CSIRO PUBLISHING
Wildlife Research, 2019, **46**, 657–668
https://doi.org/10.1071/WR18194

Does the fungus causing white-nose syndrome pose a significant risk to Australian bats?

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Abstract

Context. *Pseudogymnoascus destructans* is the fungus responsible for white-nose syndrome (WNS), which has killed millions of hibernating bats in North America, but also occurs in bats in Europe and China without causing large-scale population effects. This is likely to be due to differences in species susceptibility and behaviour, and environmental factors, such as temperature and humidity. *Pseudogymnoascus destructans* is currently believed to be absent from Australia.

Aims. To ascertain the level of risk that white-nose syndrome poses for Australian bats.

Methods. This risk analysis examines the likelihood that *P. destructans* enters Australia, the likelihood of the fungus coming in contact with native bats on successful entry, and the potential consequences should this occur.

Key results. This risk assessment concluded that it is very likely to almost certain that *P. destructans* will enter Australia, and it is likely that bats will be exposed to the fungus over the next 10 years. Eight cave-dwelling bat species from southern Australia are the ones most likely to be affected.

Conclusions. The risk was assessed as medium for the critically endangered southern bent-winged bat (*Miniopterus orianae bassanii*), because any increase in mortality could affect its long-term survival. The risk to other species was deemed to range from low to very low, owing to their wider distribution, which extends beyond the *P. destructans* risk zone.

Implications. Although Australia's milder climate may preclude the large mortality events seen in North America, the fungus could still significantly affect Australian bat populations, particularly bent-winged bats. Active surveillance is required to confirm Australia's continuing WNS-free status, and to detect the presence of *P. destructans* should it enter the country. Although White-nose Syndrome Response Guidelines have been developed by Wildlife Health Australia to assist response agencies in the event of an incursion of WNS into bats in Australia, these guidelines would be strengthened by further research to characterise Australian cave temperatures and hibernating bat biology, such as length of torpor bouts and movement over winter. Risk-mitigation strategies should focus on education programs that target cavers, show-cave managers and tourists, particularly those who have visited regions where WNS is known to occur.

Additional keywords: *Miniopterus orianae bassanii*, *Pseudogymnoascus destructans*, risk assessment, southern bent-winged bat.

Received 20 June 2018, accepted 27 July 2019, published online 4 December 2019

Introduction

Historically infectious diseases have been considered of only minimal importance in the endangerment or extinction of species (Smith *et al.* 2006). However, anthropogenic changes that increase contact among species and result in the introduction of novel pathogens to susceptible hosts in new regions have resulted in an increase in disease outbreaks and mortality (Deem *et al.* 2001). When this is linked to alterations in land use, a continuing increase in human population growth and global travel, it is not surprising that the number of new and emerging infectious diseases involving animal hosts continues to increase (Woolhouse and Gowtage-Sequeria 2005), along with their impact on already vulnerable populations. Examples of these include the high mortality rates caused by chytridiomycosis in amphibians and white-nose syndrome (WNS) in bats (Eskew and Todd 2013).

White-nose syndrome is caused by the fungus *Pseudogymnoascus destructans*, which is psychrophilic, thriving at temperatures below 15°C and ceasing growth above 20°C (Verant *et al.* 2012). However, it is quite resilient, surviving in cave sediment for up to 2 years in the absence of bats (Lorch *et al.* 2013), for over 5 years in conditions of low (30–40%) humidity (Hoyt *et al.* 2015), and up to 15 min at temperatures as high as 50°C (Shelley *et al.* 2013). Since its appearance in North America in 2006, it has killed millions of cave-dwelling, hibernating bats and has spread through much of the USA and Canada (Lorch *et al.* 2016). Subsequent surveys have identified the fungus on bats in both Europe and China (Puechmaille *et al.* 2011*c*; Hoyt *et al.* 2016*b*); however, although the fungus causes disease in bats in these areas, it is not associated with the high mortality rates seen in North America (Puechmaille *et al.* 2011*c*). Reasons for this have not been resolved, but are thought to involve a combination of factors, including species susceptibility, behaviour and environmental factors such as temperature and humidity (Hoyt *et al.* 2016*a*; Zukal *et al.* 2016). Death of infected bats appears to be the result of a cascade of physiological changes associated with the damage sustained to their wings during hibernation; this results in increased evaporative water loss and dehydration, causing the bats to wake more frequently during hibernation, thus consuming all of their energy reserves over the winter period. Because death is ultimately the result of fat depletion, WNS-related mortalities do not begin until ~120 days after bats enter hibernation and peak at ~180 days (Cryan *et al.* 2010, 2013; Lorch *et al.* 2011; Warnecke *et al.* 2013; Verant *et al.* 2014).

On the basis of preliminary screening of 325 bent-winged bats (*Miniopterus orianae bassanii* and *M. o. oceanensis*) for WNS (Holz *et al.* 2018) and a lack of reports of bats displaying WNS symptoms, *P. destructans* is believed to be absent from Australia. However, the suddenness and scale of the WNS disaster in North America has raised concerns about the potential for a similar epidemic to occur in Australian bats. This qualitative risk assessment, which summarises and updates the findings presented in a report commissioned by Wildlife Health Australia (Holz *et al.* 2016), examines the likelihood of the fungus entering Australia, the subsequent exposure of Australian bats, and the potential consequences, should this occur. The results of this assessment will inform the extent of future *P. destructans* surveillance in Australia, and assist in identifying the most important research and conservation priorities, as was done in Europe (Puechmaille *et al.* 2011*a*). It will also be used in the development of biosecurity protocols to prevent *P. destructans* entering the country, as well as WNS response guidelines to be implemented should the fungus gain access to Australian bats.

