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LETTER

Sociality, density-dependence and microclimates determine the persistence of populations suffering from a novel fungal disease, white-nose syndrome

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Abstract

Disease has caused striking declines in wildlife and threatens numerous species with extinction. Theory suggests that the ecology and density-dependence of transmission dynamics can determine the probability of disease-caused extinction, but few empirical studies have simultaneously examined multiple factors influencing disease impact. We show, in hibernating bats infected with *Geomyces destructans*, that impacts of disease on solitary species were lower in smaller populations, whereas in socially gregarious species declines were equally severe in populations spanning four orders of magnitude. However, as these gregarious species declined, we observed decreases in social group size that reduced the likelihood of extinction. In addition, disease impacts in these species increased with humidity and temperature such that the coldest and driest roosts provided initial refuge from disease. These results expand our theoretical framework and provide an empirical basis for determining which host species are likely to be driven extinct while management action is still possible.

Keywords

Adaptive management, climate change, conservation, density-dependent transmission, disease ecology, emerging infectious disease, endangered species, frequency-dependent transmission, *Geomyces destructans*, myotis, white-nose syndrome.

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INTRODUCTION

Novel pathogens introduced to naïve host communities can have devastating effects on wildlife populations, drive species to extinction and thereby decrease biodiversity (Daszak *et al.* 2000; Smith *et al.* 2006). However, the impact of multi-host pathogens differs substantially, with some species declining to extinction whereas others suffer little mortality (Riper *et al.* 1986; Harvell *et al.* 1999; Lips *et al.* 2006; LaDeau *et al.* 2007), and some may even benefit from disease-caused reductions in competitors or predators (Whitlaw & Lankester 1994). Variation in behavioural characteristics among species can lead to differences in exposure which, combined with variation in susceptibility to mortality from a disease, influence population-level impacts (Loehle 1995; Altizer *et al.* 2003; Lloyd-Smith *et al.* 2004; LaDeau *et al.* 2007; Nunn *et al.* 2008). The environment can also mediate disease impacts through direct influences on pathogen growth and persistence, or indirect effects on host physiology and behaviour (Kilpatrick *et al.* 2010; Shaman *et al.* 2010) Previous studies that have examined initial or long-term impacts of disease typically have focused on a single host (Packer *et al.* 1999; Hochachka & Dhondt 2000) or have analysed either host or environmental factors but rarely both (Dwyer *et al.* 1990; Hudson *et al.* 1998; Lips *et al.* 2006; LaDeau *et al.* 2007; McCallum *et al.* 2009). This limits strong inference about factors influencing disease-caused extinction.

Theory suggests that the scaling of pathogen transmission with population size can determine whether or not a pathogen drives a host extinct. If transmission increases with the density of hosts, there may be a threshold density below which the pathogen will die out and the host may persist (McCallum *et al.* 2001; Fenton *et al.* 2002; de Castro & Bolker 2005; Lloyd-Smith *et al.* 2005). In contrast, for pathogens where infected hosts infect the same number of individuals regardless of population size (often termed 'frequency-dependent transmission'), host extinction is more likely because pathogens will continue to be transmitted at low population densities (Getz & Pickering 1983; Lockhart *et al.* 1996). Frequency-dependent transmission is more likely if infectious contacts occur when hosts seek each other out, either to mate, or to aggregate in social groups. These behaviours contact can maintain high transmission despite population declines (Anderson & May 1991; Lloyd-Smith *et al.* 2005; Nunn *et al.* 2008; McCallum *et al.* 2009). Empirically testing how sociality influences disease impact would ideally examine population declines due to a single pathogen in a community of hosts that co-occur in the same sites, but differ in social aggregation.

White-nose syndrome (WNS) is an emerging infectious disease caused by *Geomyces destructans*, a fungus in the family Myxotrichaceae (Blehert *et al.* 2008; Lorch *et al.* 2011) that was likely recently introduced from Europe (Puechmaille *et al.* 2011; Warnecke *et al.* 2012). In North America, *G. destructans* is known to cause severe mortality in one formerly common bat species (Frick *et al.* 2010), and infect

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at least six species of hibernating bats (Table S1) (Cryan *et al.* 2010). WNS is characterised by lesions on flight membranes of bats (Meteyer *et al.* 2009) which may disrupt patterns of torpor (Warnecke *et al.* 2012) or critical physiological processes and possibly result in death by starvation or dehydration (Cryan *et al.* 2010).

