

Anticipating white-nose syndrome in the Southern Hemisphere: Widespread conditions favourable to *Pseudogymnoascus destructans* pose a serious risk to Australia's bat fauna

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Abstract There is a serious concern that white-nose syndrome (WNS), a fungal disease causing severe population declines in North American bats, could soon threaten bats on the Australian continent. Despite an 'almost certain' risk of incursion within the next ten years, and high virulence in naïve bat populations, we remain uncertain about the vulnerability of Australian bats to WNS. In this study, we intersected occurrences for the 27 cave roosting bat species in Australia with interpolated data on mean annual surface temperature, which provides a proxy for thermal conditions within a cave and hence its suitability for growth by the fungal pathogen *Pseudogymnoascus destructans*. Our analysis identifies favourable roost thermal conditions within 30–100% of the ranges of eight bat species across south-eastern Australia, including for seven species already listed as threatened with extinction. These results demonstrate the potential for widespread exposure to *P. destructans* and suggest that WNS could pose a serious risk to the conservation of Australia's bat fauna. The impacts of exposure to *P. destructans* will depend, however, on the sensitivity of bats to developing WNS, and a more comprehensive vulnerability assessment is currently prevented by a lack of information on the hibernation biology of Australian bats. Thus, given the clear potential for widespread exposure of Australia's bats to *P. destructans* demonstrated by our study, two specific policy actions seem justified: (i) urgent implementation of border controls that identify and decontaminate cave-associated fomites and (ii) dedicated funding to enable research on key aspects of bat winter behaviour and hibernation physiology. Further, as accidental translocation of this fungus could also pose a risk to other naïve bat faunas in cooler regions of southern Africa and South America, we argue that a proactive, globally coordinated approach is required to understand and mitigate the potential impacts of WNS spreading to Southern Hemisphere bats.

Key words: bats, Chiroptera, disease, exposure, extinction, pathogen.

INTRODUCTION

Australian bats might soon be exposed to the bat fungal disease called white-nose syndrome (WNS) that has caused tenfold declines in bat populations across North America since 2006 (Blehert *et al.* 2009; Frick *et al.* 2015) when *Pseudogymnoascus destructans* was introduced probably from Europe (Drees *et al.* 2017). According to a recent qualitative risk assessment (Holz *et al.* 2019), this fungal pathogen is 'almost certain' to enter Australia in the next ten years, posing a serious yet hitherto unquantified threat to Australia's cave roosting bat species. Due to its biogeographical isolation, Australia's wildlife is inherently at risk from novel invasive pathogens (Daszak *et al.* 2000). As there is no evidence that

P. destructans currently occurs in Australia (Holz *et al.* 2018), Australian bat species, like their North American counterparts, are likely to be evolutionarily naïve and hence susceptible to developing WNS (Warnecke *et al.* 2012). There is an urgent need, therefore, to quantify the vulnerability to WNS of Australian bats. Moreover, WNS could also threaten the bat faunas inhabiting cool regions of other southern continents and even high-altitude regions of the neotropics. Worldwide actions are thus required to improve preparedness to the trans-continental spread of this potentially devastating wildlife disease.

An absence of information on the hibernation biology of bats in regions outside of North America and Europe, including Australia, prevents accurate predictions of their mortality risk from WNS. Hibernation during winter is the period of vulnerability for insectivorous bats exposed to *P. destructans*. Bats in cool climates must reduce their energy expenditure

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over winter when their insect food is reduced or unavailable by the use of prolonged torpor bouts. Torpor bouts are interspersed with brief inter-bout arousal periods, which require a large proportion (~90%) of the energy consumed during hibernation (Thomas *et al.* 1990; Jonasson & Willis 2012). The low body temperature of torpid bats and their suppressed immune system during the hibernation season (Bouma *et al.* 2010) permit infection and growth by this cold-adapted fungus (Gargas *et al.* 2009). The physiopathology of WNS causes affected bats to arouse more frequently from torpor (Reeder *et al.* 2012; Warnecke *et al.* 2012) and hence to prematurely exhaust their limited overwinter body energy (fat) and/or water reserves, resulting in starvation or dehydration (Verant *et al.* 2014; Willis 2015). Mortality from WNS is restricted to bats hibernating over the winter season (Langwig *et al.* 2015a). Some tree-roosting insectivorous bat populations are known to employ multiday torpor bouts during winter in Australia (Turbill 2006; Turbill & Geiser 2008), New Zealand (Czenze *et al.* 2017), southern Africa (McKechnie & Mzilikazi 2011) and probably South America, but information is scant on torpor and activity patterns and winter energy budgets for any Austral cave roosting species (Dwyer 1964).