Table 1. Categories used to assess likelihood of entry and exposure of *Pseudogymnoascus destructans* into Australia and Australian bat populations (Murray *et al.* 2010; Snary *et al.* 2012)

Code	Category	Likelihood of occurrence
I	Insignificant	So rare that it does not merit consideration
R	Rare	Rare, but cannot be excluded
U	Unlikely	Rare, but does occur
P	Possible	May be expected to occur
L	Likely	To be reasonably expected to occur
AC	Very likely to almost certain	Occurrence is very likely to almost certainly

Materials and methods

We convened a workshop to bring together subject-matter experts, including two wildlife health researchers, three veterinary epidemiologists, two bat ecologists and two ecological modellers, to conduct an expert elicitation on the risk WNS might pose for Australian bats. Consensus of opinion on each exposure and release pathway was achieved using a Delphi Conference-like approach (Elliott *et al.* 2005). Specifically, the workshop facilitator (PH) posed a question to the group. Responses were recorded and a summary presented back to the group for comment and review. Participants were then asked to revise their responses in light of the discussion. This process continued until there was consistency of opinion across all workshop participants.

This risk assessment follows the World Organisation for Animal Health (OIE) framework of entry, exposure and consequence assessment (Murray *et al.* 2010; Jakob-Hoff *et al.* 2014). It is divided into the following three key areas:

1. What is the likelihood that *P. destructans* will enter Australia (*entry* assessment)?
2. What is the likelihood that *P. destructans* will enter a cave populated by bats after it has entered the country (*exposure* assessment)?
3. What is the likelihood of a bat species becoming affected by *P. destructans*, following exposure to the fungus (consequence assessment)?

The consequence assessment estimates the magnitude of the potential biological and environmental consequences associated with the entry, establishment and spread of *P. destructans*. Risk estimation synthesises the results arising from the entry, exposure and consequence assessments.

For the present analysis, the categories of Entry, Exposure and Consequence are defined as the probability of an event occurring at least once during a 10-year period. A time-frame longer than 10 years was considered to be an unrealistic period in which to frame management and policy decisions, and a time-frame shorter than 10 years provides insufficient opportunity for many of the less likely events to occur.

Once a probability of entry and exposure for each possible pathway had been assessed, we used the matrices in Tables 1 and 2 to estimate the likelihood of occurrence, which is the minimum of the two multiplied probabilities (Snary *et al.* 2012). Because there is no formal category between *likely* and *almost certain*, we modified the highest category to represent a range of *very likely to almost certain*.

Table 2. Table used to determine the likelihood of occurrence of white-nose syndrome (WNS) on the basis of individual probabilities of entry and exposure to *Pseudogymnoascus destructans* (Moutou *et al.* 2001; Gale *et al.* 2010; Snary *et al.* 2012)

I, insignificant; R, rare; U, unlikely; P, possible; L, likely; VL/AC, very likely to almost certain

		Entry					
		Insignificant	Rare	Unlikely	Possible	Likely	Very likely to almost certain
Exposure	Insignificant	I	I	I	I	I	I
	Rare	I	R	R	R	R	R
	Unlikely	I	R	U	U	U	U
	Possible	I	R	U	P	P	P
	Likely	I	R	U	P	L	L
	Very likely to almost certain	I	R	U	P	L	VL/AC

Table 3. Likely modes of entry of *Pseudogymnoascus destructans* into Australia, with their associated risks of entry, exposure and overall likelihood of occurrence

I, insignificant; R, rare; U, unlikely; P, possible; L, likely; VL/AC, very likely to almost certain; WNS, white-nose syndrome

Mode of entry				Entry	Exposure	Likelihood
Airborne				I	I	I
Bat-borne	Live	Accidental		R	I	I
		Illegal trade		R	I	I
		Legal trade		I	I	I
		Natural Migration		I	I	I
	Tissues	Illegal		I	I	I
		Legal		I	I	I
Paratenic host	Migratory birds			I	I	I
	Imported	Wild animal species		I	I	I
		Domestic animal species		R	I	I
Human-mediated	Tourist/traveller	Cave visitor	WNS area origin	L	R	R
		Cave visitor	Non-WNS area origin	U	R	R
		Non-cave visitor		I	I	I
	Cave researcher	Bat researcher		L	U	U
		Other cave researchers		L	U	U
	Cavers	Local		VL/AC	L	L
	Cave management	Private	Owner	I	P	I
		Private	Guide	L	P	P
		Public	Park officers	L	P	P
		Public	Infrastructure services	I	P	I
	Mining activity			R	I	I
	Mine enthusiasts	Endemic area origin		L	R	R
		Non-endemic area origin		U	R	R
	Wildlife health professional/carer			P	R	R
	Bioterrorism			I	I	I

Results and discussion

Entry assessment

The wide range of potential routes of entry and their likelihood of occurring are outlined below and summarised in Table 3.

