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WHITE-NOSE SYNDROME-AFFECTED LITTLE BROWN MYOTIS (*MYOTIS LUCIFUGUS*) INCREASE GROOMING AND OTHER ACTIVE BEHAVIORS DURING AROUSALS FROM HIBERNATION

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ABSTRACT: White-nose syndrome (WNS) is an emerging infectious disease of hibernating bats linked to the death of an estimated 5.7 million or more bats in the northeastern United States and Canada. White-nose syndrome is caused by the cold-loving fungus *Pseudogymnoascus destructans* (Pd), which invades the skin of the muzzles, ears, and wings of hibernating bats. Previous work has shown that WNS-affected bats arouse to euthermic or near euthermic temperatures during hibernation significantly more frequently than normal and that these too-frequent arousals are tied to severity of infection and death date. We quantified the behavior of bats during these arousal bouts to understand better the causes and consequences of these arousals. We hypothesized that WNS-affected bats would display increased levels of activity (especially grooming) during their arousal bouts from hibernation compared to WNS-unaffected bats. Behavior of both affected and unaffected hibernating bats in captivity was monitored from December 2010 to March 2011 using temperature-sensitive dataloggers attached to the backs of bats and infrared motion-sensitive cameras. The WNS-affected bats exhibited significantly higher rates of grooming, relative to unaffected bats, at the expense of time that would otherwise be spent inactive. Increased self-grooming may be related to the presence of the fungus. Elevated activity levels in affected bats likely increase energetic stress, whereas the loss of rest (inactive periods when aroused from torpor) may jeopardize the ability of a bat to reestablish homeostasis in a number of physiologic systems.

Key words: Arousal from torpor, bat, behavior, *Pseudogymnoascus destructans*, grooming, little brown myotis, *Myotis lucifugus*, white-nose syndrome.

INTRODUCTION

Bats are an important part of regional and global ecosystems and many species act as top insect predators. However, survival of cave-hibernating bats is in question due to the emerging infectious disease white-nose syndrome (WNS). White-nose syndrome is caused by the cold-loving fungus *Pseudogymnoascus destructans* (Pd), which invades the exposed membranes of the muzzles, ears, and wings of hibernating bats (Lorch et al., 2011). *Pseudogymnoascus destructans*, originally described in the genus *Geomyces* but transferred to *Pseudogymnoascus* by Minnis and Lindner (2013), was likely introduced from outside the United States and grows optimally between 12.5 and 15.8 C with an upper growth limit of 19.0 to 19.8 C (Verant et al., 2012), a near-perfect match for bat hibernacula (Swezey and Garrity, 2011). Bat hibernacula microclimate requirements are quite strict, and variations from these norms (to avoid the fungus) could hinder a bat's ability to survive the winter (Humphries et al., 2002). More than 5.7 million bats are thought to have died from the disease (US Fish and Wildlife Service, 2012). Little brown myotis (*Myotis lucifugus*), once one of the most common North American bat species, have been especially hard hit with declines of 91% (Turner et al., 2011) and predictions of extirpation in northeastern North America by 2026 (Frick et al., 2010).

White-nose syndrome may lead to death due to premature depletion of stored fat during hibernation, likely due to altered hibernation patterns (Reeder et al., 2012). For healthy, free-ranging little brown myotis, torpor bouts last 12–15 days (with occasional bouts of 30 or more days), being periodically interrupted by episodes of arousal to euthermic or near euthermic

temperatures (~37 C; Thomas et al., 1990) that last 1–2 hr (and occasionally longer; Jonasson and Willis, 2012). Reeder et al. (2012) found a clear link between significantly shortened torpor bout length in free-ranging little brown myotis and both the severity of Pd infection and date of death due to WNS: bats with WNS arouse from torpor approximately twice as frequently as unaffected bats. Warnecke et al. (2012) found similarly shortened torpor bouts in experimentally infected bats. This too-frequent warming rapidly depletes stored body fat reserves (each arousal bout results in the loss of 107.9 mg of fat; Thomas et al., 1990), as demonstrated by captive infected bats (Warnecke et al., 2012) which were emaciated within 3–4 mo of inoculation. The proximate mechanism underlying these frequent arousals is unknown, but water and electrolyte imbalances caused by the fungal infection may contribute (Cryan et al., 2013). Given the level of physical damage produced by Pd infection (erosions of the epidermis, destruction of apocrine and sebaceous glands and hair follicles, and destruction of blood vessels and other connective tissues; Meteyer et al., 2009), it has been suggested that infection with Pd may physically irritate bats, also contributing to the likelihood of arousal from torpor to groom irritated skin.

