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A Five-year Assessment of Mortality and Geographic Spread of White-nose Syndrome in North American Bats and a Look to the Future

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Overview

The presence of an unusual fungal infection and aberrant behavior in hibernating bats was first described in New York during winter 2006–2007. The disease was dubbed white-nose syndrome (WNS) after the most prominent field sign—white fungus on the muzzle and other areas of exposed skin. The fungus, newly described as *Geomyces destructans*, also produces characteristic skin lesions on the wing and other membranes of bats (Blehert et al., 2009; Courtin et al., 2010; Meteyer et al., 2009) and probably is the causative agent of the disease (Blehert et al., 2009; Gargas et al., 2009). In this review, we briefly summarize the current state of knowledge, including estimates of mortality for a five-state region, and describe a national plan for managing WNS. Our report is not meant to be a comprehensive review of the ever-expanding literature, but we do include a bibliography of peer-reviewed publications concerning WNS.

Geographic and Taxonomic Spread

White-nose syndrome was first noticed at Howe's Cave, near Albany, New York, in February 2006 (Blehert et al., 2009; Turner and Reeder, 2009). Currently, the presence of WNS in hibernating bats has been confirmed using histopathological criteria (Meteyer et al., 2009) at more than 190 sites in 16 states and 4 Canadian provinces (Fig. 1). Three additional states are considered suspect for the disease. Evidence of *G. destructans* has been obtained from bats not associated with any hibernaculum in Delaware, and *G. destructans* also has been identified on bats from three hibernacula in Missouri and Oklahoma through polymerase-chain-reaction (PCR) techniques, although infection in each of the three states could not be confirmed by histopathology. The detection of *G. destructans* on a bat in western Oklahoma indicates that the fungus has spread ca. 2,200 km from the original site in New York.

Infection with *G. destructans* and significant mortality associated with WNS has been documented in six species: big brown bat (*Eptesicus fuscus*), small-footed bat (*Myotis leibii*), little brown bat (*M. lucifugus*), northern long-eared bat (*M. septentrionalis*), Indiana bat (*M. sodalis*), and tricolored bat (*Perimyotis subflavus*). Rates of mortality vary among species (Table 1), although reasons for the variation are unknown. *G. destructans* also has been isolated from three additional species—southeastern bat (*M. austroriparius*), gray bat (*M. grisescens*), and cave bat (*M. velifer*)—but without histological evidence of tissue damage or reports of mortality. In summer 2009, researchers convening at a WNS Science Strategy Meeting in Austin, Texas, estimated that at least one million bats had died from WNS (Kunz and Tuttle, 2009). Given the spread to new hibernacula and significant mortality noted across the region since this estimate (Fig. 1; Table 1), we believe that the number of bats that have died from WNS is surely much greater.