The six species of bats known to be infected with Gd co-occur in the same sites, and vary substantially in abundance and sociality. Average population sizes for colonies (population and colony size are used interchangeably hereafter) of these six species during hibernation vary across four orders of magnitude (Table S1). Cluster sizes within hibernacula (groups of bats in contact with one another) can also vary by two orders of magnitude among species (Barbour & Davis 1969). A key question is whether contact and transmission rates among bats increase with colony size (i.e. are density-dependent) or whether social clustering of individuals into one or more tightly packed groups in some species might result in similar contact rates in large and small colony sizes (Nunn & Altizer 2006; Streicker *et al.* 2012). Clustering with a fixed number of neighbours in gregarious species is likely to result in elevated and constant transmission in highly gregarious species and may lead to populations declining to extinction (Lockhart *et al.* 1996; de Castro & Bolker 2005). In contrast, for species that are less likely to form clusters in hibernacula, contact and transmission among bats is predicted to be lower in smaller populations and decrease as populations decline. As a result, disease is less likely to cause extinction in these species (Lockhart *et al.* 1996; Castro & Bolker 2005).

Susceptibility to mortality from WNS, given exposure, may also be influenced by microclimate effects on host-pathogen interactions. *G. destructans* shows increasing growth across the range of hibernacula temperatures in the northeast USA, 0–15 °C (Gargas *et al.* 2009) and like many other fungi, likely grows better under more humid conditions. Across the same temperature range, host immune function, which is greatly reduced during hibernation (Moore *et al.* 2011), would be predicted to increase. Thus, dryer sites would be hypothesised to have lower disease impacts and increasing roost site temperature may increase or decrease WNS impacts depending on whether host or pathogen processes dominate.

Here we examine how colony size, sociality and environmental conditions (temperature and humidity) drive patterns of disease impact. We do so by quantifying the population growth rates of 120 populations of six species of bats in multi-host communities at 37 sites in the northeastern United States before and after the arrival of *G. destructans*. We examine both spatial patterns of population declines and how they scale with colony size, and temporal changes in clustering and population growth rates as species decline. Finally, we investigate how microclimates at roost sites in hibernacula influence the population growth rate of two declining species.

MATERIALS AND METHODS

Hibernacula surveys

Hibernacula in the New York, Vermont, Connecticut, and Massachusetts were surveyed by trained biologists from state natural resources departments between 1 December and 10 April in some years from 1979 to 2010 (Fig. S1). Visual counts were conducted during hibernacula visits and photographs were used to enhance survey accuracy. Data on clustering behaviour of the two gregarious species, little brown myotis (*Myotis lucifugus* LeConte) and Indiana myotis (*Myotis sodalis* Miller and Allen), were collected in New York by state researchers in an opportunistic subset of 45 populations prior to WNS detection, and during all (23) census counts beginning in 2009.

Determining the first year of WNS at a site

White-nose syndrome usually causes aberrant behaviour of bats during hibernation, including bats prematurely staging at hibernacula entrances, failure of bats to arouse normally in response to disturbance, and diurnal and mid-winter emergence of bats. We used the best available estimates of year of WNS detection based on reports of bats emerging onto the landscape in close proximity to hibernacula, and surveys of hibernacula entrances for bat carcasses. However, sites may have been infected with *G. destructans* prior to detection of disease when sites were not surveyed every year.

We determined the sensitivity of our results to uncertainty in the year of WNS detection by performing analyses with three sets of arrival years: the most likely year using the information described above, the latest year of WNS detection, determined by the first year a hibernacula survey was conducted and symptoms of WNS were present, and the earliest possible year of WNS detection. For this last estimate a site was considered infected in a year if the distance to the presumed site of introduction (Howes Cave) was less than the distance from Howes cave to the furthest site known to be infected. Results were qualitatively similar among all three sets of analyses so we present only the results for the most likely year.

Estimating pre-WNS growth

We calculated population trends prior to WNS infection using an average of 9.2 (range: 4–22) hibernacula surveys prior to WNS. Because counts were not conducted in consecutive years, we used a regression technique to estimate the log population growth rate. Here, the dependent variable, y_i, and the independent variable, x_i, are given by:

$$y_i = \frac{\ln\left(\frac{N_{i+1}}{N_i}\right)}{\sqrt{t_{i+1} - t_i}} \text{ and } x_i = \sqrt{t_{i+1} - t_i} \quad (1)$$

where i is an index for the hibernacula counts, t_i gives the year of count i, and N_i is the count in year i. The slope of the regression of y_i vs. x_i (with the regression forced through the origin) estimates the log population growth rate, $\ln(\lambda)$ (Morris & Doak 2002).