1. *Airborne: insignificant*. There is no evidence that the fungus is transmitted through the air even for short distances, let alone the distances needed to reach Australia. An experimental study found that unaffected bats housed 1.3 cm from infected bats did not become infected (Lorch *et al.* 2011).
2. *Bat-borne: rare–insignificant*. Accidental transport refers to inadvertent import of a live bat into the country, such as, for example, in a shipping container. Since 1999, 30 live bats have been intercepted at Australian border points as stowaways (P. Cassey, pers. obs.). Figures for the attempted illegal importation of bats and bat tissues are not available, but this is unlikely to be common, and so has been assessed the same as Accidental. Legally imported live bats in zoos have all come from Pacific countries, which are WNS free (Hibbard and Wilkins 2010). Only one study has provided evidence of a bat species migrating to, or from, Australia (the black flying-fox, *Pteropus alecto*, a tropical, tree-dwelling fruit bat; Breed *et al.* 2010). Bat tissues can be legally imported if fixed in alcohol. The fungus is destroyed by exposure to 70% ethanol for 24 h or absolute ethanol for 30 min (Puechmaille *et al.* 2011*b*). Therefore, imported tissues are unlikely to contain viable fungus.

3. *Paratenic host: rare (domestic animals)–insignificant (wildlife)*. This category refers to an animal species, other than a bat, acting as a mechanical vector for the fungus. There are no records of *P. destructans* being found on any groups of vertebrates other than bats. However, there is a knowledge gap here because no active surveillance of other species has been conducted. In this category, we included migratory birds as potential paratenic hosts to account for movement of birds within the eastern Asian–Australasian flyway (Bamford *et al.* 2008), which includes China, a country where *P. destructans* is present. Nevertheless, the probability of migrating shorebirds coming into contact with *P. destructans* in caves was assessed as being insignificant. We included imported domestic and wild animals, the former being deemed to be more common and, thus, having a higher probability, although still rare.
4. *Human-mediated.* This section has been divided into several subgroups to better explain the associated risks, because it is currently presumed that the fungus entered North America through some means of human travel (Frick *et al.* 2016).

   (a) *Tourist or traveller: insignificant–likely*. The risk of a tourist or traveller who has not visited any caves (non-cave visitor) introducing *P. destructans* is insignificant. Visitors to Australian show caves number between 500 000 and 1 000 000 annually (N. White, Australian Speleological Federation, pers. comm.). For a tourist or traveller who has visited caves (cave visitor) outside the known range of WNS, the chances of transferring the fungus are unlikely, but it could still occur, because the actual geographic distribution of *P. destructans* may be greater than is currently known. However, if the tourist or traveller has visited caves in an endemic area, it is assessed to be likely that the fungus will be transferred because there is a greater chance of it being present on the person's footwear or clothing, and tourist awareness of WNS is likely to be low.

   (b) *Cave researcher: likely*. There are currently no data to show the level of awareness about WNS in cave-bat researchers in Australia. There is a high probability of cave-bat researchers coming into contact with *P. destructans* if working in infected areas, because they frequently enter caves and move among caves. A recent study found *P. destructans* on clothing, back packs and harp traps of researchers that had visited eight different hibernacula in the eastern USA (Ballmann *et al.* 2017). Although the majority would be likely to observe the decontamination protocols, it would take only one who does not, so as to facilitate entry of the fungus from an infected area into Australia. Other cave researchers (such as archaeologists, paleontologists, or geologists) are also deemed more likely because they may be unaware of the situation of WNS overseas and the possible risks to Australian species.

   (c) *Caver: very likely to almost certain*. Although there are currently no data to show the level of knowledge about WNS in cavers visiting Australia, educational material sent to members of caving organisations, such as those circulated to registrants of the 17th International Congress of Speleology (White 2017), should help improve awareness of the risk of WNS to bats. Without educational and awareness campaigns to promote decontamination or prohibition against the use of the same equipment across regions, cavers entering Australia that have visited caves in *P. destructans*-endemic regions are very likely to introduce *P. destructans* to cave habitats in Australia. Cavers frequently enter and move among caves and are deemed to be less likely to have a scientific background than are cave researchers, or be aware of the biosecurity issues surrounding their movement and equipment. The ropes and harnesses used during caving are also difficult to disinfect. Although exact figures are unavailable, it is estimated that fewer than 100 international cavers would enter Australia annually (N. White, pers. comm.). The extent to which cavers are bringing in caving equipment that may contain *P. destructans*, is unknown. However, if, conservatively, one caver enters Australia each year from a *P. destructans* positive area with contaminated equipment, then 10 cavers could enter over 10 years, making it very likely to almost certain, that *P. destructans* would be brought into Australia over this time period.

   (d) *Cave management: likely*. We assessed the likelihood of cave-management staff inadvertently introducing *P. destructans* to Australia to be the same as that for cave researchers. Cave managers and guides visit caves as part of professional development, exchange of management ideas or for personal interest.

   (e) *Mining-related activities: rare*. The probability of mining equipment brought into Australia being contaminated with *P. destructans* is considered rare.

   (f) *Mine enthusiast (e.g. prospector): likely*, if coming from an endemic area due to entry into mines infected with *P. destructans*, and, *unlikely*, if coming from a non-endemic area. These people are deemed unlikely to be aware of the situation of WNS overseas or in Australia, nor of related decontamination protocols.

   (g) *Wildlife health professional/carer: possible*, because these people may be caring for bats affected with WNS. However, because of their profession, they are also deemed to be more likely to be highly aware of biosecurity issues associated with WNS.

   (h) *Bioterrorism: insignificant*. *P. destructans* is not a human or agricultural animal pathogen.

Exposure assessment

Bats are believed to become exposed to *P. destructans* through direct contact with infected bats or contaminated substrate (Hoyt *et al.* 2018). Given that the introduction to North American populations is thought to have been a result of human activity in caves (Frick *et al.* 2016), we assume that any introduction of the fungus into bat caves or mines inhabited by bats would be sufficient to result in exposure of resident bats.