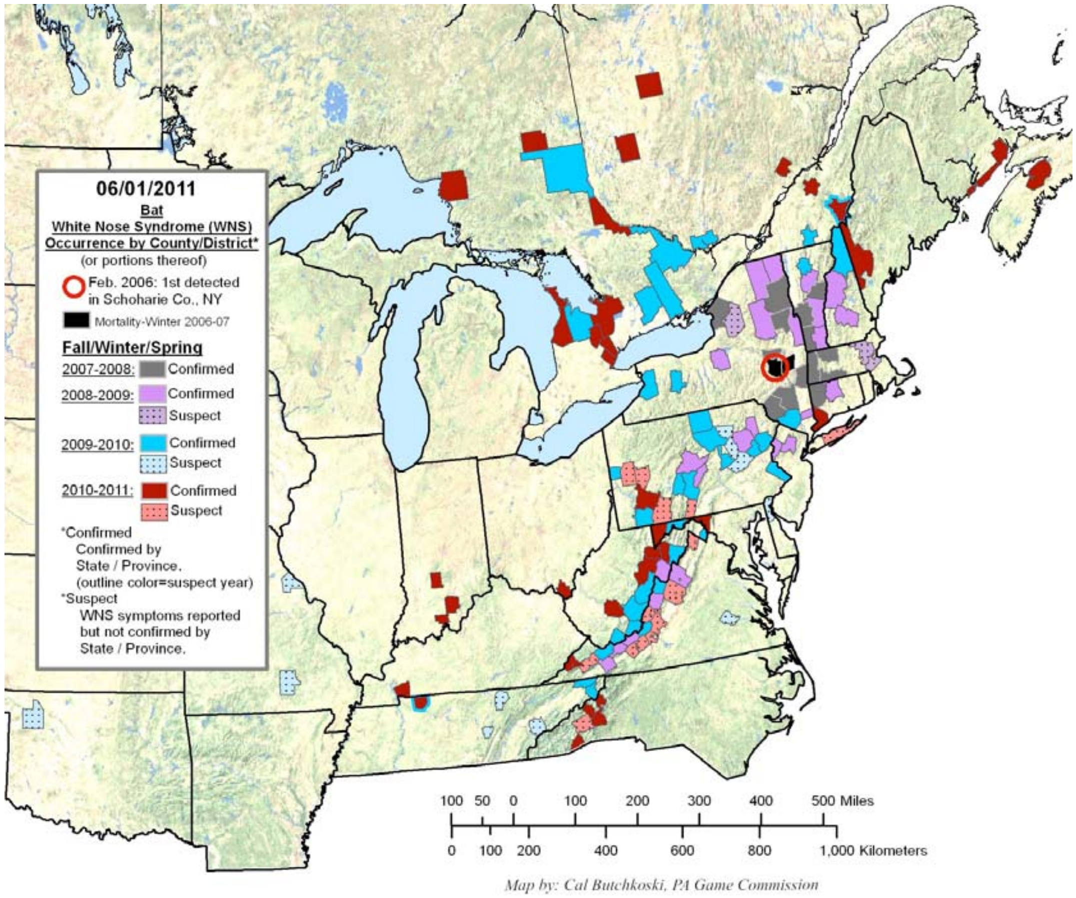

Figure 1. Current distribution of WNS in North America, showing progression of the disease over time and status ("confirmed" or "suspect") of each region as of 23 May 2011 (map may be viewed in color at http://www.fws.gov/WhiteNoseSyndrome; map by C. Butchkoski). A site (cave, county, state, etc.) is labeled as confirmed only if histopathological examination of a bat from a hibernaculum documents "a specific pattern of fungal colonization in the epidermis, which may extend to invasion of the dermis and connective tissue" (http://www.nwhc.usgs.gov/disease_information/white-nose_syndrome/wns_definitions.jsp; see details in Meteyer et al., 2009). Simple presence of hyphae or conidia, a positive fungal culture, or PCR-positive results, without fulfillment of the histopathological criteria, result in a site being categorized as suspect. In this report, a bat with simple evidence of *G. destructans* or even with histopathological signs of WNS that is found away from any hibernaculum also results in that geographic area being labeled as suspect (e.g., Delaware).

Epizootiology of WNS

Causation.—Geomyces destructans is the causative agent of the characteristic skin lesions seen on the exposed skin and in the hair follicles of affected bats (Blehert et al., 2009; Courtin et al., 2010; Meteyer et al., 2009). Although experiments are underway to determine whether *G. destructans* is the causal agent underlying WNS, the results are not yet available, and the mechanism by which an infection of the skin with *G. destructans* kills bats is unclear. In addition to studies examining the relationship between *G. destructans* and mortality, other projects that are underway include investigation of the microfauna of wing membranes and the potential roles they may play in differential survival among species or sites; exploration of various treatments for clearing fungal infection in hibernating bats; molecular studies of the transcriptome of infected and healthy individuals, which will reveal patterns of up- and down-regulated genes, thus providing insight into responses to WNS and other potential pathogens; investigations of physiological and behavioral responses/ symptoms, including water/electrolyte balance and function of the immune system; determination of variations in species susceptibility, including non-volant mammals; and examination of the relationship between microclimate of the hibernacula and progression of the disease. Although some of this research does not require definitive identification of the causative agent, the operating assumption of most biologists within the WNS-research community is that *G. destructans* is responsible for the disease.

Anecdotal observations of bats infected by *G. destructans* may shed light on the mechanisms underlying mortality. For example, affected bats exhibit aberrant behavior including altered sensory thresholds; tremors of the forearms as they crawl; flying in daylight and collisions with large stationary objects, such as the side of a building; and excessive thirst, as evidenced by licking snow or flying for prolonged periods over small areas of open water (Hendricks and Hendricks, 2010). Either starvation and/or loss of electrolytic homeostasis could potentially explain these symptoms. Courtin et al. (2010) noted reduced (but varied) fat reserves in affected bats, which is likely due to shifts in arousal patterns during hibernation (D. M. Reeder, unpublished data), whereas Cryan et al. (2010) hypothesized that fungal attacks are disrupting physiological functions of the wing, particularly the bat's ability to maintain water balance. These are areas that hopefully will receive more attention in the near future.