Scaling of WNS impacts with colony size among species

We estimated the population growth rate, λ, for each population of each species with counts both before and after WNS detection. We used the single most recent pre-WNS census as a proxy for colony size prior to onset of WNS infection, which was an average of 3.7 (range: 1–9) years before WNS detection. Our results were qualitatively similar if we excluded the two sites that were surveyed 9 years before WNS detection. For sites where the first post-WNS count was more than 1 year after WNS detection we calculated the average yearly population growth rate, λ, following the arrival of WNS by adjusting for the number of years between WNS detection at a hibernacula, and the post-WNS census via:

$$\lambda = \sqrt[t_x]{\left(\frac{N_i}{N_{i-1}}\right)} \quad (2)$$

Here, N_i is the first count post-WNS detection and count, N_{i-1} is the most recent prior count before WNS detection, and t_x is the number of years between the first post-WNS detection survey and the year prior to WNS detection. These values of λ use just two population counts and represent a single estimate of population growth rate pre- and post-WNS detection for each population. They are thus distinct from the estimates of pre-WNS population growth rates described above which use multiple counts pre-WNS detection. We used this approach because, for many populations, there was only a single count post-WNS detection and thus alternate approaches (e.g. segmented regression) would lack degrees of freedom to yield improved slope estimates over those given by eqn 2.

Statistical analysis

We examined the scaling of population declines with population size using mixed-effects generalised linear models of population growth rate, λ, with a gamma distribution and the canonical inverse link using function glmmPQL in package MASS (Venables & Ripley 2002) in R v2.15 (R Development Core Team 2012). In these mixed-effects models we treated site as a random effect, and species and $\log_{10}$ population size prior to WNS detection as fixed effects. We added one to zero values of N_i because gamma distributions must be positive. Adding other fixed values or a small fraction of the pre-WNS count produced qualitatively identical results. We tested for spatial autocorrelation using Moran's I and found no significant correlations (all $P > 0.2$).

For sites where we had counts from several years' post-WNS detection, we also analysed temporal variation in the rate of decline since WNS detection. Residuals from this analysis were not temporally autocorrelated ($P > 0.05$).

We examined changes in roosting behaviour (the fraction of bats roosting singly) pre- and post-WNS detection for two species where data were available, little brown myotis and Indiana myotis. We used a mixed-effects generalised linear model of the number of bats roosting alone with a binomial distribution, and the canonical logit link using function *lmer* in package lme4 (Bates *et al.* 2011).

We analysed the influence of temperature on WNS declines of Indiana and little brown myotis among hibernacula (data were unavailable for other species), and relative humidity for Indiana myotis (relative humidity data were unavailable for little brown myotis). We used linear regression on $\log_{10}$ transformed population growth rate (results were qualitatively identical using a generalised linear model with a gamma distribution on untransformed population growth rates). We measured relative humidity and temperature in hibernacula every 3 h between 1 December and 15 April using Hobo loggers (Onset Corporation, Bourne, MA, USA) or iButtons (Maxim Inc., Sunnyvale, CA, USA) that were placed on walls at roosting locations of each species. We could not include temperature and humidity in the larger analyses described above, because microclimates of roost locations differ among species and are poorly correlated with above ground measurements.

RESULTS

Impacts of WNS on the host community

Prior to WNS emergence, all species were increasing significantly in abundance (Fig. 1a, Fig. S2, all $P < 0.05$), although confidence intervals for λ for individual populations often overlapped 1 (Table S2). A single species, little brown myotis, dominated pre-WNS hibernacula communities (Fig. S3).

After WNS detection, population growth rates varied significantly among species, with four species declining significantly and two species with log-population growth rates that were not significantly different from 0 (Fig. 1b). For all six species, the growth rates following WNS detection were significantly lower than the pre-WNS population trend, and 32 of the 120 bat populations became locally extinct (Fig. 1, Fig. S2). WNS arrived at sites across a 4 year span (2007–2010; Figs S1 and S2), and population growth rates during the same year were significantly lower at sites where WNS was present than unaffected sites in the same region (Generalised linear mixed-effects model with a gamma distribution and inverse link of population growth rate with site as random effect and species, year and WNS presence as fixed effects: WNS effect 1.28 ± 0.35, $P = 0.0007$), suggesting that declines were more likely due to WNS than other regional factors such as weather.

The scaling of declines with population size

For all species, population growth rates were unrelated to total colony size, summed across all species (all $P > 0.2$). However,