The exposure assessments are presented in Table 3, with explanations provided below.

Table 4. Definition of categories used to assess the environmental consequences of exposure to *Pseudogymnoascus destructans* for individual bat species and for all Australian bats
Consequences are based on actual occurrences, independent of detection

Category	Bat species	All Australian bats
Insignificant	Infection with no apparent health consequences at the individual animal level	Infection with no apparent health consequences
Very minor	Infection with individual morbidities and/or mortalities, but no measurable decline in population numbers	Infection with individual morbidities and/or mortalities, but no decline in population numbers
Minor	Small population decline (<30%) in one cave	Small population decline (<30%) in one non-threatened species in one cave
Moderate	Small population decline in multiple caves, OR, moderate population decline (30–50%) in one cave	Moderate population declines (30–50%) in more than one non-threatened species in one cave OR small population declines (<30%) in one threatened species
Major	Large-scale mortality, resulting in major population decline (50–80%)	Major population decline (50–80%) of one or more non-threatened species AND/OR moderate population decline (30–50%) of one threatened species
Catastrophic	Large-scale mortality, resulting in catastrophic population decline of >80% (including extinction)	Catastrophic population declines of >80%, including extinctions, of one or more species, with widespread ecological consequences

1. *Airborne, bat-borne, paratenic host: insignificant*, for the reasons given above.
2. *Human-mediated*
   (a) *Tourist or traveller: insignificant* for the non-cave visitor; *rare* for visitors who have visited caves overseas because they would need to enter Australian caves wearing the same contaminated footwear and clothing, which would need to contain viable fungus, and for casual cave visitors, there may be long periods of time between their visits to caves.
   (b) *Cave researcher: unlikely*. If a researcher was to inadvertently facilitate entry of the fungus into Australia, they would then need to enter a bat cave without having appropriately decontaminated their equipment or clothing.
   (c) *Caver: likely*. Cavers from infected areas are deemed likely to transfer the fungus between caves, assuming that at least some will not follow guidelines on gear decontamination, and are considered less likely to be aware of the possible consequences than researchers.
   (d) *Cave management: possible*. Parks officers and guides regularly enter caves as part of their work, and could do this with their contaminated clothing and/or footwear and or equipment; however, their knowledge of WNS could be variable. If private land owners or infrastructure service providers did inadvertently bring the fungus into the country, they would be a possible risk of exposure if the caves they frequent include bats.
   (e) *Mining/mine enthusiasts: insignificant–rare*. There are few operational mines that contain bats; thus, it is unlikely that contaminated mining equipment would result in the exposure of bats. The majority of prospecting (e.g. for gold) occurs on the surface rather than within disused mines, so there is only limited likelihood of exposure of bats in mines.
   (f) *Wildlife health professional/carer: rare*. While they may come in contact with diseased bats, they will have some awareness of the disease, are likely to adopt appropriate biosecurity measures when handling bats, and are not necessarily likely to enter Australian caves.

Likelihood of occurrence

The overall likelihood of *P. destructans* being introduced and affecting bats in Australia must be based on the worst-case situation, i.e. the highest rated groups, namely, cavers and those visiting caves professionally. Although awareness of WNS appears to be increasing, there is no evidence to suggest that future fungal introductions to naïve bat populations are less likely to occur, as demonstrated by the appearance of the disease in Washington State in 2016, 2000 km from the nearest previously known WNS site (Lorch *et al.* 2016). This suggests either direct human transfer or the unintentional movement by a human of an infected bat, despite a now heightened level of awareness of WNS in the USA. It is conceivable that the fungus already entered Australia in the past, but died before being carried into a suitable cave containing bats. On the basis of these factors, our assessment suggests that entry of *P. destructans* into Australia over the next 10 years is very likely to almost certain, and subsequent exposure of bats is likely, resulting in an overall likelihood of occurrence of likely (Table 2).

Consequence assessment

The consequences of introducing *P. destructans* to Australia can be divided into two major categories, namely, environmental and economic. The economic consequences are flow-on effects from the environmental consequences, relating to the resulting loss of ecosystem services provided by insect-eating bats (Kunz *et al.* 2011). The present document primarily focuses on the environmental consequences.

The rating of environmental consequences is significantly guided by the consideration of factors that determine the impact of exposure to *P. destructans* on bat populations. Categories used to assess the environmental consequences of exposure of Australian bats to *P. destructans* are defined in Table 4.

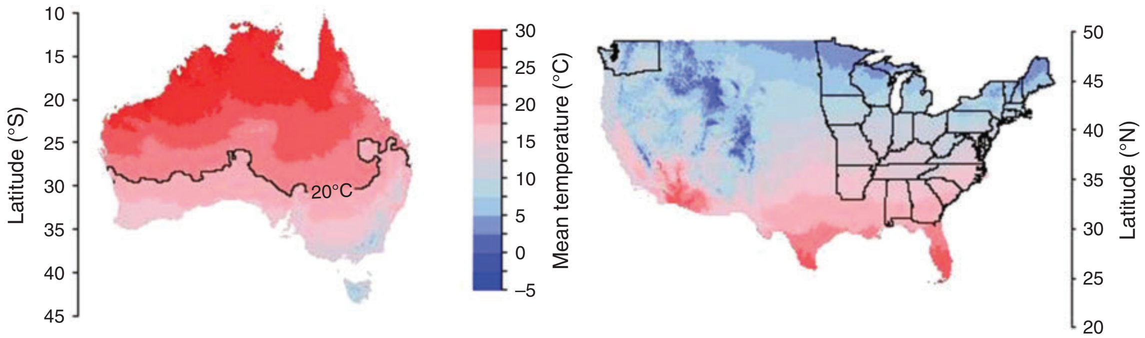

Fig. 1. Temperature maps of Australia and the USA, highlighting US states where white-nose syndrome (WNS) has been recorded (black outline) and northern limit of possible *Pseudogymnoascus destructans* growth in Australia, as shown by 20°C isotherm.

