DISEASE ECOLOGY

Context dependency of disease-mediated competitive release in bat assemblages following white-nose syndrome

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Abstract. White-nose syndrome (WNS) has caused dramatic declines of several cave-hibernating bat species in North America since 2006, which has increased the activity of non-susceptible species in some geographic areas or during times of night formerly occupied by susceptible species—indicative of disease-mediated competitive release (DMCR). Yet, this pattern has not been evaluated across multiple bat assemblages simultaneously or across multiple years since WNS onset. We evaluated whether WNS altered spatial and temporal niche partitioning in bat assemblages at four locations in the eastern United States using long-term datasets of bat acoustic activity collected before and after WNS arrival. Activity of WNS-susceptible bat species decreased by 79–98% from pre-WNS levels across the four study locations, but only one of our four study sites provided strong evidence supporting the DMCR hypothesis in bats post-WNS. These results suggest that DMCR is likely dependent on the relative difference in activity by susceptible and non-susceptible species groups pre-WNS and the relative decline of susceptible species post-WNS allowing for competitive release, as well as the amount of time that had elapsed post-WNS. Our findings challenge the generality of WNS-mediated competitive release between susceptible and non-susceptible species and further highlight declining activity of some non-susceptible species, especially *Lasiurus borealis*, across three of four locations in the eastern United States. These results underscore the broader need for conservation efforts to address the multiple potential interacting drivers of bat declines on both WNS-susceptible and non-susceptible species.

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Introduction

Emerging infectious diseases of wildlife are a key driver of biodiversity loss and global change worldwide (Daszak 2000, Brook et al. 2008). The impacts of disease can extend beyond direct mortality of susceptible species to include indirect effects on non-susceptible species which have the potential to transform entire animal communities or ecosystems (Ostfeld et al. 2008). Understanding the community-level consequences of disease is critical for conserving biodiversity in the face of global change (Brook et al. 2008).

White-nose syndrome (WNS) is an infectious disease that has caused severe declines of several cave-hibernating bat species in North America since first detection in New York in 2006 (USGS National Wildlife Health Center 2019). As of 2020, WNS occurred throughout much of the eastern and central regions of the United States and southern Canada and has been detected in several locations in the western United States (USGS National Wildlife Health Center 2019). The causative fungal agent, *Pseudogymnoascus destructans* (*Pd*), has also been confirmed present as far south as Texas and in additional western locations in Washington and California (USGS National Wildlife Health Center 2019). *Pseudogymnoascus destructans* infects the epithelial tissues of cave-hibernating bats and causes them to arouse more frequently during hibernation (Reeder et al. 2012). This increased arousal reduces fat reserves and disrupts water balance, often leading to starvation- or dehydration-induced mortality (Reeder et al. 2012). Accordingly, several species detected with WNS infections have declined by 30–99% annually (Frick et al. 2010), including four highly susceptible species (the little brown bat *Myotis lucifugus*, the federally endangered Indiana bat *M. sodalis*, the threatened northern long-eared bat *M. septentrionalis*, and the tri-colored bat *Perimyotis subflavus*) and one moderately susceptible species (eastern small-footed bat *M. leibii*) (Langwig et al. 2012). The big brown bat *Eptesicus fuscus* is susceptible to WNS and some mortality has been reported; however, due to larger body size, greater overwinter fat stores, and longer torpor bout durations when exposed to *Pd*, the species has been relatively unaffected throughout much of the WNS-impacted region (Frank et al. 2014, Moore

et al. 2018). Several tree-hibernating bat species have also tested positive for *Pd*, including the eastern red bat *Lasiurus borealis*, the hoary bat *Lasiurus cinereus*, and the silver-haired bat *Lasionycteris noctivagans*, but because they are not typically cave-hibernators or do not use deep torpor during winter, they are generally not susceptible to WNS (Johnson et al. 2013, Bernard et al. 2015).

The effects of WNS on bat assemblages may extend beyond mortality of susceptible species to include compositional effects on bat community structure (Jachowski et al. 2014, Pettit and O'Keefe 2017). The differential impacts of WNS on cave-hibernating and tree-hibernating species may drive changes in spatial and temporal niche partitioning post-WNS (Jachowski et al. 2014). Bats are thought to limit interspecific competition with species that share similar morphology (i.e., wing-loading and body size), diets, and call frequencies by reducing overlap in spatial (Arlettaz 1999, Razgour et al. 2011) and temporal niche space (Kunz 1973, Reith 1980, Adams and Thibault 2006). Many WNS-susceptible bats are smaller *Myotis* species that consume different prey than the larger non-susceptible bats (Moosman et al. 2012, Thomas et al. 2012). Thus, competition between susceptible and non-susceptible species may be more strongly related to competition for aerial foraging space than to competition for prey resources, resulting in strong spatial and temporal niche partitioning between the two groups (but see Morningstar et al. [2019] for evidence that some susceptible species may compete with non-susceptible species for prey).