In the absence of knowledge about the hibernation biology of bats, we can still quantitatively assess vulnerability to WNS with a model that predicts only the potential for exposure to the pathogen. According to a framework for predicting impacts from threatening processes (e.g. climate change), ‘vulnerability’ is a function of two essential components: ‘sensitivity’, which describes the typically negative responses of individuals or populations when experiencing the threat (governed primarily by traits that are intrinsic to an individual or population), and ‘exposure’, which describes the mostly external factors modulating whether and to what extent individuals or populations will experience the threat (Williams *et al.* 2008). We put to one side the question of sensitivity to WNS, assuming only that some negative effects are possible, and focus entirely on modelling the potential for exposure to WNS following incursion and spread of the fungal pathogen. Quantifying potential exposure represents a useful first step to planning responses to the risk of incursion. More complete models of vulnerability to WNS can be applied when species-specific information becomes available on the traits (e.g. winter behaviour and hibernation physiology) determining sensitivity to mortality from WNS (Hayman *et al.* 2016). Here, we intersect data on species occurrence locations, geographic variation in a proxy for cave roost temperatures and the thermal response curve of growth for *P. destructans* to model the potential for exposure to WNS for all Australian cave roosting bat species.

METHODS

We determined for all 27 bat species known to often roost in cave or cave-like structures in Australia (Churchill 2008) whether their occurrences were likely to contain thermal conditions suitable for the growth of *P. destructans*. Bat species hibernating in tree-roosts appear not to be susceptible to WNS (U.S. Fish and Wildlife Service 2019), possibly because tree-roosts typically are not as humid and are more variable in temperature and humidity compared to cave roosts; hence, we focused our analysis on cave roosting species only. We treated the two subspecies of large bent-winged bat (*Miniopterus orianae oceanensis* and *M. o. bas-sanii*) separately because they are recognised and likely to be upgraded to full species status (Churchill 2008; Jackson & Groves 2015). We also included one species, the chocolate wattled bat (*Chalinolobus morio*), that is primarily tree-roosting but also roosts in caves, particularly in the Nullarbor Plains region of south-western Australia.

Cave microclimate is a primary determinant of the prevalence of *P. destructans*, with the most severe die-offs from WNS in North America occurring in relatively warm and humid winter cave roosts (Langwig *et al.* 2016). Growth of *P. destructans* under high humidity occurs between critical temperatures of 0 and 19.8°C, with thermal optima of 12.5–15.8°C (Verant *et al.* 2012). There are very limited data on roost microclimates selected by overwintering bats in Australia (collated in: Holz *et al.* 2016). Mean annual surface temperature (MAST) provides a reasonable proxy of deep cave temperatures (Perry 2012) and geographic variation in MAST has been used to predict cave microclimate in key modelling studies to understand WNS vulnerability among North American bats (Hayman *et al.* 2016). We acknowledge several limitations in the use of MAST as an indicator of cave habitat suitability for *P. destructans*: (i) the geographic distribution of caves and especially those suitable for hibernation represent only a limited and potentially biased proportion of the range of occurrences for a species; (ii) temperatures can vary within caves depending on their geology, shape and air-flow characteristics (Perry 2012), and (iii) bats tend to select locations within caves during hibernation that provide temperatures somewhat below MAST (Perry 2012). Scant data on microclimate of hibernacula used by Australian cave bats indicate that selected roosts in midwinter tend to be up to 3°C colder than local MAST (Dwyer 1964; Hall 1982). These limitations reduce the precision of the relationship between MAST and thermally suitable caves but do not invalidate the usefulness of MAST as an overall predictor of geographic variation in thermal conditions within potential cave habitat. These models could be refined where finer-scale regional or cave-specific information becomes available.

For each of the 27 cave roosting species, we extracted the location (latitude, longitude) of all occurrence records (derived primarily from captures and identified acoustic echolocation recordings) listed in the Atlas of Living Australia database (www.ala.org.au) and intersected these locations with a spatial data layer of interpolated mean annual surface temperature (WorldClim Version 1.4; 10 arcminute spatial resolution; current conditions: 1960–1990; download at www.worldclim.org; Hijmans *et al.* 2005).

Australian MAST has increased on average by 1°C since 1910, with most warming occurring since 1960 (Australian Government Bureau of Meteorology and CSIRO 2018), so temperatures estimated by the WorldClim dataset will tend to be cooler than current thermal conditions. We intersected occurrence records with WorldClim data using code written by Dr Remko Duursma (package ‘speciesmap’, available at <http://remkoduursma.github.io/speciesmap>) for the program R v.3.4.2 (R Development Core Team 2009), interfaced using the program Rstudio v.1.1.423 (RStudio Team 2015). This method provided a single estimate of MAST for each 10 arcminute grid cell (~16 by 18.5 km at 30°S) that included at least one occurrence record and hence largely avoided bias linked to the spatial density of occurrence records. We calculated the proportion of all intersected 10 arcminute grid cells with mean annual temperatures between 0 and 18°C, representing the thermal range allowing growth of the fungus under high humidity conditions (Verant *et al.* 2012). We also applied a colour gradient to these MAST data to allow their visualisation as a ‘heat map’ based on a growth performance curve of *P. destructans* with a thermal optimum of 13.5°C (Verant *et al.* 2012).