Bat roosting location: cave or mine versus tree

All major population declines and mortalities caused by *P. destructans* have occurred in bats that hibernate in caves or mines (Langwig *et al.* 2012; Frick *et al.* 2015). Although the fungus has been found on some tree-dwelling bats in the USA, it has not been associated with any clinical signs or mortality (Bernard *et al.* 2015). One study, in southern Australia, found that tree-hole roosts used by bats were likely to be too warm (temperature ranged from 19°C to 25°C throughout the day) to be conducive to fungal growth (Campbell *et al.* 2010). Australian tree-roosting species also appear to be quite active during winter. One study found that tree-roosting bats were active on 89% of winter nights and actively foraging when the ambient temperature exceeded 8°C (Turbill 2008). Therefore, for tree hole-roosting bats, the consequence was deemed to be very minor, and the risk as very low.

Australian climate

(1) *Cave temperatures*. *P. destructans* ceases growth above 20°C (Verant *et al.* 2012) and will not survive for prolonged periods above this temperature. An *in vitro* study has demonstrated that *P. destructans* samples stored at 23°C for 3 weeks would not germinate (Forsythe *et al.* 2018). A survey of 204 caves across northern Australia showed that cave temperatures vary between 23.5°C and 33°C (Churchill 1991). Therefore, the consequence of the fungus being introduced into one of these bat-inhabited caves, which maintain a year-round internal temperature above 20°C, was considered to be very minor.

Whereas greatest *P. destructans* growth occurs at 13°C (Verant *et al.* 2012), temperatures in the most severely affected caves in North America range from 2°C to 15°C (Blehert *et al.* 2009). Cave temperatures in southern Australia range from 8°C to 25°C (Holz *et al.* 2016) which, although warmer than the worst-affected North American caves, are still low enough to permit fungal growth and disease.

Figure 1 compares the US climate where *P. destructans* has been found with the Australian climatic zone where *P. destructans* may be capable of establishing itself. The distributions of Australian cave bats that fall within this zone are shown in Fig. 2*a*–*f*. There are eight taxa, : southern bent-winged bat (*Miniopterus orianae bassanii*), eastern bent-winged bat (*Miniopterus orianae oceanensis*), little bent-winged bat (*Miniopterus australis*), eastern horseshoe bat (*Rhinolophus megaphyllus*), large-footed myotis (*Myotis macropus*), chocolate wattled bat (*Chalinolobus morio*), large-eared pied bat (*Chalinolobus dwyeri*) and Troughton's cave bat (*Vespadelus troughtoni*). It is apparent from these figures that Australia does not have cave bats in latitudes equivalent to the northern sections of the USA where the impact of WNS has been most severe, and that Australian conditions are likely to be more similar to the southern extent of WNS in the USA. Although WNS-related mortalities have been detected in the south-eastern USA, these have occurred in regions that experience subfreezing temperatures for extended periods during the winter months (Bernard and McCracken 2017), a scenario which does not occur in Australia. Therefore, on the basis of temperature alone, the large mortalities experienced by North American bats would not be expected to occur in Australia.

(2) *Evaporative water loss and energy depletion*. WNS is believed to kill bats through a combination of skin damage leading to increased evaporative water loss and dehydration, and increased frequency of arousal from hibernation leading to depletion of fat stores and emaciation (Verant *et al.* 2014). Bats with high evaporative water loss during hibernation, such as little brown bats (*Myotis lucifugus*) (Willis *et al.* 2011), are at increased risk because the damage caused to wing membranes by WNS exacerbates this water loss (Ehlman *et al.* 2013). When compared with two Australian bat species, at an ambient temperature of 25°C, evaporative water loss for little brown bats is three times that for Gould's wattled bats (*Chalinolobus gouldii*) and twice that for common bent-winged bats (*Miniopterus schreibersii*; Hosken and Withers 1997; Maloney *et al.* 1999; Baudinette *et al.* 2000), which should render these Australian bats less susceptible to dehydration. It has been speculated that severe mortalities occur in the regions of North America that remain below freezing throughout winter, in part because the increased evaporative water loss caused by WNS exceeds the ability of bats to obtain sufficient water from condensation inside hibernacula (Cryan *et al.* 2010; Willis *et al.* 2011). This situation is compounded by the lack of unfrozen water outside the hibernacula (Flory *et al.* 2012). Australian bats do not experience extended periods where ambient temperatures are below freezing, so there is likely to be sufficient free water available to replenish water loss.