Spatial and temporal niche partitioning may be destabilized by emerging infectious diseases (Dobson and Hudson 1986, Lips et al. 2006). For bats, Jachowski et al. (2014) found that dramatic declines of *M. lucifugus* post-WNS were associated with relaxation of spatial and temporal niche partitioning in sympatric, non-impacted bat species in northwestern New York. They inferred that non-impacted species were able to occupy locations and times of night formerly dominated by *M. lucifugus* due to reduced competition with this previously abundant species. Similarly, Thalken et al. (2018) documented increased capture rates for non-susceptible species following declines of *M. septentrionalis* post-WNS, and Morningstar et al. (2019) found

increased activity of *E. fuscus* associated with declines in *M. lucifugus* activity, with both studies inferring that less-impacted species were able to exploit spatial and dietary niche spaces vacated by WNS-susceptible bats. Although these studies suggest that disease-mediated competitive release (DMCR), that is, WNS-related declines in activity of susceptible species drives increases in non-susceptible species activity, is common, research on long-term changes in bat assemblages related to WNS across multiple locations could provide stronger insights into the generality of this pattern. These patterns have not been investigated across multiple species and sites simultaneously; thus, a broad-scale investigation of the differential effects of WNS on susceptible and non-susceptible bat species is warranted.

Of particular interest is whether similar patterns of niche relaxation occur in bat assemblages with different proportions of WNS-susceptible versus non-susceptible bats in the species pool. In the aforementioned New York and Kentucky locations, the bat assemblages had higher activity of one WNS-susceptible species, *M. lucifugus* or *M. septentrionalis*, relative to other species, and the drastic decline of the *Myotis* spp. is believed to have released the non-susceptible species from competition. Yet, locations with low activity of susceptible species pre-WNS may show little or no change in spatial or temporal niche partitioning following WNS because the susceptible species was not competitively dominant.

We investigated the assemblage-level consequences of WNS at four locations in the eastern United States that span a range of years since WNS onset. Bat assemblages at each of these locations include both highly and moderately susceptible species (*M. lucifugus*, *M. sodalis*, *M. septentrionalis*, *M. leibii*, and *P. subflavus*), henceforth referred to as susceptible species, and species that have tested positive for *Pd* presence but are relatively unaffected by WNS (*L. borealis*, *L. cinereus*, *L. noctivagans*, *E. fuscus*, and *Nycticeius humeralis*), henceforth referred to as non-susceptible species. Based on the evidence supporting disease-mediated competitive release (Jachowski et al. 2014, Thalken et al. 2018, Morningstar et al. 2019), we hypothesized that declines of WNS-susceptible species post-WNS would alter spatial and temporal niche partitioning at

each of these locations, but that specific responses would be modified by the level of activity of susceptible bat species pre-WNS and time since WNS onset. We represent these hypotheses, and the interactions between spatial and temporal overlap of susceptible and non-susceptible species and time since WNS onset with six separate models are shown in Table 1. Specifically, we hypothesized that non-susceptible species' activity would only increase at locations where susceptible species had higher activity than non-susceptible species pre-WNS (Jachowski et al. 2014). We also hypothesized that hourly activity peaks for non-susceptible species would change at these locations (Table 1), as others have found that non-susceptible bats altered temporal activity patterns post-WNS (Jachowski et al. 2014). Many bats are most active in the hours after sunset and just before sunrise (Kunz 1973, 2004); therefore, we hypothesized non-susceptible bats would increase activity during immediate post-sunset and pre-dawn periods after WNS due to relaxed competition with declining WNS-susceptible species (Jachowski et al. 2014). We further hypothesized that there would be a time-lagged WNS effect, whereby competitive exclusion would occur prior to WNS arrival and competitive release would occur several years after WNS arrival at these locations (Table 1). Finally, we hypothesized that bat activity would be higher at sampling locations closer to water sources, given many species' affinity to foraging over water (Ford et al. 2006).

METHODS

Study design

Long-term acoustic datasets of nocturnal foraging bat activity collected at four locations in the eastern United States before and after WNS was first detected at each site were used to investigate the direct and indirect effects of WNS on non-susceptible species (Appendix S1: Fig. S1; Table 2). Because the four locations varied considerably in habitats, climates, and sampling effort, high variability in observed bat activity across locations was anticipated. Thus, predictions of bat assemblage responses were tested for each study location and species separately, as opposed to an analysis of all four sites combined.

Table 1. Models used to assess competing hypotheses about the effect of spatial or temporal niche partitioning on non-susceptible bat species activity ("Susceptible" and "Hour" variables where susceptible = pooled activity of all WNS-susceptible species and hour past sunset is modeled with and without a quadratic effect), while accounting for the influence of years before or after WNS arrival (WNS) and distance to water (water).

Model	A priori hypothesis
(1) Hour × Susceptible + WNS	Competitive exclusion in *spatial and temporal* niches between non-susceptible and susceptible species in years before WNS arrival; competitive release in years after WNS arrival, and hourly activity may increase or decrease after WNS
(2) Hour × Susceptible	Competitive exclusion in *spatial* and *temporal* niches between non-susceptible and susceptible species
(3) Hour × WNS + Susceptible	Hourly bat activity peaks change from before to after WNS, and hourly activity may increase or decrease with susceptible bat species activity
(4) Hour × WNS	Hourly bat activity peaks change from before to after WNS, but this temporal trend is not affected by spatial or temporal niche partitioning with susceptible bat species
(5) WNS	Non-susceptible bat activity changes from before to after WNS, but this temporal trend is not affected by spatial or temporal niche partitioning with susceptible bat species
(6) Hour	Non-susceptible bat activity changes by hour of night but is not affected by spatial or temporal niche partitioning with susceptible bat species or by years before or after WNS
+ distance to nearest water feature	Bat activity will be higher closer to water

Notes: We included the distance to water variable in all models. An "×" indicates an interaction term.

Table 2. Attributes of four long-term acoustic sampling locations in the eastern United States, 2003–2018 (see text for details on survey duration per site).