Geographic origin.—Infection of bats by *G. destructans* without subsequent mass mortality has been recorded widely across Europe (Martinkova et al., 2010; Puechmaille et al., 2010, 2011; Šimonovičov et al., 2011; Wibbelt et al., 2010). For example, Martinkova et al. (2010) examined archived photographs taken since 1994 of greater than 6,000 bats in the Czech Republic and Slovakia, and their findings indicated the presence of *G. destructans* in those countries since at least 1995. These authors also noted that the incidence of visible fungus on the greater mouse-eared bat (*M. myotis*) increased from 2% in 2007 to 14% in 2010, but despite that increase, the population of bats actually grew. This inter-year variation could represent natural fluctuation in abundance of *G. destructans* or differential detection, but the lack of significant mortality and widespread geographic occurrence of the fungus suggest that *G. destructans* has been present in Europe for at least a decade (and likely longer) and that once the fungus becomes established in hibernacula, it persists. The lack of substantial mortality in European bats indicates that they are likely resistant to *G. destructans* and that *G. destructans* represents a novel pathogen for North American species.

Factors influencing transmission and spread.—Two modes of transmission of *G. destructans* have been proposed: bat-to-bat, via direct contact between animals, and hibernaculum-to-bat, via exposure to spores of *G. destructans* that were present on a roosting substrate, whether they were brought their by other bats or by humans. Bat-to-bat transmission is especially likely for those species that typically cluster during hibernation, such as little brown bats and Indiana bats. Given the temporal and geographical distribution of WNS, the scientific community investigating the disease generally agrees that bats can spread the fungus from site to site and to one another. The strongest evidence for interbat transmission comes from the infection of animals at numerous sites that were secured

Table 1. WNS-induced mortality of six species of hibernating bats from 42 sites in New York, Pennsylvania, Vermont,

		Species								
		Myotis lucifugus			*Myotis sodalis*			*Myotis septentrionalis*		
Site Name (Year WNS confirmed)	Pre-/Post-WNS Count Year	Pre-WNS Count[a]	Post-WNS Count	% Change	Pre-WNS Count (Year)[b]	Post-WNS Count	% Change	Pre-WNS Count	Post-WNS Count	% Change
New York										
Barton Hill Mine (2008)	2007/2011				9,393	7,398	-21%			
Baryte 'Garden of Dina' Mine (2007)	2006/2010	1	3	200%				6	0	-100%
Bartyes Cave (2009)	1986/2011	24	1	-96%				12	0	-100%
Bennett Hill Hitchcock Mine (2009)	2003/2011	17,399	1,669	-90%				26	11	-58%
Clarksville Cave (2008)	2006/2010	21	0	-100%				2	0	-100%
Eagle Cave (2009)[c]	1985/2011	2,587	4,324	67%				7	0	-100%
Gage's Cave (2007)	1985/2011	940	40	-96%				1	0	-100%
Glen Park Cave (2008)	2003/2011	151	10	-93%	1,908 (2007)	433	-77%			
Hailes Cave (2007)	2005/2011	15,374	1,496	-90%	685	0	-100%	14	4	-71%
Hasbrouck Mine (2009)	2006/2011	2,922	1,218	-58%						
Howe Cave (2006)	2005/2011	1,213	29	-98%				5	0	-100%
Howes Quarry Mine (2008)	1995/2010	42	1	-98%				6	0	-100%
Jamesville Quarry Cave (2009)	2003/2011	1,346	573	-57%	4,171 (2005)	251	-94%	2	1	-50%
Knox Cave (2007)	2001/2011	1,820	354	-81%				5	0	-100%
Lawrenceville Mine (2009)	2004/2011	293	6	-98%	57	71	25%	25	0	-100%
Main Graphite Mine (2008)	2000/2010	183,542	2,049	-99%	109 (2007)	0	-100%	440	0	-100%
Martin Mine (2008)	2004/2010	720	6	-99%				44	0	-100%
Schoharie Cavern (2007)	1999/2010	953	22	-98%				18	0	-100%
South Bethlehem Cave (2008)	2005/2011	100	0	-100%						
Walter Williams Preserve (2008)	1999/2010	87,401	16,673	-81%	13,014 (2007)	122	-99%	1	1	0%
Williams Fire Pit Mine (2008)	2002/2011	0	323	32,300%	0	718	71,800%	3	0	-100%
Williams Hotel Mine (2008)[d]	2003/2011				24,317 (2007)	6,389	-74%			
Williams Lake Mine (2008)	2003/2011	9,432	24	-100%	1,003 (2007)	11	-99%			

Virginia, and West Virginia, that have had WNS for at least 2 years.