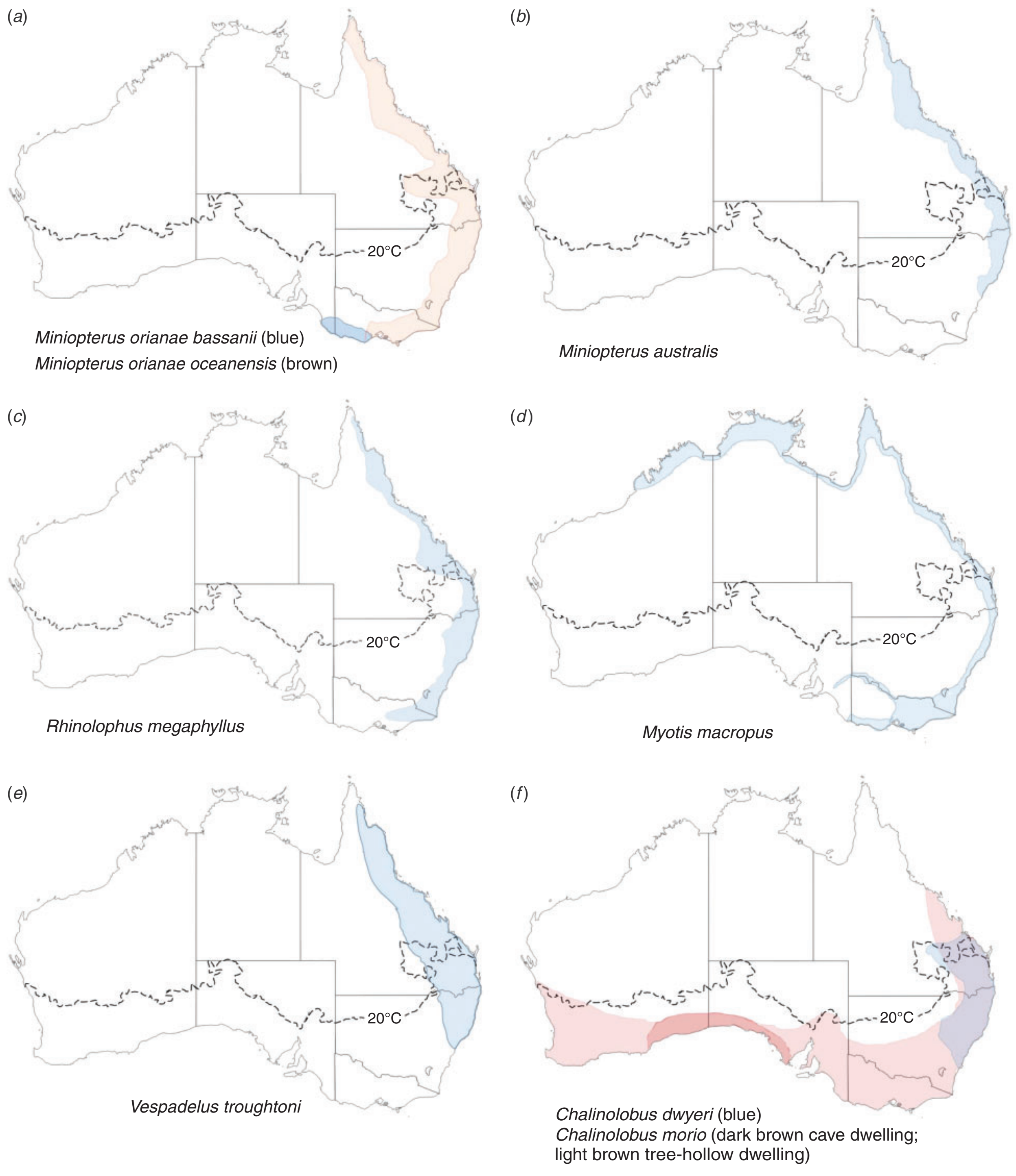

Fig. 2. (*a–f*) Distribution of Australian cave-dwelling bats that live within the potential habitable zone for *Pseudogymnoascus destructans* (Van Dyck *et al.* 2013). No species of cave-dwelling bat occurs in Tasmania (not shown on map).

Arousal from hibernation is extremely energy expensive. One arousal bout in the little brown bat consumes as much fat energy as 67 days spent in torpor (Thomas *et al.* 1990). Due to the subfreezing winter weather conditions in North America, there are no flying insects that bats could consume to replenish their energy stores. In the south-eastern USA, bats are able to feed on insects throughout winter, activity correlating with temperature (Bernard and McCracken 2017). Australian winters are mild, allowing bats to be more active and potentially offset some of the fat loss that occurs as a result of arousal from hibernation. However, insufficient prey availability over winter could still be a constraint because temperatures regularly drop below 10°C, which is the approximate threshold for flying-insect activity (Hoyt *et al.* 2016*a*). Bats that are aroused from torpor multiple times over winter because of human disturbance can use up valuable fat reserves that then may be depleted before spring when insects become more available (Speakman and Thomas 2003). Therefore, the consequences of *P. destructans* infection rousing bats repeatedly from torpor could be major.

Phylogenetic susceptibility

It has been suggested that there may be a phylogenetic component to bat susceptibility, with affected bat species coming from related families (Zukal *et al.* 2014). In a European study, common bent-winged bats and Mediterranean horseshoe bats (*Rhinolophus euryale*) carried a lower fungal load and suffered fewer WNS lesions than did other species (Zukal *et al.* 2014). These results were similar to those of a study that found a lower prevalence of *P. destructans* in Chinese bats (51%) than in North American bats (95%) living under similar environmental conditions (Hoyt *et al.* 2016*a*). Fungal load was also lower for the Chinese bats, and only 28% of Chinese bats had skin lesions, compared with 75% of North American bats. In both studies, the authors speculated that different bat species had variable levels of resistance to *P. destructans* infection (Hoyt *et al.* 2016*a*; Zukal *et al.* 2016).

Genera that have tested positive for WNS and are found in Australia are *Myotis*, *Rhinolophus* and *Miniopterus*. Therefore, they must be considered potentially susceptible to infection with *P. destructans* and the development of WNS. *Chalinolobus* and *Vespadelus* are restricted to the southern hemisphere, so their susceptibility to infection is unknown. However, because they represent a naïve population with respect to *P. destructans*, they too should be considered potentially susceptible to infection.