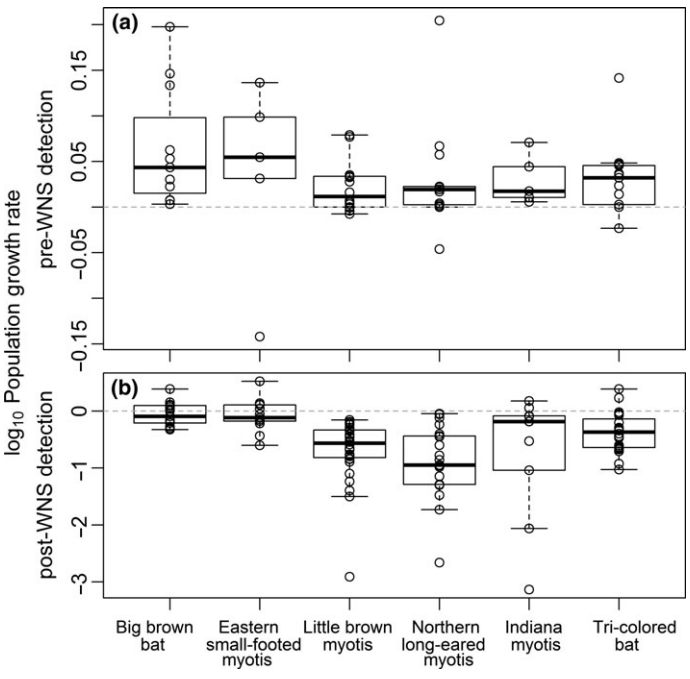

Figure 1 Population growth rates of bats pre- and post-WNS detection. (a) Box plot of $\log_{10}$ population growth rates of six hibernating bat species (a) prior to and (b) after WNS detection. The bold line indicates the median, the box encompasses the 25–75th percentiles of the data, and the whiskers extend to points within 1.5 times the inter-quantile range. The dotted grey line indicates stability and growth rates above/below 0 indicate growing/declining populations.

within-species density-dependent declines were apparent in two of the six species. Both tri-coloured bats (*Perimyotis subflavus* F. cuvier) and northern long-eared myotis (*Myotis septentrionalis* Trouessart), frequently roost solitarily or in small groups within hibernacula (Barbour & Davis 1969). In these species, declines were larger in larger pre-WNS populations (Fig. 2; Table S3), and relationships were strongest and significant only for asymptotic functions of log (colony size) (all linear relationships: $P > 0.2$). The x-intercepts of the fitted relationships imply that populations of tri-coloured bats would be expected to stabilise at an average of ~6 bats per hibernacula, but populations of northern long-eared myotis are predicted to go extinct (Fig. 2). In the other four species population growth rates were unrelated to conspecific pre-WNS population size. Of these four, the two declining species, little brown and Indiana myotis, are highly gregarious and roost in large tightly packed aggregations (Barbour & Davis 1969). In these species declines were equally severe in populations spanning four orders of magnitude, consistent with frequency-dependent transmission (Table S3, Fig. 2), and suggesting that these species might be driven to extinction by WNS.

We also examined the influence of pre-WNS population size of all other species on post-WNS population growth rates of a focal species. All but one of these 30 relationships were non-significant (all $P > 0.05$), and the single significant relationship (tri-coloured bat declines were more severe where Indiana myotis were more abundant) was relatively weak (coef. ± SE: 0.47 ± 0.21; $P = 0.04$) compared with the conspecific slope (Table S3), suggesting that this correlation may have been simply due to chance.

Temporal trends in populations and communities

Temporal analyses of population trends were consistent with predictions based on the spatial patterns of density dependence for three of the four impacted species (Figs 2 and 3). The rate of decline of tri-coloured bat populations decreased with time and populations stabilised at much lower levels 3–4 years post-WNS detection, as would be predicted if transmission were density-dependent. In contrast to this pattern of stabilisation/persistence, but also in agreement with predictions based on spatial patterns (the negative x-intercept for this species in Fig. 3), 14 populations of northern