Species: *Myotis leibii*			*Perimyotis subflavus*			*Eptesicus fuscus*					
Pre-WNS Count	Post-WNS Count	% Change	Pre-WNS Count	Post-WNS Count	% Change	Pre-WNS Count	Post-WNS Count	% Change	**Pre-WNS Grand Total**	**Post-WNS Grand Total**	**% Change**
									9,393	**7,398**	**-21%**
			1	3	200%	7	15	114%	**15**	**21**	**40%**
			1	0	-100%	1	16	1,500%	**38**	**17**	**-55%**
183	398	117%	9	6	-33%	51	51	0%	**17,668**	**2,135**	**-88%**
			59	4	-93%				**82**	**4**	**-95%**
53	43	-19%				0	1	100%	**2,647**	**4,368**	**65%**
			27	0	-100%				**968**	**40**	**-96%**
			1	2	100%	14	3	-79%	**2,074**	**448**	**-78%**
15	1	-93%	45	9	-80%	1	0	-100%	**16,134**	**1,510**	**-91%**
						1,659	729	-56%	**4,581**	**1,947**	**-57%**
88	29	-67%	42	4	-90%	13	10	-23%	**1,361**	**72**	**-95%**
			47	0	-100%	0	1	100%	**95**	**2**	**-98%**
			0	2	200%				**5,519**	**827**	**-85%**
11	5	-55%	57	0	-100%				**1,893**	**359**	**-81%**
15	4	-73%	288	6	-98%	72	37	-49%	**750**	**124**	**-83%**
721	485	-33%	194	2	-99%	18	9	-50%	**185,024**	**2,545**	**-99%**
7	9	29%	112	4	-96%	135	31	-77%	**1,018**	**50**	**-95%**
0	1	100%	55	0	-100%	0	1	100%	**1,026**	**24**	**-98%**
17	26	53%	26	5	-81%	41	20	-51%	**184**	**51**	**-72%**
34	9	-74%	13	0	-100%	220	84	-62%	**100,683**	**16,889**	**-83%**
0	2	200%	1	0	-100%	5	71	1,320%	**9**	**1,114**	**1,2278%**
3	0	-100%				131	50	-62%	**24,451**	**6,439**	**-74%**
11	7	-36%	30	0	-100%	120	270	125%	**10,596**	**312**	**-97%**

Table 1 (cont.)

Site Name (Year WNS confirmed)	Pre-/Post-WNS Count Year	*Myotis lucifugus* Pre-WNS Count	*Myotis lucifugus* Post-WNS Count	*Myotis lucifugus* % Change	*Myotis sodalis* Pre-WNS Count (Year)[a]	*Myotis sodalis* Post-WNS Count	*Myotis sodalis* % Change	*Myotis septentrionalis* Pre-WNS Count	*Myotis septentrionalis* Post-WNS Count	*Myotis septentrionalis* % Change
New York (cont.)										
Williams Mine #7-8 (2008)	2002/2011	531	33	-94%	0	18	1,800%	2	0	-100%
Williams Mine #9-10 (2008)	2002/2011	1	35	3,400%						
Williams Mine #11 (2008)	2007/2011	54	1	-98%						
New York Totals and % Difference		**326,867**	**28,890**	**-91%**	**54,657**	**15,411**	**-72%**	**619**	**17**	**-97%**
Pennsylvania										
Alexander (2008)	2006/2010	1,604	8	-100%				30	0	-100%
Durham (2009)	2004/2011	7,356	161	-98%				881	2	-100%
Mt Rock (2009)	2005/2011	20	6	-70%						
Nuangola (2008)	2008/2011	224	0	-100%				6	0	-100%
Shindle (2008)[e]	2008/2010	2,276	3	-100%				19	0	
Woodward (2009)	2010/2011	2,749	20	-99%	3	0	-100%	4	0	-100%
Pennsylvania Totals and % Difference		**14,229**	**198**	**-99%**	**3**	**0**	**-100%**	**940**	**2**	**-100%**
Vermont										
Brandon Silver Mine (2009)	2009/2011	86	4	-95%	2	3	50%	27	0	-100%
Camp Brook Mine (2009)	2009/2011	40	0	-100%				21	0	-100%
Dover Iron Mine (2009)	2009/2011	518	22	-96%				12	0	-100%
E. Magnesia Talc Mine (2009)	2009/2011	768	84	-86%				35	3	-91%
Ely Copper Mine (2009)	2004/2011	531	4	-99%				41	0	-100%
Vermont Totals and % Difference		**1,943**	**114**	**-94%**	**2**	**3**	**50%**	**136**	**3**	**-98%**
Virginia										
Breathing Cave (2009)	2001/2011	701	475	-32%				7	9	29%
Newberry-Bane (2009)	2009/2011	4,143	557	-87%	208	146	-30%			
Virginia Totals and % Difference		**4,844**	**1,032**	**-79%**	**208**	**146**	**-30%**	**7**	**9**	**29%**
West Virginia										
Cave Mountain (2009)	2007/2011	209	17	-92%						
Hamilton (2008)	2007/2011	43	1	-98%						
Trout (2009)	2007/2011	142	8	-94%	158	90	-43%	4	0	-100%
West Virginia Totals and % Difference		**394**	**26**	**-93%**	**158**	**90**	**-43%**	**4**	**0**	**-100%**
All States Combined Totals and % Difference		**348,277**	**30,260**	**-91%**	**55,028**	**15,650**	**-72%**	**1,706**	**31**	**-98%**