Understanding how the behavior of bats may be affected by Pd infection may increase our understanding of WNS pathophysiology. Unfortunately, it is difficult to study behavioral changes associated with disease when baseline information on the behavior of healthy hibernating bats is lacking. Given the clear importance of arousal from torpor in the epizootiology of the disease, understanding the behavior of both affected and unaffected bats during these arousals will shed light on the physiology and the consequences of these arousals in relation to disease. Normal behaviors that have been recorded in some bat species during these arousals from torpor include drinking, copulating, feeding, and movement within or between hibernacula (Boyles et al., 2006). In nonbat hibernators, periods of rest, including sleep, have also been shown to be associated with these arousals, potentially in support of restorative and homeostatic functions (Daan et al., 1991).

We examined the arousal behavior of WNS-affected and unaffected bats in captivity. Based upon anecdotal observations of WNS-affected bats and upon the presumption that Pd infection is physiologically and physically disruptive, we hypothesized that WNS-affected bats increase behavioral activity during arousal from torpor compared to WNS-unaffected bats. Specific predictions included an increase in the frequency or duration of locomotion (flying–crawling), grooming, and drinking, which overall would result in a decrease in the duration of resting during arousal bouts in WNS-affected bats.

MATERIALS AND METHODS

Eighty little brown myotis were brought into captivity in December 2010. Forty were collected on 14 December from an unaffected site (the site and the bats had no signs of WNS at the time of collection) in western Kentucky, and 40 were collected on 21 December from an affected site in southwestern Pennsylvania. The bats were transported to Bucknell University where they were housed in small mesh cages designed for reptiles (Reptibreeze Small Open Air Cages, Zoo Med Laboratories Inc., San Luis Obispo, California, USA) and placed in temperature- and relative humidity- (RH) controlled environmental chambers for the remainder of the winter (Conviron E7/2, Winnipeg, Manitoba, Canada). Chambers were programmed either at 4 C, 90% RH or 10 C, 90% RH and consistency of these very reliable units was confirmed with daily recording of maintained values. The WNS-affected and unaffected bats were equally distributed across temperature conditions, and affected and unaffected bats were housed in separate cages within the same hibernation chamber. Each temperature chamber housed 40 bats, 20 from the affected and 20 from the unaffected sites, housed in separate cages. In a similar housing paradigm (Lorch et al., 2011), disease transmission did not occur between infected

and uninfected bats in the same chamber but in separate cages (thus, without physical contact). We prioritized obtaining bats without excess disturbance over obtaining an equal sex distribution, which resulted in a large number of males in our study, thus precluding our ability to test for sex differences in behavior. Histologic confirmation of WNS status was not available for these bats nor was final reliable body-mass index (some of the bats were found dead with autolyzed tissue within the cages near the end of the study). However, bats collected from the affected site in Pennsylvania had visible fungal growth at the time of collection, providing strong evidence of their affected status; we refer to these as "WNS-affected bats." While the Kentucky site was considered unaffected at the time of bat collection (these bats are referred to as "WNS-unaffected bats"), the presence of Pd on a bat from this site (without mortality) was documented at the end of the hibernation season (April, 2011). However, no mortality was detected at this site throughout the entire next hibernation season (into spring 2012), which strongly suggests that the bats in this study were not affected.

