, Gotthold BS, Irvine KM, Lausen C, et al. 2021. NABat: A top-down, bottom-up solution to collaborative continental-scale monitoring. *Ambio* 50:901–913.
- Reynolds DS, Shoemaker K, von Oettingen S, Najjar S, Veilleux JP, Moosman PR. 2021. Integrating multiple survey techniques to document a shifting bat community in the wake of white-nose syndrome. *J Fish Wildl Manage* 12:395–411.
- Rodhouse TJ, Rodriguez RM, Banner KM, Ormsbee PC, Barnett J, Irvine KM. 2019. Evidence of region-wide bat population decline from long-term monitoring and Bayesian occupancy models with empirically informed priors. *Ecol Evol* 9:11078–11088.
- Schorr RA, Siemers JL. 2021. Population dynamics of little brown bats (*Myotis lucifugus*) at summer roosts: Apparent survival, fidelity, abundance, and the influence of winter conditions. *Ecol Evol* 11:7427–7438.
- Sexton JP, Montiel J, Shay JE, Stephens MR, Slatyer RA. 2017. Evolution of ecological niche breadth. *Ann Rev Ecol Syst* 48:183–206.
- Shively R, Barboza P. 2017. Range and roosting ecology of the little brown bat, *Myotis lucifugus*, in interior and northern Alaska. *Northwest Nat* 98:122–131.
- Thapa V, Turner GG, Roossinck MJ. 2021. Phylogeographic analysis of *Pseudogymnoascus destructans* paritativirus-pa explains the spread dynamics of white-nose syndrome in North America. *PLoS Pathog* 17: e1009236.
- Theobald DM, Harrison-Atlas D, Monahan WB, Albano CM. 2015. Ecologically-relevant maps of landforms and physiographic diversity for climate adaptation planning. *PLoS One* 10:e0143619.
- Thomas DW, Fenton MB, Barclay RMR. 1979. Social behavior of the little brown bat, *Myotis lucifugus*. I. Mating behavior. *Behav Ecol Sociobiol* 6:129–136.
- Turner GG, Meteyer CU, Barton H, Gumbs JF, Reeder DM, Overton B, Bandouchova H, Bartonička T, Martinkova N, et al. 2014. Nonlethal screening of bat-wing skin with the use of ultraviolet fluorescence to detect lesions indicative of white-nose syndrome. *J Wildl Dis* 50:566–573.
- Turner GG, Sewall BJ, Scafina MR, Lilley TM, Bitz D, Johnson JS. 2022. Cooling of bat hibernacula to mitigate white-nose syndrome. *Conserv Biol* 36:e13803.
- Twente JW. 1960. Environmental problems involving the hibernation of bats in Utah. *Proc Utah Acad Sci* 37: 67–71.
- Udell BJ, Straw BR, Cheng T, Enns KD, Frick WF, Gotthold BS, Irvine KM, Lausen C, Loeb S, et al. 2022. Status and trends of North American bats summer occupancy analysis 2010–2019. North American Bat Monitoring Program, USGS. <https://ecos.fws.gov/ServCat/Reference/Profile/144755>. Accessed March 2023.
- USFWS (US Fish and Wildlife Service). 2022. White-nose syndrome occurrence map—by year. <https://www.whitenosesyndrome.org/where-is-wns>. Accessed November 2022.
- van Schaik J, Janssen R, Bosch T, Haarsma AJ, Dekker JJA, Kranstauber B. 2015. Bats swarm where they hibernate: Compositional similarity between autumn swarming and winter hibernation assemblages at five underground sites. *PLoS One* 10:e0130850.
- Vanderwolf KJ, Campbell LJ, Goldberg TL, Blehert DS, Lorch JM. 2021a. Skin fungal assemblages of bats vary based on susceptibility to white-nose syndrome. *ISME J*. 15:909–920.
- Vanderwolf KJ, Kyle CJ, Faure PA, McAlpine DF, Davy CM. 2021b. Skin pH varies among bat species and seasons and between wild and captive bats. *Conserv Physiol* 9:coab088.
- Verant ML, Bohuski EA, Richgels KLD, Olival KJ, Epstein JH, Blehert DS. 2018. Determinants of *Pseudogymnoascus destructans* within bat hibernacula: Implications for surveillance and management of white-nose syndrome. *J Appl Ecol* 55:820–829.
- Verant ML, Boyles JG, Waldrep W Jr, Wibbelt G, Blehert DS. 2012. Temperature-dependent growth of *Geomyces destructans*, the fungus that causes bat white-nose syndrome. *PLoS One* 7:e46280.
- Verant ML, Meteyer CU, Speakman JR, Cryan PM, Lorch JM, Blehert DS. 2014. White-nose syndrome initiates a cascade of physiologic disturbances in the hibernating bat host. *BMC Physiol* 14:10.
- Vonhof MJ, Russell AL, Miller-Butterworth CM. 2015. Range-wide genetic analysis of little brown bat (*Myotis lucifugus*) populations: Estimating the risk of spread of white-nose syndrome. *PLoS One* 10: e0128713.
- Warnecke L, Turner JM, Bollinger TK, Lorch JM, Misra V, Cryan PM, Wibbelt G, Blehert DS, Willis CKR. 2012. Inoculation of bats with European *Geomyces destructans* supports the novel pathogen hypothesis for the origin of white-nose syndrome. *Proc Natl Acad Sci U S A* 109:6999–7003.
- Washington Department of Fish and Wildlife. 2021. Where is white-nose syndrome in Washington? <https://wdfw.wa.gov/species-habitats/diseases/bat-white-nose#wns-where>. Accessed March 2022.
- Weller TJ, Rodhouse TJ, Neubaum DJ, Ormsbee PC, Dixon RD, Popp DL, Williams JA, Osborn SD, Rogers BW, et al. 2018. A review of bat hibernacula across the western United States: Implications for white-nose syndrome surveillance and management. *PLoS One* 13:e0205647.
- Weller TJ, Scott SA, Rodhouse TJ, Ormsbee PC, Zinck JM. 2007. Field identification of the cryptic vespertilionid bats, *Myotis lucifugus* and *M. yumanensis*. *Acta Chiropterol* 9:133–147.
- Wibbelt G, Kurth A, Hellmann D, Weishaar M, Barlow A, Veith M, Prügler J, Göröfö T, Grosche L, et al. 2010.

- White-nose syndrome fungus (*Geomyces destructans*) in bats, Europe. *Emerg Infect Dis* 16:1237–1243.
- Wilder AP, Kunz TH, Sorenson MD. 2015. Population genetic structure of a common host predicts the spread of white-nose syndrome, an emerging infectious disease in bats. *Mol Ecol* 24:5495–5506.
- Wilson JM, Reimer JP, Allaire D, Lausen CL. 2014. Diversity and distribution of bats in the Northwest Territories. *Northwest Nat* 95:197–218.
- Zhang T, Chaturvedi V, Chaturvedi S. 2015. Novel *Trichoderma polysporum* strain for the biocontrol of *Pseudogymnoascus destructans*, the fungal etiologic agent of bat white nose syndrome. *PLoS One* 10: e0141316.

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