RESULTS

The distribution of MAST indicating the potential for cave habitats with a thermal climate suitable for *P. destructans* included much of south-eastern Australia south of approximately 30°S, and further north to 26°S in elevated regions of the Great Dividing Range (Fig. 1). Of the 27 bat species known to often roost in cave or cave-like structures in Australia (Churchill 2008), eight species have occurrences that overlap with MAST values indicative of cave roost temperatures suitable for growth of *P. destructans* (Fig. 2, Table 1). All eight potentially exposed species occurred in the cooler south-eastern portion of Australia excluding the island of Tasmania that does not support any cave roosting bats. All occurrences of the critically endangered southern bent-winged bat *Miniopterus orianae bassanii* intersected with a narrow band of MAST from 12 to 15°C spanning the optimal temperature for growth by *P. destructans*. For the eastern bent-winged bat *M. o. oceanensis*, two-thirds (68%) of occurrences had estimated cave roost temperatures permitting growth by *P. destructans*, with a broad mode between 13 and 18°C in the thermal range of high growth rates. One-third (32%) of occurrences for the little bent-winged bat *Miniopterus australis* had suitable roost temperatures for growth by *P. destructans*, reflecting the more northerly limit of its range and more coastal distribution compared to the other *Miniopterus* species. Three more cave roosting species had a minimum of 43% of occurrences, and one further cave-dwelling species had just 2% of occurrences containing roost temperatures suitable for growth by *P. destructans*. For the chocolate wattled bat *Chalinolobus morio*, 85% occurrence

records had estimated cave roost temperatures permitting growth by *P. destructans* but the species uses tree hollows primarily over most of this range (apart from Nullarbor Plains region, where MAST values are just within the upper limit for fungal growth).

DISCUSSION

Our analysis indicates that cave temperatures suitable for growth of *P. destructans* are likely to be found across a large proportion of the ranges of nearly one-third of Australian cave-dwelling bat species. Of these species facing potential exposure, two are listed as threatened with extinction at the national level, including *M. o. bassanii* as critically endangered, and seven are listed as threatened with extinction at the state level. Given the likelihood of incursion of *P. destructans* into Australia was rated as ‘almost certain’ within the next ten years by a multi-agency risk assessment workshop (Holz *et al.* 2019), and evidence of catastrophic effects on evolutionarily naïve bat populations elsewhere (Frick *et al.* 2015), the potential for widespread exposure to the fungus suggests that WNS poses a serious impending risk to the conservation of Australia’s bat fauna.

Several factors could reduce the vulnerability to WNS among Australian bats (Holz *et al.* 2019), despite the potential for exposure to the fungal pathogen as shown in our study. Humidity is important for growth by *P. destructans* and hence will affect potential

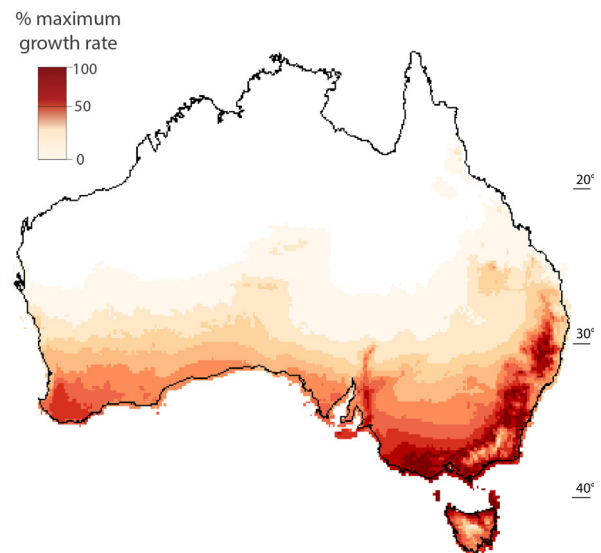


Fig. 1. Estimated spatial extent of cave roost thermal conditions suitable for growth by *Pseudogymnoascus destructans* throughout Australia, as indicated by coding of mean annual surface temperatures according to the thermal growth performance curve of *P. destructans* (darker colour density indicates higher fungal growth rates).