Bats were housed at two temperatures as part of a separate study assessing survivorship by temperature, but we had no a priori expectations of differences in behavior during arousal bouts in relation to hibernation temperature. On the date of their arrival, data on forearm length, weight, sex, and reproductive condition were recorded. Custom-made temperature-sensitive dataloggers (Reeder et al., 2012) were attached to the back of each bat to monitor skin temperature (T_{skin}) across the hibernation season. Temperatures were recorded every 30 min. Loggers weighed approximately 1.1 g and each was given a unique paint color and marking combination to facilitate visual identification of the bats through remote video monitoring. Each of the four groups was monitored using one Vandal Proof 420 Lines High Resolution Sony CCD Infrared (IR) Day and Night Weatherproof CCTV Security Camera (Rhino, McGraths Hill, Australia) connected to a 1,000 or 1,500 GB hard drive DVR (PRO Series 4 Channel Digital Video Recorder DVR by Falco, Selangor Darul Ehsan, Malaysia). The cameras were infrared equipped and motion sensitive and thus did not disturb the bats (Mistry and McCracken, 1990), only recording when motion was detected. The bats were allowed to hibernate until 21 March 2011, but cages and chambers were opened approximately every week for removal of any bats that died and for removal of individual bats for a testing of thermoregulatory preferences as part of a different study.

To examine behavior during arousal bouts, behavioral data were recorded and analyzed in tandem with T_{skin} data. For each individual bat, torpor was defined as when T_{skin} was 10 C or more below its highest temperature (T_{max}). The T_{max} varied for each individual but on average was 24.8 C. Duration of an arousal episode (when T_{skin} was within 10 C of T_{max}) was calculated to the nearest 30 min. For every half-hour period of arousal recorded by the dataloggers, video from the same period was analyzed if the warm bat could be identified ($n=62$ euthermic periods across all groups). When an identifiable bat aroused with one or more unidentifiable bats, these instances were excluded from the analysis to avoid misidentifying the focal bat. When the same bat was recorded for more than one arousal over the course of the hibernation period, data were averaged. As we were only able to record temperature every 30 min, and thus able to pair thermal data with video-recorded behaviors only within 30 min windows, it is possible that behavior was missed that occurred either before or after an arousal bout was detected. However, analyses of the video recordings indicated that this was not the case. The final consolidated dataset included behavioral observations during arousal bouts for 31 individual bats distributed to the four treatment groups as follows: 4 C and WNS-affected ($n=6$), 4 C and WNS-unaffected ($n=11$), 10 C and WNS-affected ($n=10$), and 10 C and WNS-unaffected ($n=4$).

An ethogram of behavior exhibited by little brown myotis during arousal bouts was created based on behaviors previously recorded for bats (from active season observations; Burnett and August, 1981) and those recorded from the videos (Table 1). Durational behaviors were scored as total time spent engaged in a behavior and included locomotion (crawling and flying), resting, self-grooming, and drinking. Instances of drinking, self-grooming, and flying were also scored as the frequency per 30-min arousal interval. No instances of yawning were ever recorded and only one instance of urination was ever recorded, so these were excluded from the analysis. "Detectable time" refers to the portion of a bat's 30-min arousal period where they showed motion of any kind (which triggered video recording). Bats that were aroused but not detected by video were considered to be in "euthermic rest" and bats that exhibited brief bouts of no motion during otherwise active periods were scored as being "inactive." There were a few instances in which one bat could be

TABLE 1. Ethogram of captive little brown myotis' (*Myotis lucifugus*) behavior during arousals from hibernation.

Behavioral category	Behavior	Description
Locomotion	Crawling	When a bat is moving around the frame using its arms and legs to propel itself.
	Flying	When a bat "jumps" or attempts to fly from one side of the cage to another.
Not physically active	Rest	When a bat is euthermic but not detected with motion-sensitive cameras ("undetectable") because it is not exhibiting locomotion or other active behaviors.
	Inactive	When a bat is not showing any locomotion or other behaviors but is recorded with motion-sensitive cameras (inactive bouts occurring in otherwise detectable periods).
Foraging	Drinking	Taking water into the mouth via the water trough; head remains in a downward position.
Other behaviors	Yawning	Opening the mouth widely, usually done while resting.
	Self-grooming	When a bat appears to touch its fur or wings using its mouth or foot, either structurally or functionally.
	Urinating	When a bat is faced head up and liquid is seen to run down the side of the cage; seldom occurs while bat is face down.

identified for 60 to 90 min. In these cases, behavioral data were averaged across 30-min periods to compare results for all individuals.