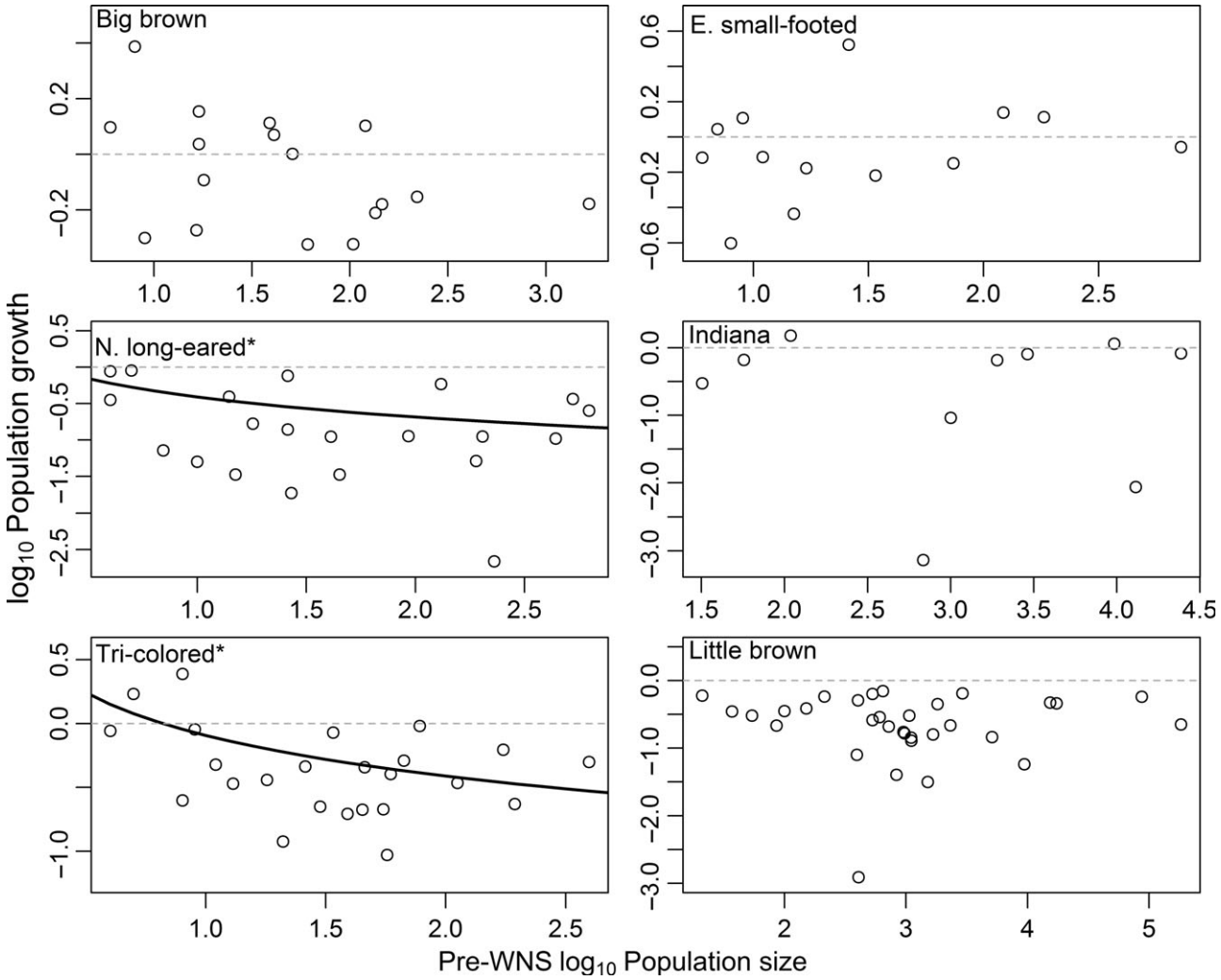

Figure 2 The influence of pre-WNS population size on population growth rate following WNS detection. Fitted lines and asterisks (*) following species names identify species in which pre-WNS population size was significantly negatively correlated with population growth rates following WNS detection. The curves show the fitted relationships, which are linear on the inverse scale used in the generalised linear model.

long-eared myotis became locally extinct within 2 years after WNS detection and no population remained after 5 years (Fig. 3). Population growth rates of Indiana myotis (which exhibited no evidence of density-dependent declines), showed little evidence for reduced declines over time (Fig. 3, Table S4). Somewhat surprisingly, declines of the fourth impacted species, little brown myotis, attenuated significantly over time with most remaining populations reaching stability within 4 years of WNS detection (Fig. 3; Table S4), despite no spatial evidence of density-dependent declines (Fig. 2).

Amelioration of declines in little brown myotis and the contrast with continuing declines in Indiana myotis may have been related to greater changes in social behaviour in little brown myotis following declines. Prior to WNS detection, both these species hibernated almost entirely in clustered aggregations (Fig. 4; fraction roosting individually: little brown myotis 1.16% ± 1.1%; Indiana myotis 0.29% ± SE 0.12%). After WNS detection, a significantly higher fraction of populations of both species roosted individually (little brown myotis: 44.5% ± 9.42%; Indiana myotis 9.6% ± 6.1%), but Indiana myotis, which continued to decline, remained far more social (Fig. 4; Table S5). For both species, the number of bats roosting singly after WNS detection was 17 times greater at each site than before WNS detection, despite greatly reduced population sizes, implying that individual bats changed clustering behaviour, rather than disease simply eliminating all but singly roosting individuals.

Overall, the differential impacts of WNS on different species resulted in changes in bat community composition pre- and post-WNS detection with the two least-impacted species, big brown bats (*Eptesicus fuscus* Palisot de Beauvois) (Wilcoxon signed rank test, $P < 0.001$) and eastern small-footed myotis (*Myotis leibii* Audubon and Bachman) ($P = 0.008$) making up significantly larger percentages of hibernating bat colonies post-WNS (Fig. S3).