[a] A blank indicates that no data on that species were provided by the state agency.
[b] Some sites in New York had visits to survey specifically for Indiana bats (*Myotis sodalis*) on dates more recent than the full site survey presented; in these
[c] Eagle Cave represents a significant increase, but this anomaly is likely due to the 25 years since the previous survey.
[d] The survey of the Williams Hotel Mine does not include counts for little brown bats (*Myotis lucifugus*), because the state biologist omitted them for
[e] Shindle Iron Mine was confirmed in December 2008, and although it qualified as 2 years, the site should be considered one full season of mortality; it

Myotis leibii			*Perimyotis subflavus*			*Eptesicus fuscus*					
Pre-WNS Count	Post-WNS Count	% Change	Pre-WNS Count	Post-WNS Count	% Change	Pre-WNS Count	Post-WNS Count	% Change	**Pre-WNS Grand Total**	**Post-WNS Grand Total**	**% Change**
0	2	200%	34	0	-100%	17	12	-29%	**584**	**65**	**-89%**
0	12	1200%				7	61	771%	**8**	**108**	**1,250%**
						61	6	-90%	**115**	**7**	**-94%**
1158	**1033**	**-11%**	**1042**	**47**	**-95%**	**2573**	**1478**	**-43%**	**386,916**	**46,876**	**-88%**
0	1	100%	16	1	-94%	0	1	100%	**1,650**	**11**	**-99%**
2	0	-100%	167	16	-90%	1	1	0%	**8,407**	**180**	**-98%**
1	1	0%	20	2	-90%	79	54	-32%	**120**	**63**	**-48%**
			12	9	-25%	36	2	-94%	**278**	**11**	**-96%**
			39	0	-100%				**2,334**	**3**	**-100%**
3	4	33%	30	0	-100%	17	4	-76%	**2,806**	**28**	**-99%**
6	**6**	**0%**	**284**	**28**	**-90%**	**133**	**62**	**-53%**	**15,595**	**296**	**-98%**
9	1	-89%	4	1	-75%	9	3	-67%	**137**	**12**	**-91%**
			0	1					**61**	**1**	**-98%**
			6	0	-100%				**536**	**22**	**-96%**
			0	0		8	5	-38%	**811**	**92**	**-89%**
122	90	-26%	5	6	20%	146	126	-14%	**845**	**226**	**-73%**
131	**91**	**-31%**	**15**	**8**	**-47%**	**163**	**134**	**-18%**	**2,390**	**353**	**-85%**
0	8	800%	513	408	-20%	12	21	75%	**1,233**	**921**	**-25%**
4	1	-75%	233	219	-6%	7	4	-43%	**4,595**	**927**	**-80%**
4	**9**	**125%**	**746**	**627**	**-16%**	**19**	**25**	**32%**	**5,828**	**1,848**	**-68%**
			151	8	-95%	6	2	-67%	**366**	**27**	**-93%**
			437	2	-100%				**480**	**3**	**-99%**
4	3	-25%	432	63	-85%	25	12	-52%	**765**	**176**	**-77%**
4	**3**	**-25%**	**1020**	**73**	**-93%**	**31**	**14**	**-55%**	**1,611**	**206**	**-87%**
1303	**1142**	**-12%**	**3107**	**783**	**-75%**	**2919**	**1713**	**-41%**	**412,340**	**49,579**	**-88%**

instances the year of the survey for Indiana bats follows the number of Indiana bats.

potential inaccuracies.
only was included because the mortality could not increase significantly with another year.

from human visitation and where no management or handling of bats occurred prior to arrival of WNS, such as the Shindle Iron Mine in Mifflin County, Pennsylvania (G. Turner, unpublished data).