Hibernation

White-nose syndrome lesions and mortalities have occurred only during periods of hibernation (Langwig *et al.* 2015). Therefore, for bats that do not hibernate, the consequence of exposure and risk is insignificant. However, all insectivorous bats in southern Australia enter periods of torpor or hibernation during winter for several weeks at a time (Turbill and Geiser 2008). Recent research on southern bent-winged bats indicated that they may be more active during winter than originally thought (van Harten *et al.* 2018). White-nose syndrome is a slowly progressive disease that kills bats by causing them to rouse from hibernation more frequently, thus accelerating the depletion of their fat reserves. The impact that WNS may have on bats that hibernate for short periods of time or already have a high level of winter activity is not known, and there are no comparable data available from other species or populations exposed to WNS. Therefore, a conservative approach should be adopted. The likely consequence of exposure to *P. destructans*, therefore, remains major.

Disease transmission and dispersal

(1) *Clustering and colony size*. The size of bat colonies and their propensity to aggregate in groups (cluster) can affect the outcome for WNS-affected bat colonies. In the USA, the impact of disease on solitary species, such as northern long-eared bats (*Myotis septentrionalis*) and tri-coloured bats (*Perimyotis subflavus*), was lower in smaller populations, whereas in socially gregarious species, such as little brown bats and Indiana bats (*Myotis sodalis*), declines were equally severe regardless of population size (Langwig *et al.* 2012). The Langwig *et al.* (2012) study found that, after the introduction of WNS, more little brown bats began to roost individually, which resulted in a decrease in WNS-related mortality.

In Australia, large-footed myotis colonies usually contain 10–15 individuals, but may occasionally hold several hundred. Eastern horseshoe bat colonies usually contain 5–50 bats, except for maternity colonies, which can contain up to 5000 bats. However, horseshoe bats typically hang individually rather than clustering tightly together. Chocolate wattled bats cluster in groups from 10 to 1000. Bent-winged bats often occupy maternity sites in the tens of thousands, but, outside the breeding season, it is more usual for individuals to roost in smaller groups, or even singly, although clusters of a thousand or more are not uncommon (Van Dyck *et al.* 2013).

It could be expected that smaller colonies of Australian bat species that hang individually, such as horseshoe bats, would be less affected by WNS, whereas the disease impact on species that cluster together, such as bent-winged bats, would be similar regardless of population size. However, this density-dependent pathogen transmission is confounded by the ability of the fungus to survive for long periods in the environment. Therefore, small bat populations with low densities and bat species that roost individually, such as northern long-eared bats, can still be severely affected and potentially driven to extinction (Langwig *et al.* 2012; Frick *et al.* 2017). Hoyt *et al.* (2018) demonstrated that northern long-eared bats were connected to only 7.3% of other bats by direct physical contact, but to 24.7% of other bats by indirect contact such as through a contaminated environment. This helps explain the large mortalities witnessed in this species, despite their solitary behaviour.

(2) *Bat movement*. On the basis of the temporal and geographical distribution of WNS in the USA, bats are capable of spreading the fungus from site to site and to each other. Therefore, bats using multiple caves or sharing caves with other species will facilitate the spread of the fungus. Southern bent-winged bats roost with eastern bent-winged bats and large-footed myotis in some caves, and eastern bent-winged bats may roost with little bent-winged bats, eastern horseshoe bats and large-footed myotis. All Australian bats move among multiple caves, including over winter. For example, southern bent-winged bats have been recorded travelling up to 70 km between caves in a night (van Harten *et al.* 2018), which could potentially enhance fungal spread. Therefore, the effect of bat movement on the likely consequences of a WNS incursion is assessed to be major.

In summary, on the basis of the available information, for large-scale mortalities to occur, several criteria need to be satisfied:

1. bats need to roost and hibernate in caves or mines that maintain temperatures below 20°C during an extended hibernation season, because *P. destructans* does not grow and can survive only for a limited time above this temperature (Forsythe *et al.* 2018);

Table 5. Consequence score for each of the cave-dwelling bat species from southern Australia, based on the parameters affecting the spread and pathogenesis of white-nose syndrome (WNS), and the species' ecology and biology

None of the bats occur in regions where the temperatures are regularly below freezing

Species	Consequence	Comment
Southern bent-winged bat (*Miniopterus orianae bassanii*)	Moderate	Critically endangered; large maternity colonies where individuals cluster tightly together, but lower hibernation density, although some over-wintering colonies can consist of thousands of bats that may represent a significant proportion of the total population, and any impact could be a tipping point for the conservation of this subspecies. The entire population occurs within the risk zone (<20°C mean annual temperature).
Eastern bent-winged bat (*Miniopterus orianae oceanensis*)	Minor	Large maternity colonies, with smaller colonies in winter. Individuals cluster tightly together throughout the year. About 50% of the entire distribution occurs within the risk zone.
Little bent-winged bat(*Miniopterus australis*)	Minor	Large colonies especially north of the risk zone. About 70% of the Australian distribution and 90% of the world population occurs outside the risk zone.
Eastern horseshoe bat (*Rhinolophus megaphyllus*)	Minor	Often in small colonies, although thousands can roost together in maternity caves. Individuals roost separately rather than in tight clusters. Share the same caves as eastern and little bent-winged bats. About 50% of the Australian distribution occurs within the risk zone.
Chocolate wattled bat (*Chalinolobus morio*)	Very minor	Medium colony size. A very small proportion of the entire population is cave-dwelling, but within the area where this species does roost in caves, the majority of the population uses caves. Outside this area, most of the distribution lies within the risk zone.
Large-eared pied bat (*Chalinolobus dwyeri*)	Very minor	Roosts in small, shallow sandstone caves and mines where temperatures are likely to vary seasonally. Colonies are very small in size and geographically disparate, and, hence, likely to be at lower risk. Over 75% of the entire distribution occurs in the risk zone.
Large-footed myotis (*Myotis macropus*)	Very minor	Small colony size, with individuals roosting together in clusters. Shares caves with bent-winged bats. Over 60% of the entire distribution occurs outside the risk zone.
Troughton's cave bat (*Vespadelus troughtoni*)	Very minor	Roosts in small shallow sandstone caves and mines where temperatures are likely to vary seasonally. Colonies are very small in size and geographically disparate, and, hence, likely to be at lower risk. About 50% of the entire distribution occurs in the risk zone.