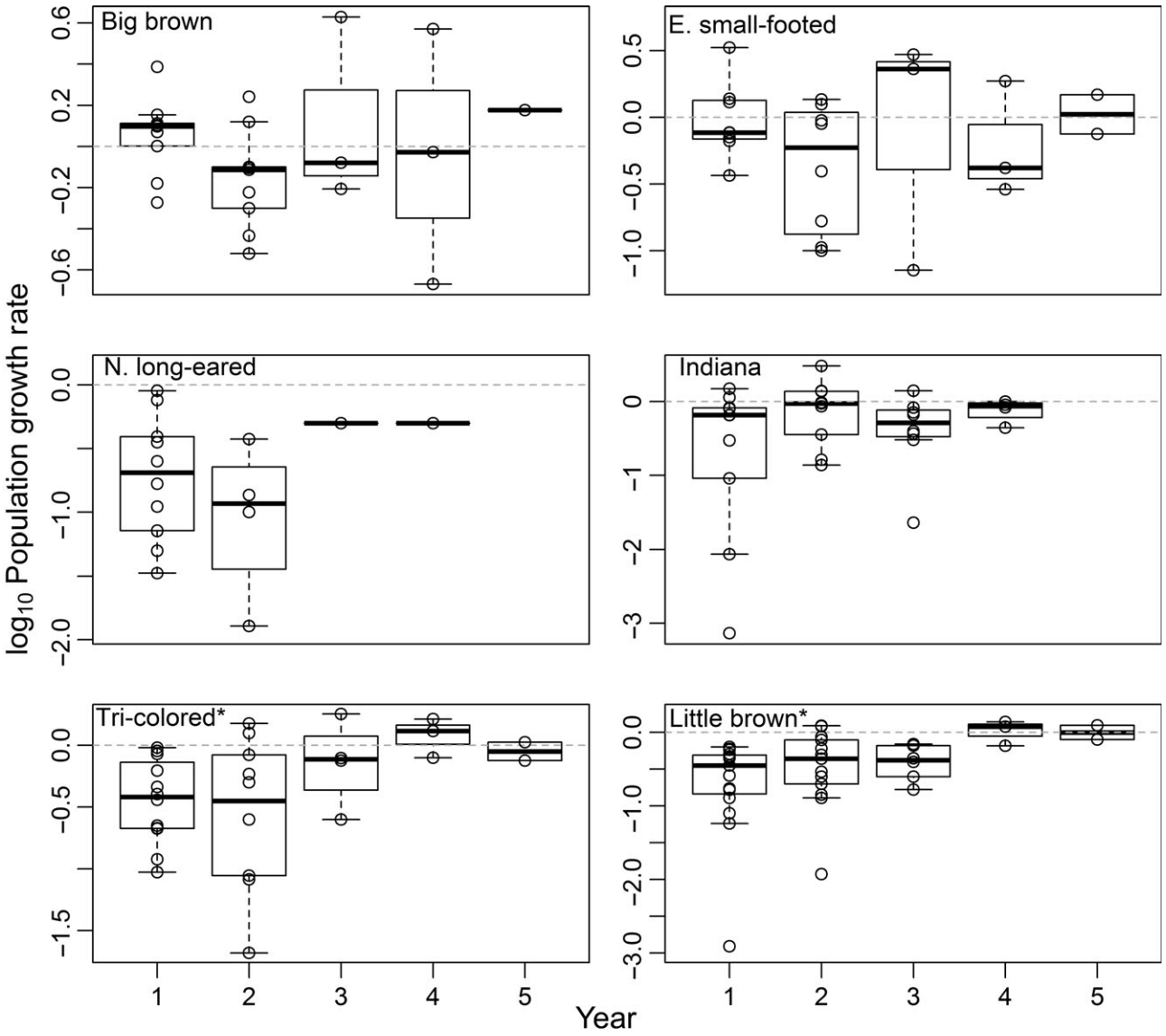

Figure 3 Population trends for six bat species in the 5 years post-WNS detection. An asterisk (*) following the species name denotes species in which population growth rates increased significantly with years since WNS detection. Boxplot details are described in Fig. 1.

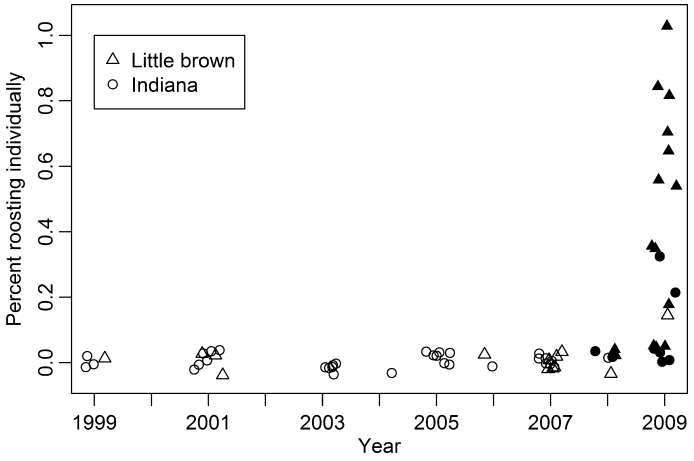

Figure 4 Clustering behaviour of little brown and Indiana myotis in hibernacula before (open symbols) and after (filled symbols) WNS detection. Points show the fraction of each population of each species roosting individually. A small amount of random variation was added to each point to show overlapping symbols.