Each bat was not active as soon as it aroused from torpor (based on T_{skin}), so we calculated durational behaviors as a percentage of the 30 min that they were aroused (based on T_{skin}) and as a percentage of the time they were showing "detectable" activity. For example, if a bat did not show activity until 10 min after it aroused and then groomed for 4 min, crawled for 8 min, drank for 1 min, and crawled for another 7 min, the total percentage time for grooming would be 4 min/30 min, but the detectable time percentage would be 4 min/20 min (Fig. 1).

Within- and between-observer reliability was calculated by observations of 12, 30-min, randomly selected (using a random number generator) segments of captive bat footage (also used in the main data set) by the main observer (S.A.B.) and a secondary observer. Reliability was assessed with Pearson correlation coefficient or, when necessary, the nonparametric Spearman correlation coefficient. Martin and Bateson (2007) suggest 0.70 as a reasonable correlation and, with the exception of "drinking" and "'resting," correlation coefficients generally greatly exceeded this value (within-observer reliabilities ranged from 0.78–0.99 and between-observer reliabilities ranged from 0.70–0.94). Low correlations for drinking behavior (0.64 within-observer and 0.70 between-observers) are likely due to the rarity and cryptic nature of this behavior (especially given the position of the cameras), which skews the correlation calculations. Similarly, "resting" or "inactive" during detectable times was rare and challenging to score (0.85 within-observer and 0.62 between-observers).

Data are represented as mean±SE. Data for each behavior were compared between bats at each temperature and by WNS status. Normality was assessed with Shapiro-Wilk's test and homogeneity of variances was assessed with Levine's test. If data were normally distributed and variances were homogeneous, a univariate analysis of variance was performed. If data were not normally distributed or not homogeneous (and normality or homogeneity of variance could not be achieved with a transformation), data were analyzed nonparametrically using either Kruskal-Wallis or Mann-Whitney *U*-tests to detect differences between groups. All statistics were calculated using SPSS 18.0 (IBM Corporation, Somers, New York, USA).

RESULTS

The sex ratio of bats in this study was highly skewed toward males; thus, we were unable to examine sex differences in behavior. Body mass index (forearm length/mass) did not differ between groups at the start of hibernation. As we had predicted, there were no significant differences between the behaviors of bats of the same WNS status housed at

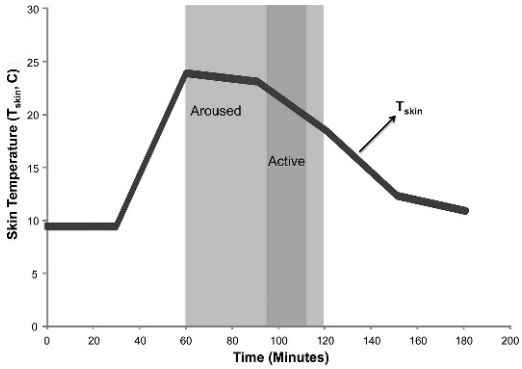

FIGURE 1. Example arousal profile of a little brown myotis (*Myotis lucifugus*), in captivity, and unaffected by white-nose syndrome. Solid line indicates skin temperature (T_{skin}) over time. The period of arousal (when T_{skin} is within 10 C of the bat's T_{max}) is indicated in light gray. The period of behavioral activity (when bat movement was detected by the motion sensitive cameras) is indicated in dark gray.

different temperatures; thus, data from the different temperature groups were combined. The WNS-affected and unaffected bats did not differ in torpor bout length (6.48±0.76 vs. 6.55±0.53 days) or arousal bout length (57.16±4.22 min vs. 39.9±1.69 min), although our ability to determine differences in arousal bout length when temperatures were only recorded every 30 min was limited (Reeder et al., 2012).