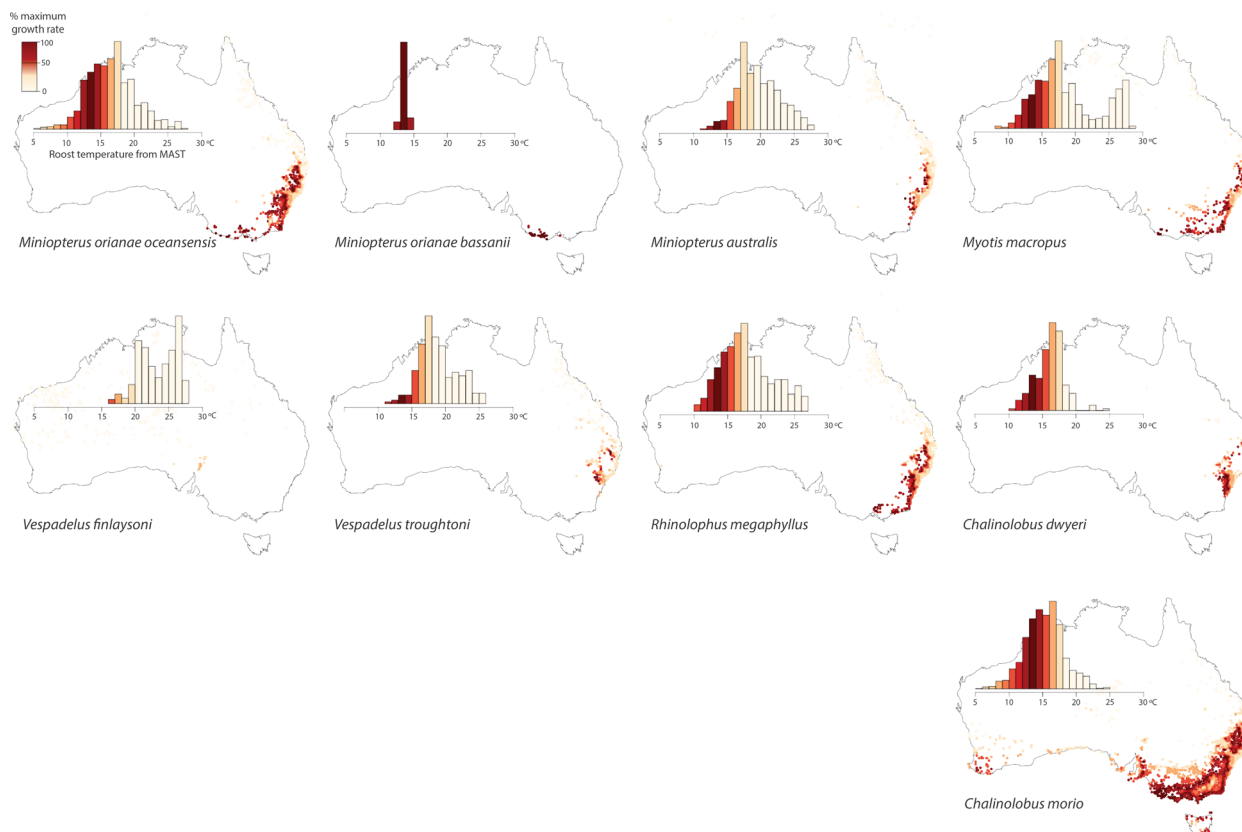


Fig. 2. Potential for exposure to the fungal pathogen *Pseudogymnoascus destructans* causing white-nose syndrome among Australian cave roosting bat species. Species occurrences are coded according to cave roost temperature predicted from mean annual surface temperature with the density of colour indicative of the temperature-dependent growth rate of *P. destructans* (darker colour density indicates higher fungal growth rates). Note that *Chalinolobus morio* is primarily a tree-roosting species that sometimes roosts in caves (primarily in the Nullarbor Plain region).

exposure in the roost. Humidity is very high in the winter cave roosts used by *Miniopterus orianae oceanensis* (Hall 1982), *M. o. bassanii*, and probably also *Rhinolophus megaphyllus*, but the relatively shallow cave-like roosts used by *Vespadelus troughtoni*, *Chalinolobus dwyeri* and *Myotis macropus* (Churchill 2008) are generally less humid and hence would be suboptimal for fungal growth. Sensitivity of individual bats to mortality from WNS is largely dependent on the thermal energetics of hibernation (Reeder *et al.* 2012; Warnecke *et al.* 2012), including body fat levels (Cheng *et al.* 2019), and their interaction with immune responses (Moore *et al.* 2018). Torpor use is widespread among Australian bats (Geiser 2006; Geiser & Körner 2010), but winter conditions might be sufficiently mild to prevent hibernating bats from developing WNS symptoms or reduce the likelihood of consequential mortality. In laboratory experiments, infected little brown bats *Myotis lucifugus* had significantly shorter torpor bouts than controls after just 27 days, and mortalities from WNS began after 71 days, while hibernating at 7°C and 97% humidity (Warnecke *et al.* 2012). Hibernation patterns of Australian

bats have been measured for several tree-roosting species (*Nyctophilus gouldi*, *N. geoffroyi* and *Chalinolobus morio*) in a region with a cool temperate climate (MAST: 13.2°C) on the elevated northern tablelands of eastern Australia. These species employed multiday torpor bouts lasting up to 15 days interrupted by short arousals over a period of 2–3 months during winter (Turbill 2006; Turbill & Geiser 2008). Shorter torpor bouts and increased nightly activity were observed throughout winter during occasional brief periods of milder weather conditions (Turbill 2008; Turbill & Geiser 2008). The cave roosting *M. o. oceanensis* in a similar climate often appeared torpid during winter and lost on average 22% of their pre-hibernation body mass over the winter season (Dwyer 1964). In a subtropical coastal habitat, another tree-roosting species (*N. bifax*) was recorded using torpor often during winter, including multiday bouts lasting up to 5 days during cooler periods (Stawski *et al.* 2009), indicating that degrees of hibernation are employed even in relatively mild climates (Geiser & Stawski 2011). Thus, exposure will be less severe for bats overwintering in dryer roosts, and sensitivity of bat populations facing

Table 1. Proportion of occurrence records for all Australian cave roosting bat species with roost temperatures predicted from annual surface temperature within the range of 0 and 18°C that is suitable for growth of the fungal pathogen (*Pseudogymnoascus destructans*) causing white-nose syndrome