Environmental influences

Across sites within a species, population growth rate of Indiana myotis post-WNS detection decreased with the relative humidity at hibernation sites within a hibernacula, but was unrelated to temperature (Fig. 5a: univariate linear regression for relative humidity coefficient ± SE: -0.18 ± 0.060; $P = 0.024$; Fig. 5b: coefficient for temperature in a multiple regression model with relative humidity: -0.17 ± 0.13; $P = 0.23$) and was uncorrelated with total pre-WNS population size or any two-way interaction terms (all $P > 0.05$). For populations of little brown myotis, which roosted across a larger range of temperatures, the effect of microclimate temperature was stronger and statistically significant (Fig. 5c; coef. ± SE: -0.099 ± 0.034, $P = 0.017$). As for Indiana myotis, population growth rates at this subset of sites were unrelated to total pre-WNS population size or interaction with temperature (both $P > 0.05$). In summary, populations of both species in the coolest and driest hibernacula were stable in the first year after WNS detection (Fig. 5).

DISCUSSION

In the past three decades a number of pathogens have invaded new regions and caused declines across entire communities of hosts (Riper *et al.* 1986; Lips *et al.* 2006; LaDeau *et al.* 2007). An outstanding question is which factors determine whether or not disease will cause extinctions, and which populations or species will persist? Although theory has identified several potentially important factors (Castro & Bolker 2005), empirical analyses of disease impacts on multiple host species infected with the same pathogen and varying in sociality are absent, despite the importance of assessing the risk of extinction for effective conservation (Martin *et al.* 2012).

We have shown that differences in sociality can influence the impacts of disease on populations. Declines were higher in larger winter colonies of two solitary species, northern long-eared myotis and tri-coloured bats (Fig. 2). These species rarely form large clusters (Barbour & Davis 1969) and, as a result, contact among individuals of these species would be expected to increase with colony size, resulting in density-dependent transmission. Saturating functions of density were a better fit to the declines for both species than linear functions suggesting that increases in contact rate asymptote with colony size as suggested by theory (McCallum *et al.* 2001). In contrast, in little brown and Indiana myotis, which clustered in tight aggregations during hibernation prior to WNS detection (Davis & Hitchcock 1965; Thomson 1982), we found that declines were equally severe across a large range of colony sizes. This suggests that clustering behaviour facilitated high transmission regardless of colony size, with infected individuals having approximately the same number of contacts in small colonies as they did in larger populations. This pattern is consistent with transmission being frequency-dependent, which conflicts with expectations of how populations transmit non-sexually transmitted pathogens and puts these species at risk of extinction. In these analyses, we implicitly assumed that transmission of Gd occurred directly from bat-to-bat, or if indirect transmission (e.g. bat – substrate – bat) happens, that it was proportional to conspecific density, as might be the case if contact with individual surfaces was species-specific.

The unexpected change we observed in social behaviour following WNS detection (Fig. 4) reveals how altered social aggregation can allow a species to persist, and suggests that theoretical predictions using a static scaling of transmission with host density may need revision. An increase in the number and fraction of little brown myotis roosting individually after populations declined likely results in each bat having fewer neighbours during hibernation and lower pathogen exposure. It is worth noting that the impact of WNS on this species was still severe, with populations stabilising at only 2–20% of the pre-WNS population size. The smaller changes in sociality observed in Indiana myotis apparently were not large enough to reduce transmission and disease impact to allow for populations to stabilise, and this puts this species at a high risk of extinction.

We found little support for total colony size or the abundance of individual heterospecifics as significant predictors of declines. This likely resulted in part from the fact that the species with density-dependent declines (tri-coloured bats and northern long-eared myotis) were never dominant at sites (Fig. S3). Nonetheless, it suggests that the total number of individuals within a hibernaculum is not determining transmission intensity, and that interactions among species are playing a relatively minor role in transmission. We caution that this analysis is purely observational and based on population trends rather than infection data, and thus should be treated as a hypothesis to be tested with data on the infectiousness of each species, and while accounting for other factors, such as environmental conditions.