The responses of a bat to WNS are surely contributing to the spread of the disease. Severely infected bats emerge prematurely from hibernation, and if they survive long enough and enter a different hibernaculum, the likelihood of transmission is probably high, because they presumably carry a large load of fungal spores. Many bats swarm at one site, yet hibernate at another (Humphrey and Cope, 1976), suggesting that infected bats know the location of other hibernacula. If infected bats survive the winter, their ability to retain viable spores and transmit *G. destructans* to healthy colony members in summer is unknown. Likewise, male bats that use hibernacula throughout summer may transmit *G. destructans* to other bats or sites during fall swarming.

Although bats are surely transmitting *G. destructans* to one another, more controversial is the occurrence of inadvertent human-assisted spread of the disease. Fungal spores are durable and easily can become attached to clothing or gear. Caving equipment used at a confirmed site did carry fungal spores having the distinctive shape of those of *G. destructans* (J. Okoniewski, unpublished data), and further research on this mode of transmission is ongoing. If in fact *G. destructans* was transported to North America from Europe, anthropogenic transmission via contaminated gear or clothing (and not bat-to-bat transmission) is the most parsimonious scenario for the initial infection. Furthermore, movement of the fungus to clean sites, hundreds or thousands of kilometers beyond the original epicenter in New York, might explain the rapid spread of WNS. To date, evidence for the anthropogenic spread of *G. destructans* remains largely anecdotal, but this fact does not diminish the very real risks posed by human action. Unintentional, human-assisted movement of pathogens is certainly not without historical precedent (e.g., the chytrid fungal disease in amphibians—Rosenblum et al., 2010) and is a grave concern to managers of animal health worldwide.

Significant variation exists in the time between detection of visible fungus and mass mortality. At some sites, we have observed the appearance of visible fungus on only a few animals during a particular winter, with further development of the disease and deaths not occurring until the next year or even later (e.g., Layton Fire Clay Mine, Fayette County, Pennsylvania). In other cases (e.g., Shindle Iron Mine), the progression from detection of a single bat with visible fungus to large-scale mortality has happened in a matter of weeks.

Once a bat is exposed to *G. destructans* at a particular location, a myriad of factors could influence progression of WNS. Understanding these factors is facilitated by considering the disease triangle (Fig. 2), which relates the potential dynamics of the host (bats of potentially multiple species), the pathogen (presumably *G. destructans*), and the environment (the hibernacula, but possibly active-season environments), as well as interactions between these variables. For example, questions such as how many spores are needed to establish infection (the loading dose) are best studied by considering the species of bat (different species and perhaps different sexes may vary in susceptibility), the time of year, and the nature of the hibernaculum (e.g., infections in sites with ambient temperature below the optimal growth temperature of *G. destructans* may progress more slowly). Likewise, understanding the timing of spread within a site and the rate of death once the fungus is visible will require analyses of these same variables.

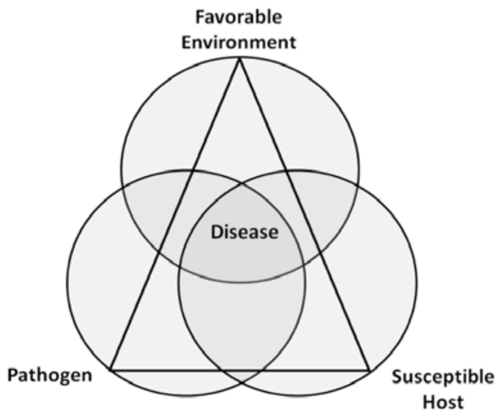

Figure 2. The disease triangle, showing the interrelationships between hosts, pathogens, and environment. A disease (WNS) occurs when a specific pathogen (presumably *Geomyces destructans*) infects susceptible hosts (hibernating bats) under certain environmental conditions (cold damp hibernacula, in which bats use torpor and effectively suppress their immune systems, allowing relatively unchecked fungal growth).

Patterns of Mortality

What is the overall decline of hibernating bats? Are there differences in mortality among species? Are there changes in mortality as the disease progresses across a region? These are some of the most frequently asked questions regarding the impacts of WNS, and biologists are just now starting to examine such issues. Unfortunately, answering these questions relies on accurately estimating/counting the number of bats in hibernacula, and multiple confounding variables make this a difficult task.

Difficulties encountered during winter surveys.—One variable affecting the accuracy of winter surveys is behavioral differences among species. For example, some species, such as big brown bats and small-footed bats are tolerant of low ambient temperatures and hibernate in highly variable conditions. They are often the last bats to enter and the first to leave a hibernaculum. Counts of these species, even those made in midwinter, often vary tremendously. This is likely due to variation in average ambient temperatures during a particular winter, which in turn affects whether the bats are in a particular cave or mine.