Table 6. Table used to estimate the risk as a result of likelihood of occurrence (first column) and consequence (first header row)

Table based on the Biosecurity Import Risk Analysis Guidelines 2016: managing biosecurity risks for imports into Australia (DAWR 2016)

Category	Insignificant	Very minor	Minor	Moderate	Major	Catastrophic
Insignificant	Insignificant	Insignificant	Insignificant	Insignificant	Insignificant	Very low
Rare	Insignificant	Insignificant	Insignificant	Insignificant	Very low	Low
Unlikely	Insignificant	Insignificant	Insignificant	Very low	Low	Medium
Possible	Insignificant	Insignificant	Very low	Low	Medium	High
Likely	Insignificant	Very low	Low	Medium	High	Very high
Very likely to almost certain	Insignificant	Very low	Low	Medium	High	Very high

2. bats need to be susceptible to infection with *P. destructans* and the development of WNS;
3. bats need to live in regions with extended cold seasons, with ambient weather and temperatures that require repeated and extended bouts of torpor, with limited foraging activity, for 2–6 months.

Rating of environmental consequences

To describe the likely consequences of an exposure of Australian bats to *P. destructans*, the definitions shown in Table 4 have been applied. On the basis of the criteria discussed, we assigned a separate consequence score for each of the cave-dwelling bat species from southern Australia (Table 5).

The risk of WNS for Australian bats was then determined on the basis of the likelihood and consequence scores. The consequences of exposure to *P. destructans* were deemed to be moderate for the southern bent-winged bat, which is listed as *Critically endangered* (DSE 2013) and exists entirely within the critical temperature band for WNS. Consequences for eastern bent-winged bats, little bent-winged bats and eastern horseshoe bats were rated as minor, and consequences for chocolate wattled bats, large-eared pied bats, large-footed myotis and Troughton's cave bats were classed as very minor (Table 5).

The likelihood of occurrence that Australian bats will be exposed to *P. destructans* over the next 10 years has been determined to be likely. On the basis of a consequence assessment of moderate for southern bent-winged bats, the risk of WNS is assessed as medium. For the other species, the risk is deemed to be low for eastern bent-winged bats, little bent-winged bats and eastern horseshoe bats and very low for chocolate wattled bats, large-eared pied bats, large-footed myotis and Troughton's cave bats, using the matrix outlined in Table 6.

Conclusions

- The overall likelihood of *P. destructans entering* Australia via human transmission (e.g. tourist, caver, researcher), was assessed as being very likely to almost certain to occur at least once within the next 10 years.
- The overall likelihood of entry leading to *exposure* was assessed as being likely to occur at least once within a 10-year period, leading to an *overall likelihood assessment of entry and exposure of* likely.
- Our assessment of the consequences of an incursion of *P. destructans* into Australia relies on information about many factors involved with the epidemiology and pathogenesis of WNS in other countries, some of which are not yet sufficiently known. However, on the basis of our knowledge and expertise, we predict that there is a risk to southern Australian cave-dwelling bat populations from WNS, although the large-scale mortalities seen in North America are unlikely.
- Lower mortality rates associated with WNS may be significant for the survival of the southern bent-winged bat which, as a result of other threatening factors, is already listed as *Critically endangered* and whose entire population lies within the low-temperature zone. For other bat species whose distributions extend well outside this zone, higher mortality rates due to WNS might affect only their southern populations.
- The confidence in the present risk assessment would be significantly improved by a greater understanding of whether *P. destructans* is currently present in Australia. The conclusions of the risk assessment may be substantially changed if this pathogen is detected. An ongoing surveillance program could determine whether the agent is present but not causing disease (and, therefore, of no concern), or detect it as soon as possible after introduction. Assuming that *P. destructans* is currently absent from Australia, on the basis of an absence of the fungus in a pilot prevalence survey (Holz *et al.* 2018), and the absence of clinical signs and detected population impacts, White-nose Syndrome Response Guidelines have been developed by Wildlife Health Australia in consultation with stakeholders (Wildlife Health Australia 2017), so as to assist response agencies in the event of an incursion of WNS into bats in Australia. These guidelines would be strengthened by further research into cave temperatures and hibernating-bat biology, as well as education programs targeting cavers, show-cave managers and tourists.

Conflicts of interest

Thomas Prowse is an Associate Editor for *Wildlife Research*.

Acknowledgements

The authors acknowledge Wildlife Health Australia and the Australian Government Department of Agriculture and Water Resources for contributing funding for this project. The authors also acknowledge the helpful reviewer comments, which have significantly improved the manuscript.

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