Study location and references	Lat/Long	Size (ha)	Elev (m)	Dominant forest type	NSP	Sample point placement	Bat species present	Year WNS	MYS	Hour	Acoustic detectors	Acoustic software
Fort Drum, NY (Ford et al. 2011)	44°03′32.8″N 75°46′11.1″W	43K	125–278	Northern hard woods	71/255	<100 m water feature; forest tracks, canopy gaps, emergent wetlands	MYLU, MYSO, MYSE, MYLE, PESU, EPFU, LANO, LABO, LACI	2008	May–Sept./ 2003-2017	0–11	Anabat II (weather-proofing, mic. exposed pre-2011, in PVC post-2011)	Kaleidoscope Pro classifier 4.2.0
Fernow Experimental Forest, WV (Ford et al. 2006)	39°00′0″N 79°67′0″W	1.4K	533–1112	Allegheny/ northern hard-woods and oak	4/4	Near 1 pond and 3 1st or 2nd order streams	MYLU, MYSO, MYSE, MYLE, PESU, EPFU, LANO, LABO, LACI	Winter 2010–2011	May–Sept./ 2004–2006, 2012, 2013, 2016	0–12	Anabat II and Wildlife Acoustic SMZCs (no weather-proofing)	Analook 4.8p
Fort Pickett, VA (St. Germain 2012)	37°04′23.6″N 77°58′20.8″W	16K	75–110	Piedmont mixed pine hard woods	84/82	Random - stratified across 6 habitat types	MYLU, MYSO, MYSE, PESU, EPFU, LANO, LABO, LACI, NYHU	Winter 2010–2011	May–Aug./ 2007, 2016	0–12	Anabat II (weather-proofing with mic. exposed)	Analook W (Beta version 3.2)
Wisconsin	43°04′05.3″N 87°53′26.1″W	10/113	188–260	Deciduous boreal	2/2	Urban Ecology Center and Schmeeckle Reserve	MYLU, MYSE, PESU, EPFU, LANO, LABO, LACI	Spring 2014– Winter2015	May–Sept./ 2007-2017	0-11	Anabat II (weather-proofing)	Kaleidoscope Pro classifier 4.2.0

Notes: EPFU, *Eptesicus fuscus*; Hour, Hours sampled post-sunset; LABO, *Lasiurus borealis*; LACI, *Lasiurus cinereus*; LANO, *Lasionycteris noctivagans*; MYLE, *Myotis leibii*; MYLU, *Myotis lucifugus*; MYS, months and years sampled; MYSE, *Myotis septentrionalis*; MYSO, *Myotis sodalist*; NSP, Number of sampling points pre- and post-WNS; NYHU, *Nycticeius humeralis*; PESU, *Perimyotis subflavus*; Year WNS, Year WNS 1st detected.

Sites were revisited that were acoustically sampled prior to WNS by our team and collaborators in temperate forest bat assemblages of northwestern New York, central and southern Wisconsin, north-central West Virginia, and southeastern Virginia (Table 2). These study areas were selected based on the availability of pre-WNS acoustic data and the ability to address our study objectives (i.e., locations that varied in the range of time elapsed since WNS was first detected). Four non-susceptible bat species were detected across all four sites, including *L. borealis*, *L. cinereus*, *L. noctivagans*, and *E. fuscus* (Table 2). One non-susceptible species, *N. humeralis*, occurred only in Virginia (Table 2). Three susceptible species (*M. lucifugus*, *M. septentrionalis*, and *P.*

subflavus) were detected across all four sites, whereas *M. sodalis* were detected in three of four sites, and *M. leibii* were detected in low numbers at two of four sites (Table 2; Appendix S1: Table S1). Sampling points (georeferenced locations where acoustic detectors were placed) were revisited at each of the four study areas to collect acoustic data on nocturnal foraging bat activity following the same sampling protocol used in the pre-WNS studies (Table 2). An attempt was made to sample the same locations during the same months and hours of night as in the pre-WNS studies. However, owing to the high number of sampling points and varying annual project objectives, not all points were relocated or resampled over the exact same time periods within the summer pre- to post-WNS, and sampling effort pre- to post-WNS was not always equal (Table 2; Appendix S1: Table S1). Sampling points were established across a range of habitat conditions, including forest tracks, forest canopy gaps, and riparian areas, but proximity to water features was prioritized at some locations to maximize detection of multiple species (Table 2). The number of sampling points and number of years sampled varied by study area (Table 2).

Study area description

The four study areas represent a range of habitats, land uses, and physiographic conditions (Table 2). Fort Drum is an approximately 43,750-ha U.S. Army installation located where several ecoregions converge. Caves occurring in limestone "karst" formations to the west and east of Fort Drum provide hibernation sites for bats (Ford et al. 2011). Topography in the region is rolling and elevations range from 125 to 278 m. Approximately 57% of Fort Drum is covered with northern hardwood-dominated forest types, and approximately 20% of the installation area contains small lakes, ponds, and wet meadows (Jachowski et al. 2014). White-nose syndrome was first detected on Fort Drum in 2008.

The Fernow Experimental Forest is a 1473-ha Allegheny hardwood forest in the central Appalachian Mountains of West Virginia used for forest management research by the USDA Forest Service (Ford et al. 2005). The forest has a mix of older-aged forest, mid-successional stands, and both fire-suppressed and fire-altered conditions. Elevations range from 533 to 1112 m, and the

topography is steep and mountainous (Adams et al. 2012). Several small cave systems nearby serve as winter hibernacula for bats within the Experimental Forest in the underlying Greenbrier Limestone, including Big Springs Cave, a Priority III *M. sodalis* hibernaculum (Ford et al. 2005). White-nose syndrome was first detected in Fernow Experimental Forest in 2010 within this hibernaculum (Table 2).