Timing of surveys may also play a significant role in differences among bat counts. Because winter surveys of some WNS-affected sites have been pushed from the typical mid-winter period to a time closer to natural emergence (to reduce potential stress on bats), early emerging species, such as big brown bats, and/or individuals affected with WNS may have already left, thus biasing these censuses. Finally, species preferences in roosting location during hibernation (e.g., northern long-eared bats prefer deep cracks) can result in significant underestimates of some species.

Even though most state agencies that perform the counts attempt to assign the same experienced surveyors to the same sites, misidentification of species is possible, especially for those bats that cluster in mixed-species groups and for those that are structurally similar. The physical size of the site, number of bats present, number of passages that surveyors cannot access, and amount of disturbance during the hibernating period can undermine accurate censuses.

The arrival of WNS in a site further affects the accuracy of counts. One of the hallmark signs that a site is affected is the shifting of roost sites within the hibernaculum and the premature exit of affected bats in winter, often months before food is available. Depending upon the time of the survey, this phenomenon may result in underestimates of winter abundance, whereas in other sites, numbers may initially increase during the first year of infection. For example, at Hall's Cave in Huntingdon County, Pennsylvania, total population size jumped from 75 bats before

WNS to 1,800 bats during the winter that WNS arrived, with a drop to 31 bats in the following year; surveys of surrounding sites did not detect similar changes in numbers. It is difficult to draw conclusions from the small number of these occurrences, but the increases may be due either to movement of bats away from nearby, high-mortality sites or to movement of bats within the site from hidden passages to areas closer to the entrance where they are more easily counted. The more pertinent question regarding the derivation of mortality numbers is whether or not to use these peaks in any estimate.

Prior to the arrival of WNS in new geographic areas, the collection of accurate population counts will allow a better understanding of WNS-related declines than may currently be possible in affected areas of the East. In addition, inclusion of data from the active season (e.g., counts at maternity colonies, acoustic surveys, and trapping during fall swarming—Brooks, 2011; Dzal et al., 2010) ultimately may help achieve a more accurate picture of total declines.

Current status of bat populations.—For the analysis presented herein, we utilized data for 42 sites from five states—New York, Pennsylvania, Vermont, Virginia, and West Virginia (Table 1). We limited our analysis to sites with confirmed mortality for at least 2 years, to control for some of the variation described earlier and have focused on counts derived from a consistent level of effort across years. Although some sites have many historical counts where numbers could have been averaged, many others do not, so for consistency, we present only data from the most recent census conducted prior to WNS and the latest count following confirmation of the disease. To reduce stochastic variation and/or issues relating to small samples, we added the count for each species at each site within a state to obtain average mortality estimates per species per state. We then combined data from all states to obtain an estimate of regional change in species composition and abundance. Finally, we aggregated all counted bats, regardless of species, to report the overall change in the total hibernating population for each state and the region. Note that the important number is the percent change in species by state, not absolute numbers, because our 42 sites represent only a fraction of known hibernacula in the region.

At our 42 sites, we saw a precipitous decline in the number of hibernating bats after WNS, from 412,340 to 49,579 animals, for an overall decrease of 88% (Table 1). All six species declined, but there were notable differences among species. Northern long-eared bats decreased by 98% (1,706 to 31 bats); little brown bats, 91% (348,277 to 30,260); tricolored bats, 75% (3,107 to 783); Indiana bats, 72% (55,028 to 15,650); big brown bats, 41% (2,919 to 1,713), and small-footed bats, 12% (1,303 to 1,142). The species with smaller reductions are hopefully less susceptible or more resistant to *G. destructans*, but it is possible that they are just declining at a slower rate, with total mortality rates eventually reaching those of the other species.

When examined by state, we see an overall decline of 98% in Pennsylvania, 88% in New York, 87% in West Virginia, 85% in Vermont, and 69% in Virginia. Although differences among states in overall mortality may be real, undersampling of sites and biased sampling of certain species (e.g., Indiana bats) also may contribute. As previously mentioned, increased accuracy of surveys and eventual inclusion of active-season data will improve our understanding of mortality by species and region. Unfortunately, our mortality estimates are in line with the mathematical models of Frick et al. (2010), who predict that the once-abundant and ubiquitous little brown bat has the potential to become extinct in the Northeast in only 7–30 years; a similar fate may await

Indiana, northern long-eared, and tricolored bats.

The differences in mortality among species also have affected composition of the hibernating assemblage (Fig. 3). For example, prior to WNS, little brown bats comprised 84.5% of all hibernating bats at the 42 sites used in this analysis, with Indiana bats at 13.4%. After WNS, little brown bats now represent only 61% of all bats, and Indiana bats have increased to 31.6% of the overall population.