Behavioral differences were found between WNS-affected and unaffected bats (Table 2). Firstly, WNS-affected bats showed a significantly higher percentage detectable time (54.7±5.6%) than did unaffected bats (28.6±3.2%), indicating that they were generally more active during each arousal bout than were unaffected bats (as detected by the triggering of the motion-sensitive video cameras). As a consequence, WNS-affected bats' time spent resting while aroused from torpor was significantly lower (undetectable or resting 45.3±5.6% vs. 71.4±3.3%). Resting or inactive rates during periods of detection (when cameras were triggered by prior movement) were low and did not significantly differ by WNS status.

There were no differences in locomotor behavior between affected and unaffected bats as a function of the percentage of total time aroused (total locomotion or crawling only) or frequency (flying). However, because of the large difference in percentage of time detected for the portion of arousal bouts in which bats were active, WNS-affected bats spent significantly less time locomoting (largely due to crawling) than did affected bats. Rather than locomoting during their active periods, WNS-affected bats displayed significantly higher rates of grooming. These much-higher rates are clearly evident when grooming as a function of total time aroused is considered. WNS-affected bats groomed 21.9±3.5% of the total time aroused (vs. 1.1±0.5% for unaffected bats) and initiated grooming bouts significantly more frequently than did unaffected bats. Contrary to our predictions, significant differences in drinking frequencies or total time were not found.

These behavioral differences are best visualized as activity budgets (Fig. 2), where one can clearly see that WNS-affected bats have largely replaced periods of inactivity or rest during arousal from torpor (and to a lesser extent, time spent locomoting) with grooming. Given the much lower rates of grooming in unaffected bats, we could not quantitatively compare the specific nature of grooming between groups. However, in general, grooming efforts were focused on the wing membranes with bats putting their head under one wing and licking along the membrane until they reached the fifth digit. Less often bats groomed their ventral fur or used the hind foot to scratch near the top of the head.

DISCUSSION

As predicted, WNS-affected bats significantly altered their behavior during arousal bouts relative to unaffected bats. Specifically, WNS-affected bats spent significantly more time active (recorded

TABLE 2. Captive behavior durational means. *P*-values are given for white-nose syndrome (WNS)-affected and unaffected comparisons for little brown myotis (*Myotis lucifugus*) from Kentucky and Pennsylvania, USA, observed in the laboratory.

Behavior	WNS-unaffected mean±SEM (%)	WNS-affected mean±SEM (%)	Test statistic	*P*-value
% of total time detectable (active behavior triggered recording with motion-sensitive cameras)				
	28.6±3.2	54.7±3.2	Univariate ANOVA[a] $F_{1,27}=21.011$	<0.001*
Inactive (during periods of activity)				
% Total time	1.4±0.6	2.4±1.6	Kruskal-Wallis H=0.187	0.980
% Detectable time	4.2±1.5	5.0±3.9	Kruskal-Wallis H=0.995	0.802
Locomotion				
% Total time (all locomotion)	24.3±2.9	29.4±4.4	Univariate ANOVA	0.145
% Detectable time (all locomotion)	84.5±2.7	55.0±7.1	Univariate ANOVA $F_{1,27}=8.450$	0.007*
% Total time (crawling only)	23.4±2.7	29.0±4.4	Kruskal-Wallis H=3.950	0.267
% Detectable time (crawling only)	82.1±3.0	54.2±7.1	Univariate ANOVA $F_{1,27}=7.267$	0.012*
Flight frequency per 30 min interval	2.61±1.06	1.41±0.33	Kruskal-Wallis H=0.324	0.955
Grooming				
Frequency per 30 min interval	0.29±0.12	1.10±0.13	Kruskal-Wallis H=12.133	<0.001*
% Total time	1.1±0.5	21.9±3.5	Kruskal-Wallis H=16.581	<0.001*
% Detectable time	3.4±1.5	37.8±6.0	Kruskal Wallis H=16.581	<0.001*
Drinking				
Frequency per 30 min interval	0.93±0.20	0.41±0.13	Kruskal-Wallis H=7.310	0.063
% Total time	1.7±0.5	1.0±0.3	Kruskal-Wallis H=0.465	0.465
% Detectable time	7.9±2.5	2.2±0.7	Kruskal-Wallis H=3.541	0.316

[a] ANOVA = analysis of variance.