Fort Pickett is a 16,870-ha Army National Guard Maneuver Training Center in southeastern Virginia (St. Germain 2012). Fort Pickett is approximately 36 km from the Fall Line between the Piedmont physiographic region and the Coastal Plain physiographic region and is largely dominated by lower Piedmont mixed pine-hardwood forests interspersed among open and forested live-fire and maneuver training lands, pine savannas, and managed pine plantations (St. Germain 2012). The topography consists of rolling hills and both broad and narrow valleys with an elevation range from approximately 75–110 m. Fort Pickett lies approximately 100 km east of karst formations with cave systems that support hibernating bats. Though not near any known hibernacula, WNS was first detected at Fort Pickett in the winter of 2010–2011 (Table 2).

The two sampling points in Wisconsin included one at the Urban Ecology Center in Milwaukee and another to the northwest at the University of Wisconsin Stevens Point Schmeeckle Reserve. The Urban Ecology Center site is surrounded by an urban environmental matrix and numerous deciduous forest woodlots and green spaces. The Schmeeckle Reserve site is a 113-ha conservancy area surrounded by a matrix of urban structures, a golf course, forest woodlots, and agricultural lands. Schmeeckle Reserve occurs within a deciduous-boreal transition zone and the topography at both locations is generally flat, with elevations ranging from 190 to 205 m at the Urban Ecology Center and from 330 to 340 m at the Schmeeckle Reserve. White-nose syndrome was detected in nearby counties in Wisconsin from spring 2014 through winter 2015 (White-Nose Syndrome Response Team 2019).

Acoustic sampling

Bat echolocation passes were passively recorded at all sampling points in each of the four study areas using zero crossing, frequency-

division Anabat II bat detectors (Titley Scientific, Brendale, Queensland, Australia) (Table 2); SMZC and SM2 detectors (Wildlife Acoustics Inc., Maynard, Massachusetts, USA) were also used in Virginia and West Virginia. All acoustic surveys were conducted from May to August or September (Table 2). Detectors recorded bat activity from dusk to dawn (Table 2). Detectors were attached at the top of tripods approximately 1.5 m high in New York, attached to permanent posts in Wisconsin at 3 m high, and attached to tree branches or boles in the early years and to poles with detached microphones in the later years at West Virginia and Virginia. PVC weatherproofing techniques were used to protect acoustic recorders at some study areas, while no weatherproofing was used at other locations (Table 2), but weatherproofing methods were similar before and after WNS within each study area except at Fort Drum. At this location, units were placed in weatherproof boxes with the microphone exposed until 2010. From 2011 and thereafter, a PVC tube was attached to protect the microphone from rain as described by Britzke et al. (2010). These investigators did not find differences in detection probability between PVC tube weatherproofing techniques and exposed microphones. Acoustic surveys were conducted in New York from 2003 to 2017 (WNS impacts detected in 2008), in West Virginia from 2004 to 2006 (pre-WNS) and in 2012, 2013, and 2016 (post-WNS), in Virginia in 2007 (pre-WNS) and 2016 (post-WNS), and in Wisconsin from 2007 to 2017 (WNS detected in the nearest counties during winter 2015–2016) (Table 2).

Acoustic data processing

Most echolocation passes were analyzed using Kaleidoscope Pro classifier (Wildlife Acoustics Inc.), but some of the early pre-WNS data were analyzed visually in Analook (Titley Scientific) (see Table 2 and citations within for detailed descriptions of acoustic analysis methods). When results from Kaleidoscope Pro were compared to visual expert classifications in Analook, Nocera et al. (2019a) found minimal difference in total activity by individual bat species at the nightly level.

The resulting processed acoustic data were used to tally the number of identifications per hour at each sampling point and night for each species at all four study areas. These tallies of species-level hourly bat passes at each site are commonly used as an index of bat activity (Hayes 1997, Law and Chidel 2002, Gehrt and Chelsvig 2004, Owen et al. 2004, Razgour et al. 2011). Although such indices do not account for variation in detection probability (Anderson 2001, MacKenzie et al. 2006), if sampling methods are standardized (as is the case in this study *within* each study area) such indices can be used to infer population trends over time, make comparisons across environmental gradients, and provide an efficient and reliable method for quantifying trends in activity and competition in bat assemblage studies (Link and Sauer 1998, Razgour et al. 2011, Barlow et al. 2015, Gibb et al. 2019).

Spatial analysis of environmental variables

A geographic information system (GIS) proximity analysis was used to calculate distance to water for each individual detector location at the four study sites. The ArcMap 10.6.1 (ESRI, Redlands, California, USA) Merge tool was used to combine multiple USGS National Hydrography Datasets into a single waterbody layer. The near tool in ArcMap was used to calculate the distance from each sampling point to the nearest stream or waterbody.

Because forest loss is a major threat to bat biodiversity (Frick et al. 2019), we also used GIS to assess changes in forest habitat extents from before to after WNS across all four study areas. We found minimal change in forest cover across the four sites (Appendix S1: Table S2); thus, forest cover change was not hypothesized to impact bat activity at our study areas and was not included as a covariate in bat activity models described below.