Scientific name	Common name	Conservation status [†]	% Occurrences
<i>Miniopterus australis</i>	Little bent-winged bat	VU (NSW)	32
<i>Miniopterus orianae bassanii</i>	Southern bent-winged bat	CR (National, VIC); EN (SA)	100
<i>Miniopterus orianae oceanensis</i>	Eastern bent-winged bat	VU (NSW, VIC)	68
<i>Myotis macropus</i>	Large-footed myotis	VU (NSW); EN (SA)	55
<i>Vespadelus finlaysoni</i>	Finlayson's cave bat	Not listed	2
<i>Vespadelus troughtoni</i>	Eastern cave bat	VU (NSW)	43
<i>Rhinolophus megaphyllus</i>	Eastern horseshoe bat	VU (VIC)	56
<i>Chalinolobus dawyeri</i>	Large-eared pied bat	VU (National, NSW, QLD)	86
<i>Chalinolobus morio</i> [‡]	Chocolate wattled bat	Not listed	85

[†]Species classified as threatened with extinction (CR = Critically Endangered; EN = Endangered; VU = Vulnerable) in national or state legislation (National: Environment Protection and Biodiversity Protection Act 1999; NSW: Biodiversity Conservation Act 2016; VIC: Flora and Fauna Guarantee Act 1988; SA: National Parks and Wildlife Act 1972; QLD: Nature Conservation Act 1992). [‡]Primarily tree-roosting with a cave roosting population occurring in the Nullarbor Plain region.

exposure could be alleviated by shorter winter seasons, shorter torpor bouts during hibernation and some winter foraging opportunities for bats in relatively mild Australian climates. These conditions might allow better resistance to infection and reduce the severity of symptoms of WNS among at least some population of Australian bats in areas of potential exposure.

Other factors could exacerbate the vulnerability to WNS among Australian bats. Evolutionary naïveté to the pathogen is supported as the underlying cause of the devastating impacts of WNS among North American bats (Warnecke *et al.* 2012). Indeed, persisting bat populations show evidence of adaptive changes that enhance resistance to WNS (Donaldson *et al.* 2017; Langwig *et al.* 2017; Gignoux-Wolfsohn *et al.* 2018; Harazim *et al.* 2018). Australia's unique wildlife is inherently at risk from novel invasive pathogens due to its long-term biogeographical isolation (Daszak *et al.* 2000), and Australian bats could thus be more evolutionarily naïve than their distant North American relatives and relatively more susceptible to the pathophysiology of WNS (Verant *et al.* 2014). In addition, some bats in warmer climates are known to select the coldest sections of caves during winter hibernation (Perry 2012), which may lead to underestimates of exposure to *P. destructans* and hence vulnerability to WNS. For instance, as activity declined during early winter, eastern bent-winged bats moved to roost in locations that were 2–3°C colder than mean cave temperature (Hall 1982). Such selection of relatively cold (and humid) winter roosting locations within caves could expose bats in warmer climates to increased prevalence of *P. destructans*, and at lower elevations and latitudes than we have identified here. There is a need for research to describe the microclimate of winter cave hibernacula and roost selection behaviour for different species of Australian bats. Clustering behaviour also increases the

sensitivity of bats to WNS (Turner *et al.* 2015) and Australian bent-winged bats (*Miniopterus* spp.) form tight clusters when hibernating over winter (Dwyer 1964). Finally, even if direct mortality from WNS is unlikely, the disease might cause important non-lethal negative consequences, including disruptions to torpor patterns and hence seasonal energy budgets, tissue damage and chronic physiological effects, including the costs of recovery from the disease (Davy *et al.* 2016), all of which could reduce the long-term fitness of Australian cave roosting bats and hence exacerbate pre-existing threats to their conservation (Holz *et al.* 2019).

Given the rapid and catastrophic impact of WNS on bat populations in North America (Frick *et al.* 2015), and the estimated widespread extent of cave roost thermal conditions suitable for growth by *P. destructans* in Australia (Fig. 1), a proactive and precautionary approach is critical to minimising impacts in the likely event of an Australian incursion. Such actions should include pre-arrival measures involving tightening of biosecurity to prevent accidental introduction of *P. destructans* on fomites, such as boots and caving equipment, and facilitating research to provide key missing information required to improve modelling of vulnerability, and post-arrival measures including limiting public access to hibernation roost sites, implementing WNS decontamination protocols and other mechanisms that reduce the spread of the pathogen and possibly also its impact on populations of threatened or high-risk species (Wildlife Health Australia 2017).

Current pre-arrival measures include a multistakeholder drive for increased awareness of the risk of WNS among Australia's caving (Australian Government Department of Agriculture and Water Resources 2017; Australian Speleological Federation 2018) and bat enthusiasts communities (Australasian

Bat Society 2017). However, at present, caving activities and equipment are not explicitly identified on Australia's incoming passenger declarations so that instead it is left to cavers and bat enthusiasts to identify these voluntarily. Furthermore, the Australian Border Force as yet has no specific protocols in place for decontaminating and, if necessary, confiscating fomites that potentially carry *P. destructans*; so even when fomites are reported voluntarily it is not clear that this is then followed by an appropriate biosecurity response. Therefore, we strongly urge the Australian government specifically to (i) amend its Incoming Passenger Card (Australian Border Force 2018) to include 'caves' explicitly in the question 'Have you been in contact with farms, farm animals, wilderness areas or freshwater streams/lakes etc in the past 30 days?'; and (ii) implement targeted protocols at its borders for identifying and processing fomites that potentially carry *P. destructans*.