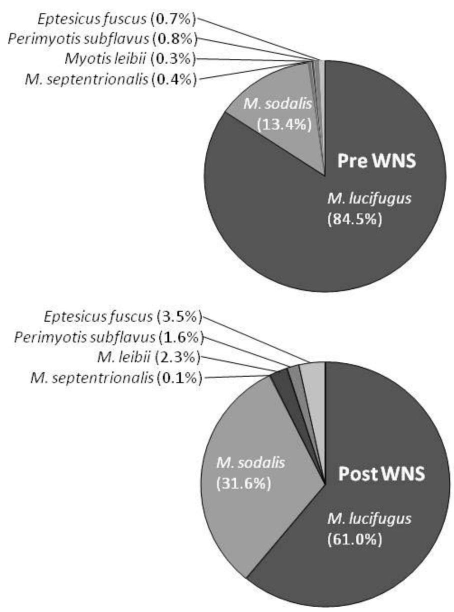

Figure 3. Changes in overall species composition for the six affected species of bats after 2 years of WNS-associated mortality (Table 1).

The National Plan

A final version of a national response plan, *A National Plan for Assisting States, Federal Agencies, and Tribes in Managing White-Nose Syndrome in Bats*, was released in May 2011 (http://www.fws.gov/WhiteNoseSyndrome/). The purpose of the national plan is to guide the reactions of federal, state, and tribal agencies and their partners to WNS. The plan has been developed with input from multiple agencies and establishes an organizational structure for the national response, with defined roles for agencies, stakeholders, and the research community. Oversight of implementation of the plan is provided by two committees—an executive committee and a steering committee—both of which were formally established during winter 2010–2011. The plan also officially institutes seven working groups to address the myriad needs of a national response: communications and outreach, conservation and recovery, data and technical information management, diagnostics, disease management, disease surveillance, and epidemiological and ecological research. The national plan will integrate and support state and regional response plans for WNS and is not intended to replace planning at the local/regional level.

The national plan for WNS is based on similar disease-response plans that have been implemented in the past (e.g., chronic wasting disease in cervids—http://www.cwd-info.org/index.php/fuseaction/policy.policy), and is essentially a formalization of coordinated efforts that were initiated in 2008. The final version of the plan is intended to be static, although implementation of the plan will be an adaptive process, allowing incorporation of new information and guidance, as they become available and/or necessary. The individual working groups will be responsible for developing and maintaining the various components of the action items identified for each element of the plan. The implementation of national strategies will help standardize management practices, including disease surveillance and population monitoring, to ensure consistency in data collection and to facilitate interpretation of results at the continental scale. Because the national plan incorporates a number of actions and efforts that have been used to address WNS over the past 3 years, many elements of the plan are already in service. Existing and future guidance will continually be improved upon so that the WNS implementation plan will be an evolving system rather than a static document.

The Future of White-nose Syndrome?

While WNS continues to spread, not all news is bad news and several surprising findings offer rays of hope. For example, WNS has been confirmed in two hibernacula in West Virginia that harbor nearly 50% of the entire population of the endangered Virginia big-eared bat (*Corynorhinus townsendii virginianus*). Despite mortality of other species in those sites, no fungal infection has been found in the Virginia big-eared bat. Likewise, although *G. destructans* was detected in Oklahoma and Missouri in 2009–2010, histological examination showed that the infected bats were not suffering from WNS, and no new cases were detected in 2010–2011 in either state. Only one of four sites in Tennessee in which *G. destructans* was detected in 2009–2010 was confirmed by histology in 2010–2011, and despite an active surveillance program in Kentucky, WNS was not detected in that state until late spring 2011. Finally, limited evidence from the Northeast, mainly in the form of consistent annual counts at a few locations, suggests that some populations may have stabilized, albeit at much smaller sizes than before WNS. For example, surveys that occurred at Hailes Cave in New York before WNS estimated a hibernating population of 15,374 bats. Following the advent of WNS, annual surveys from winter 2007–2008 to 2010–2011, recorded 7,258; 1,443; 1,000; 1,198; and 1,496 bats.

Despite these few sources of optimism, the overall predictions for WNS are dire and researchers have really just begun to understand how the putative pathogen affects bats and spreads between individuals and populations. As many as 25 species of hibernating bats in North America may be susceptible to *G. destructans*, representing millions of individuals. To succeed in combating this threat, the size of the research community that is involved must increase significantly, with concomitant increases in funding. Efforts must be made not only to study the basic biology of this newly emerging disease, but also to generate a toolkit of mitigation strategies. Only when armed with more information and with mechanisms for fighting WNS can we truly have hope for the bats that hibernate in North America's mines and caves.

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