* Significant at $P<0.05$.

as detectable time) during their arousal bouts than did unaffected bats. This increased level of activity likely has energetic consequences. Although arousal periods account for approximately 1% of the total time budget during winter, because metabolic rate greatly increases with increased body temperature, approximately 80–90% of the energy (depot fat) used during hibernation is consumed during these periodic arousals from torpor (Thomas et al., 1990). The amount of depot fat expended during each arousal episode (not including flight or other activity) for hibernating little brown myotis is approximately 107.9 mg (Thomas et al., 1990). Increasing activity during these bouts in all likelihood makes each bout more costly. Given the relatively tight linkage between number of arousals and death from Pd infection (Reeder et al., 2012), even a moderate increase in energy

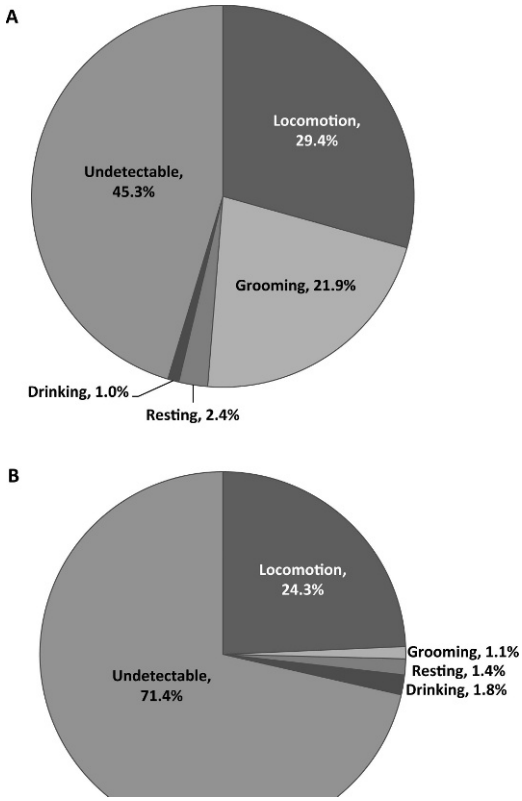

FIGURE 2. Average activity budget for a (A) white-nose syndrome (WNS)-affected ($n=16$) and (B) WNS-unaffected ($n=15$) little brown myotis (*Myotis lucifugus*), as portions of time aroused.

used during an arousal (e.g., a 1.5-times increase in metabolic rate or loss of depot fat per arousal) will hasten mortality.

As illustrated by their energy budget (Fig. 2), the increase in detectable time in WNS-affected bats (54.7% compared to 28.6% in unaffected bats) is nearly fully explained by a large and significant increase in the percentage of time spent grooming (21.9% vs. 1.1%) and a moderate (but not statistically significant) increase in the percentage of total time spent locomoting (29.4% vs. 24.3%). Contrary to our predictions, differences in other aspects of behavior between WNS-affected and unaffected bats were not found, especially with regard to flight (which may have been limited due to the size of the cages) and to drinking (perhaps due to the rarity of the behavior). Field observations of WNS-affected and unaffected bats during the previous year, using identical video camera systems (Brownlee-Bouboulis and Reeder, unpubl.), documented nearly all of the WNS-affected bats in a cluster flying away (out of view) during arousal bouts, whereas unaffected bats remained largely clustered throughout hibernation. While this may be due to the increased arousal bout frequency (or shortened torpor bout lengths) documented in free-ranging WNS-affected bats (Reeder et al., 2012), increased flying in affected bats may occur in unrestricted but not restricted settings (i.e., when not in a cage). Although we did not detect differences in drinking behavior, it is an important behavior to document considering the suggestion that electrolyte imbalances are affecting bats with WNS (Cryan et al., 2013). Evidence for drinking in excess would support the notion that bats are trying to correct fluid imbalances, and field observations of WNS-affected bats drinking water and eating snow during arousal bouts suggest that this remains a likely consequence of Pd infection.