Current post-arrival measures include strategies for control of the spread of WNS and measures that could reduce its impact, with high priority activities being the identification and engagement of stakeholders, disease surveillance, cave closures, biosecurity and decontamination, education and conservation activities (Wildlife Health Australia 2017). However, the effectiveness of these post-arrival measures would benefit greatly from 'research to inform risk and response' (Wildlife Health Australia 2017). Our study has made the potential for exposure to *P. destructans* following incursion species-specific and spatially explicit and so facilitates more efficient deployment of limited WNS management resources. However, to quantify the vulnerability of species to WNS, information on exposure must be combined with information on the traits that determine WNS sensitivity; hence, research on winter behaviour and hibernation physiology of most at-risk bats in particular is key for enabling informed decisions about effective management at each of the invasion front, epidemic and recovery stages of the disease (Langwig *et al.* 2015b).

In response to the WNS epidemic, US Fish and Wildlife Services have allocated more than \$46 million since 2008 to support research and fieldwork on WNS (U.S. Fish and Wildlife Service 2019). This direct injection of funding and additional resourcing from multiple agencies of North America and Canada and non-government organisations has led to an enormous increase in relevant knowledge about the biology of bats and fungal pathogen. These recent studies have honed techniques for monitoring bats and their responses to WNS, such as long-term video surveillance (Hayman *et al.* 2017) and experimental testing of possible amelioration (e.g. by habitat manipulation; Boyles & Willis 2010). From this intense period of research, we can identify the

population-specific traits most informative of sensitivity to WNS. Key factors include behavioural traits such as selection of roost microclimate, clustering and colony size, arousal cues and winter foraging activity, and physiological traits such as pre-hibernation body fat accumulation, torpor-arousal patterns, metabolic rates during torpor and arousal, and pathophysiological and immunological responses to the fungal infection (Willis 2015, 2017; Hayman *et al.* 2016). We thus urge relevant agencies in Australia to make funding available (e.g. as competitive grants) for focused research programmes that will deliver this crucial missing information.

Finally, although our study focuses on Australian bats, there is a clear potential for catastrophic impacts of this fungus on naïve bat populations in other Southern Hemisphere continents. The warm tropics are presumably a natural barrier to dispersal for the cold-adapted fungus (although cool mountainous tropical regions could be at risk, e.g. for bats in the Tropical Andes). The high prevalence in recently infected North American bat colonies, and increasing human translocation of pathogens (Fisher *et al.* 2012), enhances the risk of trans-hemispheric incursions of *P. destructans*. Our mapping shows that caves across a substantial area of south-eastern Australia provide thermally suitable conditions for this cold-growing fungus. Mapping of climatic suitability for *P. destructans* in South America also indicates overlap with the ranges of several endemic species (Escobar *et al.* 2014). We are not aware of any WNS vulnerability assessments for African bats, but elevated regions in southern Africa contain suitable climates and some African bats employ a degree of hibernation (McKechnie & Mzilikazi 2011). Overall, given the potential for accidental trans-hemispheric spread of *P. destructans*, it is clear that a proactive, globally coordinated response, which must include targeted research, is needed to help prevent WNS from impacting Southern Hemisphere bats.

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AUTHOR CONTRIBUTIONS

Conceptualization-lead, formal analysis-lead, writing-original draft-equal, writing-review & editing-equal: C.T. Conceptualization-supporting, formal analysis-supporting, writing-original draft-equal, Writing-review & editing-equal: J.A.W.