Modeling bat activity

Separate analyses of the pooled activity of WNS-susceptible and non-susceptible species activity were conducted to explore general patterns at each of the four study areas and more detailed models were also fit for each non-susceptible species to explore individual species responses to WNS-induced declines of susceptible species and other predictor variables of interest (Table 1). We were unable to fit detailed models of susceptible species activity due to few

detections post-WNS. For the detailed suscepti-ble species models, zero-inflated generalized lin-ear mixed models (GLMMs) of bat activity (number of bat passes per hour for either WNS-susceptible or non-susceptible species) were fit as a function of hour past sunset, years before or after WNS (either a pre- or post WNS categorical variable at West Virginia and Virginia due to a gap in the time series, or a continuous time vari-able at New York and Wisconsin), distance to water, and activity of non-susceptible or suscep-tible species' activity, respectively. Models with an interaction between "hour past sunset" and "years before or after WNS" or "susceptible/non-susceptible species activity" were also fit to assess whether bats were changing the hours of night in which they were most active in relation to time since WNS or susceptible/non-susceptible bat activity, or both. All "hour past sunset" mod-els were fit with and without quadratic effects to assess whether the shape of the hourly activity function changed post-WNS. Models were also fit with effects for the hour past sunset, WNS-susceptible/non-susceptible species, and years before or after WNS *only* to test whether there was support for these factors individually. All models also included random effects for the sampling night within each sampling point to account for (1) repeated measures per sampling point, (2) extra sampling effort post-WNS at Fort Drum, and (3) night and weather effects, that is, rain. Each sampling night represented a unique day within the time period of the survey (Table 2).

All models were fit using the glmmTMB pack-age (Brooks et al. 2017) in R version 4.0.3. Zero-inflated models were chosen because of the high frequency of zero observations in our hourly bat activity data and because zero-inflated models were supported over models that lacked zero-inflation (lower AIC values; Burnham and Anderson 2002) during exploratory data analy-sis. Predictor variables were included in the zero-inflated GLMMs in the conditional count compo-nent but not the zero-inflation component of the full model. These models were fit with both Pois-son and negative binomial distributions and the best distribution was selected based on the lowest AIC value (Burnham and Anderson 2002).

After selecting the best-fitting distribution with our global model, AIC model selection was used

to rank the different GLMMs representing our hypotheses (Table 1). All models with ΔAIC < 4 were considered to be supported by the data per (Burnham and Anderson 2002). For the best sup-ported models, the predicted effects of hour past sunset and years before or after WNS on bat spe-cies activity were estimated using the plot_model function in the sjPlot package (v2.6.2, Ludecke 2018). Model fit was assessed using the r2 func-tion in the sjstats package (v0.17.2, Ludecke 2018)), based on the Nakagawa and Schielzeth (2013) R-squared calculation for GLMMs.

Results

Declines were found in the pooled activity of both WNS-susceptible and non-susceptible spe-cies across all locations except Fort Drum, New York, where pooled non-susceptible species activity increased post-WNS (Fig. 1a, b). The pooled activity patterns were only partially reflected in individual non-susceptible species' responses at each location. At Wisconsin, two of three non-susceptible species decreased in activ-ity post-WNS (Figs. 1, 2). In West Virginia, the overall response for non-susceptible species was a decrease in activity post-WNS (Fig. 1a), but this pattern largely reflected decreases in activity for *Lasiurus borealis* (Fig. 2). Two other non-susceptible species (*E. fuscus* and *L. noctivagans*) slightly increased in activity post-WNS and *L. cinereus* remained unchanged post-WNS (Fig. 2). In Virginia, the overall response for non-susceptible species was a decrease in activity post-WNS (Fig. 1a), which largely reflected decreases in activity by *E. fuscus*, *Lasiurus borealis*, and *N. humeralis* (Fig. 2). One species, *L. cinereus*, slightly increased, and *L. noctivagans* activity did not change appreciably pre- to post-WNS.