Our results demonstrate how environmental conditions can modulate disease impacts. We found that declines in Indiana myotis were greater under more humid conditions, which suggest that growth of the fungus, and either intensity or prevalence of infections may be higher in more humid conditions. We also found that for little brown myotis declines were higher in hibernacula with higher temperatures. This suggests that, for this species, increased pathogen growth observed in the lab across the range of temperatures measured in hibernacula, 3–15 °C (Fig. 5) (Gargas *et al.* 2009; Chaturvedi *et al.* 2010), is more important than increases in host immune function, if any. It is possible that the lower declines observed in Indiana myotis compared to little brown myotis may be partly due to the cooler temperatures where Indiana myotis hibernate (Table S1; Fig. 5).

In the four decades prior to WNS detection, bat populations were growing at an average of 8% per year. WNS has reversed this trend and changed the composition of bat communities. Our find-

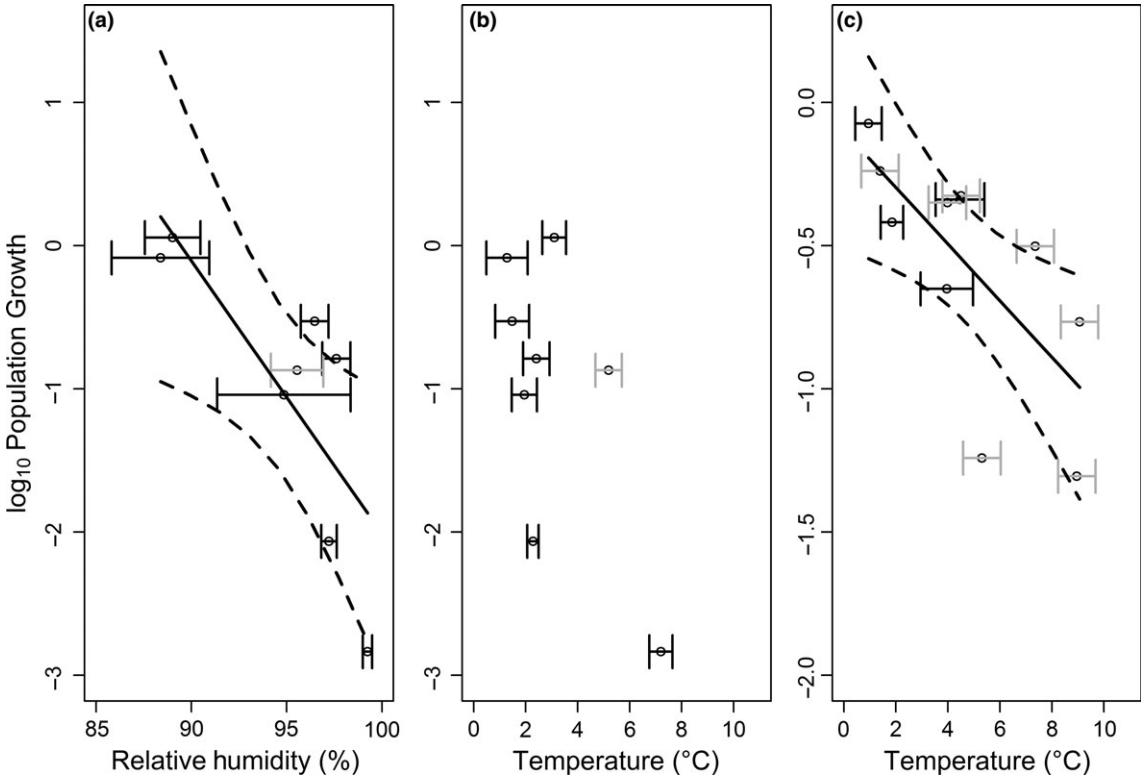

Figure 5 Influence of environmental factors on declines post-WNS detection. (a) Relative humidity and (b) Mean temperature of Indiana myotis roosts at seven hibernacula in New York State. (c) Mean temperature of little brown myotis roosts from 11 sites in New York State. Black error bars show standard error and grey bars show mean standard error estimated from all points.

ings illustrate how among-species variation in sociality, the scaling of declines with colony size and dynamic changes in clustering behaviour influence long-term persistence of species suffering from disease. Geographical variation in sociality and population size, that is widespread in bats and other species (Barbour & Davis 1969; Nunn & Altizer 2006), combined with changes in behaviour in response to disease (Funk *et al.* 2009), will modulate impacts as pathogens spread following introduction. More broadly, our results highlight key factors that can determine the impact of a pathogen on a community of co-occurring hosts, and provide an empirical basis for assessing risk of extinction from disease.

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AUTHOR CONTRIBUTIONS

All authors conceived of and designed the study. ACH and KEL collected the data. KEL, WFF, JTB and AMK analysed the data. KEL, WFF and AMK wrote the paper. All authors contributed to revising the manuscript.

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