REFERENCES

- Australasian Bat Society (2017) [Cited 19th December 2018.] Available from URL: <http://www.abs.gov.au/AUSSTATS/abs@.nsf/1020492cfcd63696ca2568a1002477b5/87e6462fceb8b8ca256c3f007bd582!OpenDocument>.
- Australian Border Force (2018) [Cited 19th December 2018.] Available from URL: [https://www.abf.gov.au/entering-and-leaving-australia/crossing-the-border/at-the-border/inc-oming-passenger-card-\(ipc\)](https://www.abf.gov.au/entering-and-leaving-australia/crossing-the-border/at-the-border/inc-oming-passenger-card-(ipc)).
- Australian Government Bureau of Meteorology & CSIRO (2018) State of the Climate 2018.
- Australian Government Department of Agriculture and Water Resources (2017) [Cited 19 December 2018.] Available from URL: <http://www.agriculture.gov.au/pests-diseases-weeds/animal/white-nose-syndrome>.
- Australian Speleological Federation (2018) [Cited 19th December 2018.] Available from URL: <https://asconferece2019.com/stop-the-spread-of-wns-and-invasive-species/>.
- Blehert D. S., Hicks A. C., Behr M. *et al.* (2009) Bat white-nose syndrome: an emerging fungal pathogen? *Science* **323**, 227.
- Bouma H. R., Carey H. V. & Kroese F. G. M. (2010) Hibernation: the immune system at rest? *Journal of Leukocyte Biology* **88**, 619–24.
- Boyles J. G. & Willis C. K. R. (2010) Could localized warm areas inside cold caves reduce mortality of hibernating bats affected by white-nose syndrome? *Frontiers in Ecology and the Environment* **8**, 92–8.
- Cheng T. L., Gerson A., Moore M. S. *et al.* (2019) Higher fat stores contribute to persistence of little brown bat populations with white-nose syndrome. *Journal of Animal Ecology* **88**, 591–600.
- Churchill S. (2008) *Australian Bats*, 2nd edn. Allen & Unwin, Crow's Nest.
- Czenze Z. J., Brigham R. M., Hickey A. J. R. & Parsons S. (2017) Winter climate affects torpor patterns and roost choice in New Zealand lesser short-tailed bats. *Journal of Zoology* **303**, 236–43.
- Daszak P., Cunningham A. A. & Hyatt A. D. (2000) Emerging infectious diseases of wildlife – threats to biodiversity and human health. *Science* **287**, 443.
- Davy C. M., Mastrotonaco G. F., Riley J. L., Baxter-Gilbert J. H., Mayberry H. & Willis C. K. R. (2016) Conservation implications of physiological carry-over effects in bats recovering from white-nose syndrome. *Conservation Biology* **31**, 615–24.
- Donaldson M. E., Davy C. M., Willis C. K. R., McBurney S., Park A. & Kyle C. J. (2017) Profiling the immunome of little brown myotis provides a yardstick for measuring the genetic response to white-nose syndrome. *Evolutionary Applications* **10**, 1076–90.
- Drees K. P., Lorch J. M., Puechmaille S. J. *et al.* (2017) Phylogenetics of a fungal invasion: origins and widespread dispersal of white-nose syndrome. *mBio* **8**, e01941–17.
- Dwyer P. D. (1964) Seasonal changes in activity and weight of *Miniopterus schreibersii blepotis* (Chiroptera) in north-eastern NSW. *Australian Journal of Zoology* **12**, 52–69.
- Escobar L. E., Lira-Noriega A., Medina-Vogel G. & Townsend Peterson A. (2014) Potential for spread of the white-nose fungus (*Pseudogymnoascus destructans*) in the Americas: use of Maxent and NicheA to assure strict model transference. *Geospatial Health* **9**, 221–9.
- Fisher M. C., Henk D. A., Briggs C. J. *et al.* (2012) Emerging fungal threats to animal, plant and ecosystem health. *Nature* **484**, 186–94.
- Frick W. F., Puechmaille S. J., Hoyt J. R. *et al.* (2015) Disease alters macroecological patterns of North American bats. *Global Ecology and Biogeography* **24**, 741–9.
- Gargas A., Trest M. T., Christensen M., Volk T. J. & Blehert D. S. (2009) *Geomyces destructans* sp. nov. associated with bat white-nose syndrome. *Mycotaxon* **108**, 147–54.
- Geiser F. (2006) Energetics, thermal biology, and torpor in Australian bats. In: *Functional and Evolutionary Ecology of Bats* (eds A. Zubaid, G. F. McCracken & T. Kunz) pp. 5–22. Oxford University Press, New York.
- Geiser F. & Körtner G. (2010) Hibernation and daily torpor in Australian mammals. *Australian Zoology* **35**, 204–15.
- Geiser F. & Stawski C. (2011) Hibernation and torpor in tropical and subtropical bats in relation to energetics, extinctions, and the evolution of endothermy. *Integrative Comparative Biology* **51**, 337–48.
- Gignoux-Wolfsohn S. A., Pinsky M. L., Kerwin K. *et al.* (2018) Genomic signatures of evolutionary rescue in bats surviving white-nose syndrome *bioRxiv*, 470294.
- Hall L. S. (1982) The effect of cave microclimate on winter roosting behaviour in the bat, *Miniopterus schreibersii blepotis*. *Australian Journal of Ecology* **7**, 129–36.
- Harazim M., Horáček I., Jakešová L. *et al.* (2018) Natural selection in bats with historical exposure to white-nose syndrome. *BMC Zoology* **3**, 8.
- Hayman D. T. S., Pulliam J. R. C., Marshall J. C., Cryan P. M. & Webb C. T. (2016) Environment, host, and fungal traits predict continental-scale white-nose syndrome in bats. *Scientific Advances* **2**, e1500831.
- Hayman D. T. S., Cryan P. M., Fricker P. D. & Dannemiller N. G. (2017) Long-term video surveillance and automated analyses reveal arousal patterns in groups of hibernating bats. *Methods in Ecology and Evolution* **8**, 1813–21.
- Hijmans R. J., Cameron S. E., Parra J. L., Jones P. G. & Jarvis A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**, 1965–78.
- Holz P., Hufschmid J., Boardman W. *et al.* (2016) Qualitative risk assessment: White-nose syndrome in bats in Australia. A report prepared for Wildlife Health Australia.
- Holz P. H., Lumsden L. F., Marendá M. S., Browning G. F. & Hufschmid J. (2018) Two subspecies of bent-winged bats (*Miniopterus orianae bassanii* and *oceanensis*) in southern Australia have diverse fungal skin flora but not *Pseudogymnoascus destructans*. *PLoS ONE* **13**, e0204282.
- Holz P., Hufschmid J., Boardman W. *et al.* (2019) Does the fungus causing white nose syndrome pose a significant risk to Australian bats? *Wildlife Research*, in press.
- Jackson S. & Groves C. (2015) *Taxonomy of Australian Mammals*. CSIRO Publishing, Clayton South.
- Jonasson K. A. & Willis C. K. R. (2012) Hibernation energetics of free-ranging little brown bats. *Journal of Experimental Biology* **215**, 2141–9.
- Langwig K. E., Frick W. F., Reynolds R. *et al.* (2015a) Host and pathogen ecology drive the seasonal dynamics of a fungal disease, white-nose syndrome. *Proceedings of the Royal Society B: Biological Sciences* **282**, 20142335.
- Langwig K. E., Voyles J., Wilber M. Q. *et al.* (2015b) Context-dependent conservation responses to emerging wildlife diseases. *Frontiers in Ecology and the Environment* **13**, 195–202.
- Langwig K. E., Frick W. F., Hoyt J. R. *et al.* (2016) Drivers of variation in species impacts for a multi-host fungal disease of bats. *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**, 20150456.
- Langwig K. E., Hoyt J. R., Parise K. L., Frick W. F., Foster J. T. & Kilpatrick A. M. (2017) Resistance in persisting bat