Partial support was found for the hypothesis that non-susceptible species' hourly activity would only increase at locations where suscepti-ble species had higher activity than non-susceptible species pre-WNS, that is, New York and West Virginia. These locations had higher activity of one or more WNS-susceptible species than non-susceptible species pre-WNS (Appendix S1: Table S1) and saw declines in activity of all susceptible species to nearly zero (Fig. 1b). These were the only locations where activity of non-susceptible species notably
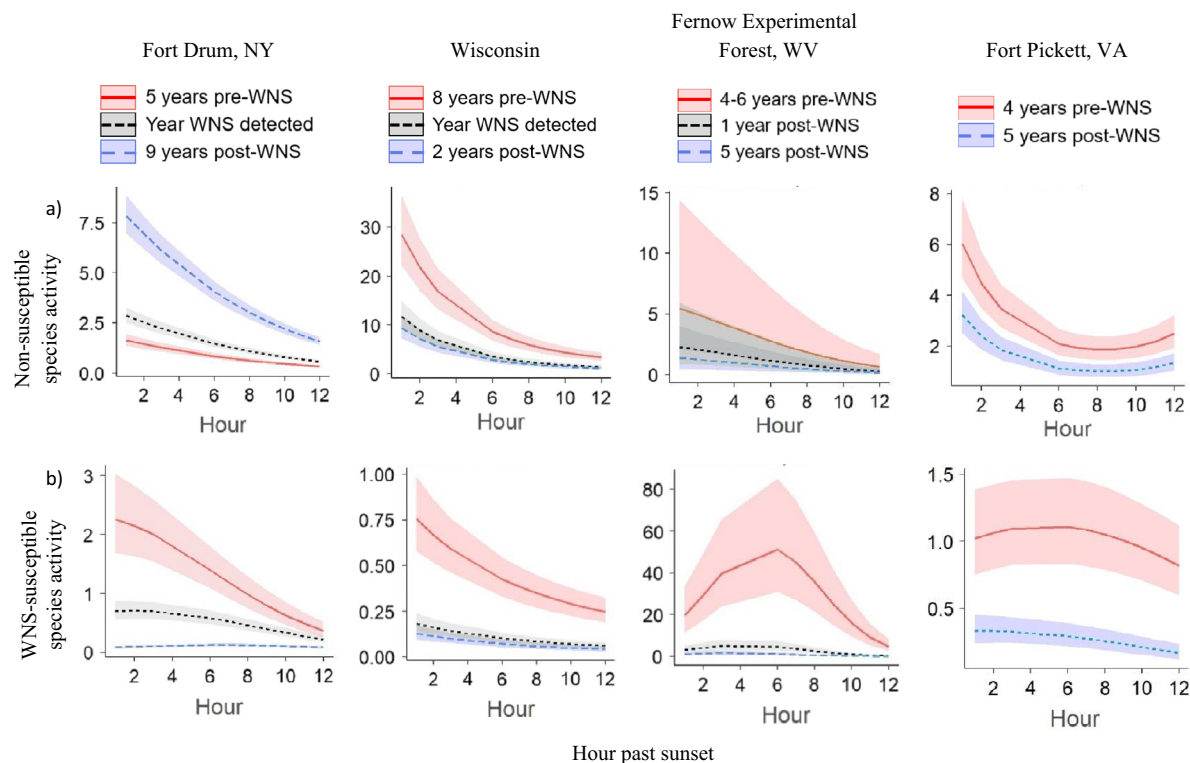
Fig. 1. Predicted hourly mean activity (+/− 95% CI) of WNS non-susceptible (a) and WNS-susceptible (b) species before and after white-nose syndrome (WNS) was detected at four long-term acoustic sampling locations in the eastern United States, 2003–2018 (see text for details on survey duration per site).

increased post-WNS (Fig. 2). However, one non-susceptible species (*Lasiurus borealis*) decreased in activity at West Virginia, and two non-susceptible species' activity levels did not change appreciably pre- to post-WNS (*E. fuscus* in New York and *L. cinereus* in West Virginia. Thus, the only strong evidence indicating that non-susceptible bats were being released from competition with susceptible bats was found at Fort Drum, New York, where three of four non-susceptible species' activity increased post-WNS. Furthermore, minimal evidence was found to support the hypothesis that non-susceptible species would alter their temporal niches to occupy post-sunset and pre-dawn periods. Nightly activity peaks generally flattened as species' activity decreased, but peak activity periods did not change for most species (Figs. 1, 2).

Nearly all supported models (ΔAIC < 4) of non-susceptible species activity included hour past sunset, years before or after WNS, and activity of potential competing susceptible species

(Appendix S1: Tables S3–S4). Although these variables were identified as consistent predictors of bat activity, the marginal variation explained by fixed effects in our models for most species ranged from 5% to 96% (Appendix S1: Table S3). Additionally, <1% marginal variation was explained by top-ranked models for one species (*L. cinereus*) in West Virginia due to infrequent detections that limited our predictive capacity for these species. Similarly, <5% variation was explained by the models for *L. cinereus* in Wisconsin and Virginia.

Discussion

Understanding the direct and indirect effects of disease on animal communities is critical for conserving biodiversity in the face of global change (Brook et al. 2008, Ostfeld et al. 2008). Yet, research on the impacts of WNS has largely been directed toward declines of susceptible bat species, and assessments of how WNS affects the activity of entire bat assemblages are less

common (but see Brooks 2011, Ford et al. 2011, Jachowski et al. 2014, Nocera et al. 2019*b*). Furthermore, assemblage-level investigations of the direct and indirect effects of WNS across multiple distinct regions with unique bat assemblages are unprecedented. Through a long-term dataset of bat acoustic activity at multiple locations preceding and following WNS arrival, we showed that activity of WNS-susceptible, cave-hibernating bat species decreased significantly from pre-WNS levels to low levels at all four study locations. We further show that non-susceptible species were more likely to increase in activity post-WNS at locations with a greater opportunity for competitive release to occur, that is, locations where WNS-susceptible species had similar (New York) or higher activity (West Virginia) than non-susceptible species pre-WNS (Fig. 1). At the other locations, non-susceptible species already had six times (Virginia) to thirty times (Wisconsin) higher activity than the susceptible species before WNS (Fig. 1), so there was likely little opportunity for competitive release to occur. These findings suggest that disease-mediated competitive release in response to WNS may be dependent on the relative activity of the pre-WNS bat assemblage at each site.

Our finding that increases in non-susceptible species activity will likely only arise at locations with a greater opportunity for competitive release to occur aligns with the hypothesis put forward by Jachowski et al. (2014) that there might be an abundance threshold above which susceptible bat species with high activity suppress the activity of competing non-susceptible bat species pre-WNS and that WNS-induced declines of susceptible species might open niches for competing non-susceptible species to occupy. However, strong evidence for this effect was only found at Fort Drum, New York, which was overwhelmingly dominated by the activity of one susceptible species pre-WNS, *M. lucifugus*. A similar, but weaker, increase was found for two of four non-susceptible species in West Virginia, another site characterized by similarly high relative *M. lucifugus* activity pre-WNS, followed by dramatic declines of species (Appendix S1: Table S1). The weaker increase in West Virginia may reflect a time-lag effect since data from West Virginia have only been collected up to five years post-WNS versus nine years post-WNS in New York. In the absence of stressors such as WNS and wind energy, adult bats have high annual survival rates, and most species have low reproductive rates and recruitment (Barclay and Harder 2003). Therefore, it may take years for any strong increases in non-susceptible species activity to occur due to competitive release, especially if the population sizes are already low at a given location.