It is possible that the differences we documented between WNS-affected and unaffected bats are due to geographic differences between our study groups (WNS-affected bats were from southwestern Pennsylvania and unaffected bats from western Kentucky). However, our findings of similar differences in free-ranging WNS-affected and unaffected bats the previous year, in which the distance between affected and unaffected sites was only ~130 km (Brownlee-Bouboulis and Reeder, unpubl. data) suggest that we are not geographically biased. Another potential bias is that excessive grooming can be caused by stress, as might occur in captivity (Katz and Roth, 1979). However, if this was the case, grooming rates should have been similar in affected and unaffected bats.

Our failure to find a difference in torpor bout length between WNS-affected and unaffected bats is likely due to too much disturbance (opening of cages, occasionally removing bats for a separate study). However, this disturbance should have affected each group of bats similarly and thus does not negate the significant behavioral differences seen during arousal bouts between WNS-affected and unaffected bats. Additionally, our failure to find predicted behavioral differences in some measures may be because at least some of our bats did not reach the endpoint (clinical morbidity or morality) that occurs in severely affected free-ranging bats. Thus, the behavioral changes we saw may only be a part of the full range of behaviors seen in WNS-affected free-ranging bats.

It is clear that the WNS-affected bats in this study greatly increased the amount of time they spend grooming, at the expense of time that would otherwise be spent resting. Although increased grooming supports the notion that WNS-affected bats are irritated by the fungal infection in their skin (which might then lead, in part, to increased arousals from torpor), we are unable to distinguish between this idea and the notion that affected bats simply become aware of the infection upon arousal from torpor, which then leads to excessive grooming. One consequence of increased grooming could be increased geographic spread of WNS, as it appears WNS-affected bats are ingesting fungal spores which may remain viable after passing through the digestive tract. Some affected bats emerge from hibernacula early and may switch hibernacula (Turner et al., 2011) while those that survive to spring emerge from the hibernacula and promptly migrate to their summer roosts (potentially stopping at various hibernacula along the way); thus, Pd spores may be dispersed to new locations as the bat's digestive track becomes active.

In addition to needing to better understand the consequences of excessive grooming for winter energy balance, equally important is our need to understand the consequences of significantly decreased amounts of resting or inactivity during arousal bouts. As is the case with nonbat hibernators (Daan et al., 1991), we found that healthy bats may remain motionless for some time during arousal bouts (typically at either the beginning or the end of a bout). It is generally accepted that torpor is incompatible with sleep and that one of the functions of euthermic bouts during hibernation may be to correct sleep deficits (Trachsel et al., 1991). Thus, periods of inactivity during arousal bouts (recorded as "undetectable time") may serve to meet sleep needs. In addition to helping restore sleep deficits, arousals from torpor are thought to return a number of physiologic systems, including the immune system, to homeostasis (Luis and Hudson, 2006), and presumably some of this restoration occurs during periods of "euthermic rest," especially those that occur at the start of an arousal. Therefore, decreased euthermic rest may represent a significant cost to WNS-affected bats in terms of their ability to achieve the requisite corrections that are a part of arousals from torpor. These cyclic warming periods reflect a continuous balancing act between physiologic necessity and energy availability, and the fact that every mammalian hibernator arouses periodically suggests that arousals are obligatory and provide benefit (Carey et al., 2003). Further studies on physiologic processes that occur during arousal bouts, and especially during periods of rest or inactivity, will shed light on the consequences of the loss of "rest" in euthermic WNS-affected bats.

As a cold-loving fungus, Pd is an unusual pathogen against which little brown myotis do not appear to possess significant behavioral or physiologic adaptations. In contrast to the "sickness behaviors" exhibited by many species in response to infection, which serve to enhance the ability to fight a pathogen

(Hart, 1988), the changes documented in response to WNS in little brown myotis appear to be detrimental. Both the presumably increased energetic cost of being more active (by grooming) and the lack of presumably restorative rest during arousal bouts likely contribute to, rather than ameliorate, mortality.

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