- populations after white-nose syndrome invasion. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **372**, 20160044.
- McKechnie A. E. & Mzilikazi N. (2011) Heterothermy in Afrotropical mammals and birds: a review. *Integr. Comp. Biol.* **51**, 349–63.
- Moore M. S., Field K. A., Behr M. J. *et al.* (2018) Energy conserving thermoregulatory patterns and lower disease severity in a bat resistant to the impacts of white-nose syndrome. *J. Comp. Physiol. B.* **188**, 163–76.
- Perry R. W. (2012) A review of factors affecting cave climates for hibernating bats in temperate North America. *Environ. Rev.* **21**, 28–39.
- R Development Core Team (2009) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Reeder D. M., Frank C. L., Turner G. G. *et al.* (2012) Frequent arousal from hibernation linked to severity of infection and mortality in bats with white-nose syndrome. *PLoS ONE* **7**, e38920.
- RStudio Team (2015) *RStudio: Integrated Development for R*. RStudio, Inc., Boston.
- Stawski C., Turbill C. & Geiser F. (2009) Hibernation by a free-ranging subtropical bat (*Nyctophilus bifax*). *J. Comp. Physiol. B.* **179**, 433–41.
- Thomas D. W., Dorais M. & Bergeron J.-M. (1990) Winter energy budgets and cost of arousals for hibernating little brown bats, *Myotis lucifugus*. *J. Mammal.* **71**, 475–9.
- Turbill C. (2006) Thermoregulatory behavior of tree-roosting chocolate wattled bats (*Chalinolobus morio*) during summer and winter. *J. Mammal.* **87**, 318–23.
- Turbill C. (2008) Winter activity of Australian tree-roosting bats: influence of temperature and climatic patterns. *J. Zool.* **276**, 285–90.
- Turbill C. & Geiser F. (2008) Hibernation by tree-roosting bats. *J. Comp. Physiol. B.* **178**, 597–605.
- Turner J. M., Warnecke L., Wilcox A. *et al.* (2015) Conspecific disturbance contributes to altered hibernation patterns in bats with white-nose syndrome. *Physiol. Behav.* **140**, 71–8.
- U.S. Fish and Wildlife Service (2019) [Cited 24th September 2019.] Available from URL: <https://www.whitenosesyndrome.org/>.
- Verant M. L., Boyles J. G., Waldrep W. Jr, Wibbelt G. & Blehert D. S. (2012) Temperature-dependent growth of *Geomyces destructans*, the fungus that causes bat white-nose syndrome. *PLoS ONE* **7**, e46280.
- Verant M. L., Meteyer C. U., Speakman J. R., Cryan P. M., Lorch J. M. & Blehert D. S. (2014) White-nose syndrome initiates a cascade of physiologic disturbances in the hibernating bat host. *BMC Physiol.* **14**, 10.
- Warnecke L., Turner J. M., Bollinger T. K. *et al.* (2012) Inoculation of bats with European *Geomyces destructans* supports the novel pathogen hypothesis for the origin of white-nose syndrome. *Proc. Natl Acad. Sci.* **109**, 6999–7003.
- Wildlife Health Australia (2017) White-nose Syndrome Response Guidelines Version 1.0.
- Williams S. E., Shoo L. P., Isaac J. L., Hoffmann A. A. & Langham G. (2008) Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol.* **6**, e325.
- Willis C. K. (2015) Conservation physiology and conservation pathogens: white-nose syndrome and integrative biology for host-pathogen systems. *Integr. Comp. Biol.* **55**, 631–41.
- Willis C. K. R. (2017) Trade-offs influencing the physiological ecology of hibernation in temperate-zone bats. *Integr. Comp. Biol.* **57**, 1214–24.