Although some evidence was found to indicate that non-susceptible bats increased their activity post-WNS in locations with a greater opportunity for competitive release, limited support was found for the hypothesis that bats would shift their temporal niches post-WNS, as almost no species altered their activity peaks pre- to post-WNS (Fig. 2). Thus, temporal niche alteration may be highly dependent upon the level of niche partitioning within bat assemblages (Adams and Thibault 2006). Indeed, investigators have found evidence of temporal niche partitioning in some bat assemblages (Kunz 1973, Reith 1980), but not in others, especially when each species forages on different prey or in different habitats (Saunders and Barclay 1992, Hickey et al. 1996). Furthermore, nocturnal activity patterns can vary considerably. Some investigators have found that activity for several North American insectivorous bat species peaks post-sunset and often again near sunrise after a second emergence period (Kunz 1973, 2004), whereas others have found that peak activity periods can vary considerably across species and locations (Adams and Thibault 2006), or even within a species but across different locations, that is, riparian and upland sites (Menzel et al. 2005).

The variability in competitive release across sites may also be related to the variation in morphology, diets, and foraging habitat among the species considered in this study (Appendix S1: Table S5). Although many species consume similar prey, they often forage in different habitats and the average body size and wing loading of non-susceptible species is generally larger than for susceptible species (Appendix S1: Table S5). Competitive interactions may be more strongly related to indirect exclusion of non-susceptible species within the aerial space when there are larger numbers of susceptible species present. For example, with interactions between species
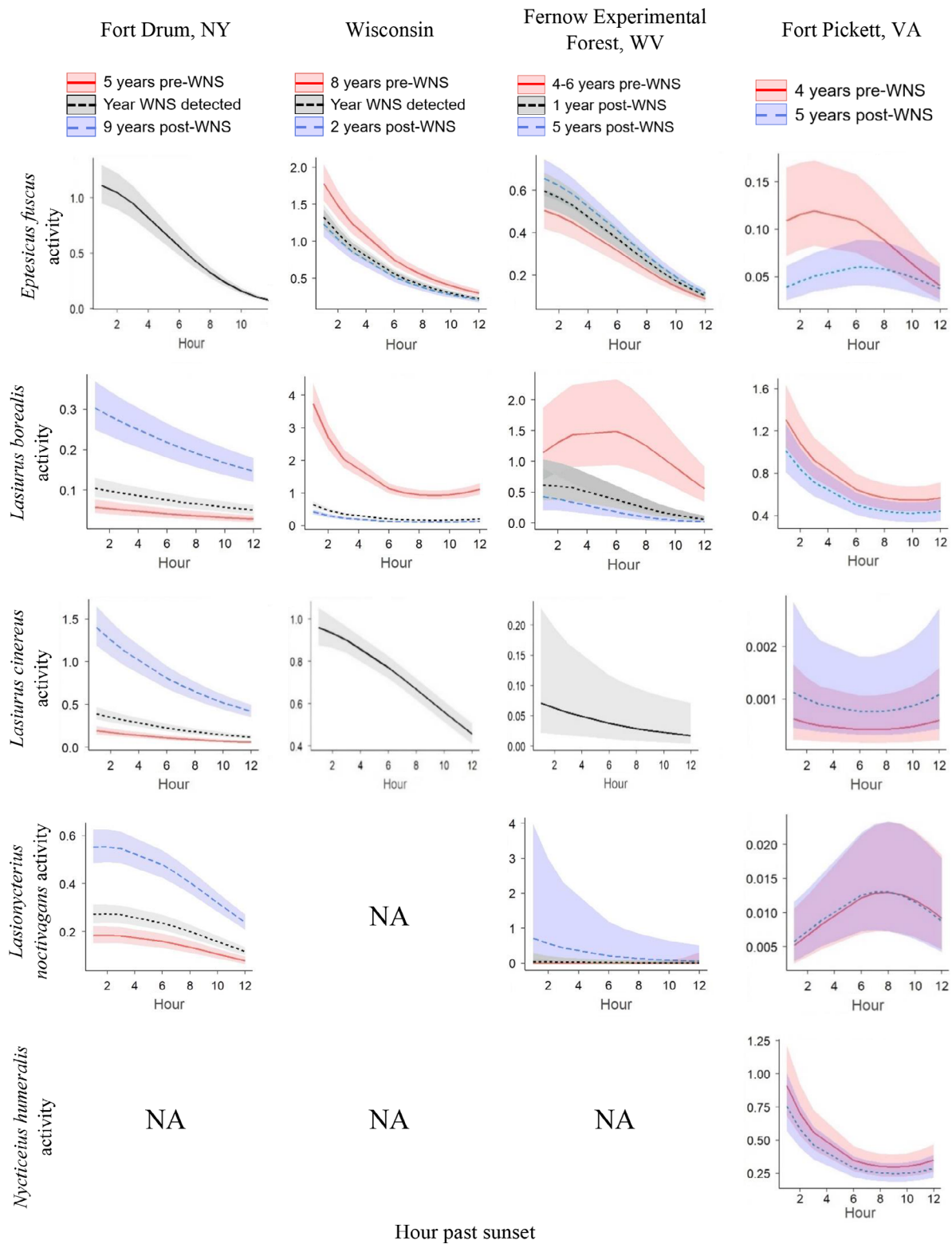
Fig. 2. Predicted hourly mean activity (+/− 95% CI) of individual non-susceptible bat species pre- and

(Fig. 2. *Continued*)

post-WNS (white-nose syndrome) at four long-term acoustic sampling locations in the eastern United States, 2003–2018 (see text for details on survey duration per site). Results are from the highest ranking model (lowest ΔAICc) among all supported models (ΔAICc < 4). Plots in grey indicate that all supported models (ΔAICc < 4) did not include an effect for WNS. NA = species rare or not detected. Note that axis ranges differ per graph to increase clarity.

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such as *M. lucifugus* and *E. fuscus*, there is likely little direct competition over prey, as the two species typically consume different diets (Appendix S1: Table S5). Rather, competition is more likely related to the sheer numbers and amount of activity of *M. lucifugus* in the aerial space creating other foraging or space utilization challenges for *E. fuscus* (or some of the other non-susceptible species) such as from auditory interference (Jones et al. 2018). However, Morningstar et al. (2019) found that, post-WNS, *E. fuscus* shifted their diet to include prey formerly consumed by *M. lucifugus*, indicating that competition between susceptible and non-susceptible bats for prey may also occur. The mixed evidence on mechanisms of competition across diverse geographic bat assemblages suggests that pre-WNS competition between non-susceptible and susceptible species may be moderate to weak overall, or there may be limited temporal niche partitioning among non-susceptible and susceptible bats pre-WNS. The latter point appears to be demonstrated by our data, as temporal activity patterns across species were relatively similar pre- to post-WNS (Fig. 2). Changes in temporal partitioning related to WNS may become more apparent in regions where competition for limited water resources is high. Future research that assesses temporal niche shifts between susceptible and non-susceptible bat species in arid regions would be valuable.

Our results also indicate that activity of some non-susceptible species, *especially L. borealis* and possibly *E. fuscus*, is declining alongside declines in susceptible species activity (Figs. 1, 2), especially in Wisconsin and Virginia. Declines in non-susceptible species activity in Wisconsin were likely not related to WNS, as bats were only surveyed during the first two years post-WNS and bat activity was already low the year WNS was detected in Wisconsin (Figs. 1, 2). We also acknowledge that data from only two sampling

points may be insufficient to provide an accurate assessment of the temporal change in bat activity in northeastern Wisconsin. Yet, except for our observation of decreased activity of *L. borealis* post-WNS, our findings align with those of Hueb-schman (2019), where declines were detected from mist-net capture success over the same period as our study (2007–2017) at ten locations in southwest Wisconsin. We do not have data to infer which factors are driving declines of two non-susceptible species (*E. fuscus* and *L. borealis*) in Wisconsin and three non-susceptible species (*E. fuscus*, *L. borealis*, and *N. humeralis*) in Virginia. However, these findings align with recent long-term studies that found similar evidence for population declines in several non-susceptible species over the past two decades (Hammerson et al. 2017, Rodhouse et al. 2019). These studies attribute such population declines in part to the expansion of wind energy development over the same period, given that migratory bat species that are typically of low susceptibility to WNS are disproportionately impacted by wind energy development (Cryan and Barclay 2009, Arnett and Baerwald 2013) and that the short-distance migrant species *E. fuscus* may also experience significant mortality from wind facilities at some locations (Jain et al. 2011, Grodsky et al. 2012). Other drivers of bat declines have also been suggested, for example, climate variation (Faure-Lacroix et al. 2020) and declines of insect prey abundance (Goulson 2019). Thus, we echo the calls of others for a wider long-term research agenda to understand how multiple interacting threats may be impacting susceptible and non-susceptible bat populations (Faure-Lacroix et al. 2020).

CONCLUSIONS

Emerging infectious wildlife diseases are among the top threats to biodiversity worldwide (Daszak 2000, Brook et al. 2008), and diseases

can have transformative or mediating effects on keystone species (Collinge et al. 2008), community interactions and food webs (Lafferty 2008, Selakovic et al. 2014), biological invasions (Dunn and Hatcher 2015), and ecosystem functions (Eviner and Likens 2008). Opportunities to understand how diseases transform communities are rare, and opportunities to assess the impact of diseases across geographically distinct assemblages are rarer still. Our findings suggest that although relaxation of spatial and temporal niche partitioning between susceptible and non-susceptible bats post-WNS may occur, such patterns do not appear to generalize across multiple bat assemblages. Specifically, we suggest that increases in non-susceptible species activity will likely only arise at locations with a greater opportunity for competitive release, that is, when susceptible species have higher activity than non-susceptible species pre-WNS and drastically decline following disease arrival. These findings challenge the generality of WNS-mediated competitive release between susceptible and non-susceptible species. Our results also add further evidence to highlight a broader pattern of some non-susceptible species declining in the eastern United States (Winhold et al. 2008, Hammerson et al. 2017, Rodhouse et al. 2019). Collectively, our findings suggest that while WNS as an emerging infectious disease is having a strong impact on bat communities, to develop appropriate conservation strategies, there is a need to investigate the effects of multiple potential interacting drivers of bat declines (e.g., disease, turbine mortality, insect abundance, climate variability) on both WNS-susceptible and non-susceptible species.

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Data Availability

Data are available from Mountain Scholar Digital Repository: http://dx.doi.org/10.25675/10217/233937.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3825/full