Using Stochastic Modeling to Predict the Effect of Culling and Colony Dispersal of Bats on Zoonotic Viral Epidemics

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Abstract

Frequent outbreaks of emerging infectious diseases originating from wild animals have highlighted the necessity of managing wildlife populations to prevent zoonotic spillover, and the appropriate development of management protocols required attention on gaining a better understanding of viral dynamics in wild animal populations. In east Australia, there have been outbreaks of Hendra virus (HeV) infection in horses and humans following spillover from the virus's reservoir hosts, flying foxes (family Pteropodidae), and bat culling and colony dispersal have been proposed as appropriate management strategies. A key factor relating to flying fox population structure that influences HeV dynamics is that these bats form metapopulations, and consequently, to assess this factor, we designed an epidemic dynamics model of HeV transmission, focusing on bat metapopulation dynamics. Specifically, using flying fox movement data, we stochastically simulated models for a hypothetical metapopulation of flying foxes to examine the impact of metapopulation-related parameters, and subsequently simulated probable scenarios of culling and colony dispersal to estimate their effects on the probability of epidemic occurrence. Modeling of the hypothetical metapopulation revealed that a reduction in the number of large-sized colonies would lead to an increase in the probability of epidemic occurrence within the bat population, whereas the strong spatial coupling among colonies was found to dilute the effects of altering the number of colonies and the number of bats in each colony through culling or colony dispersal of bats on the probability that an epidemic within the bat population would occur. Culling and colony dispersal scenarios showed no significantly beneficial effect with respect to reducing the probability of an HeV epidemic occurring in flying foxes, and may indeed prove counterproductive. In conclusion, the modeling results indicate that bat culling and colony dispersal may not be an effective strategy to control HeV epidemics.

Keywords: culling, colony dispersal, flying fox, Hendra virus, metapopulation, stochastic simulation

Introduction

IN 1994, THE FIRST identified outbreaks of the previously unknown Hendra virus (HeV) in horses and humans were reported in eastern Australia (Field et al. 2001). A few years later, Pteropid bats (commonly known as flying foxes) were identified as natural reservoir hosts of HeV (Young et al. 1996). HeV infections spill over from flying foxes to horses and subsequently to humans. HeV infections have a high case mortality in both horses and humans (Field et al. 2007). All four flying fox species found in Australia—the black flying fox (*Pteropus alecto*), gray-headed flying fox (*Pteropus poliocephalus*), little red flying fox (*Pteropus scapulatus*), and spectacled flying fox (*Pteropus conspicillatus*)—can be in-

fected with HeV (Field et al. 2011). In subtropical eastern Australia, however, the black flying fox appears to play a particularly important role as reservoir hosts for HeV spillover events (Smith et al. 2014).

The emergence of zoonotic diseases from wildlife has threatened human public health. Frequent outbreaks of fatal infectious diseases emanating from wildlife have increased interest in controlling infectious diseases in their reservoir populations before the etiologic agent spillover (Daszak et al. 2000). A possible strategy to control the spillover risk is to manage the population structure of wildlife (McCallum 2016). Culling has been used in attempts to reduce risk of spillover of zoonotic diseases originating from wildlife, which have threatened human or livestock health (Wobeser

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2002). However, the strategy might result in counterproductive outcomes if it was implemented without an accurate assessment of the outcomes. For example, the culling of badgers has not been as successful as expected in managing the spillover of cattle tuberculosis from badgers to British cattle. Although TB incidence in cattle was reduced in areas where badgers were culled, the social and spatial disturbances of the badger group caused by the culling of badgers led to increased incidence in cattle in adjoining areas (Donnelly et al. 2006). Modeling studies could be effectively used to predict probable outcomes and to evaluate and guide wildlife population control programs (McCallum 2016). In particular, modeling studies enable the investigation of a broader range of scenarios than is possible with experimental or empirical studies alone (Beeton and McCallum 2011).

With regard to potential population management, a factor that has a key bearing on HeV dynamics is that flying foxes in Australia form metapopulations (Field et al. 2007), which are defined as groups of spatially separated subpopulations of the same species among which individuals regularly move (Hanski and Gilpin 1991). From a metapopulation perspective, it has been suggested that changes in the movement patterns of flying foxes in response to increasing urbanization might be associated with an increased risk of HeV spillover (Plowright et al. 2011). Accordingly, it would be essential to include the metapopulation structure of flying foxes in models that are designed to realistically simulate the culling and colony dispersal of these bats and predict how these management actions may affect the risk of HeV spillover.

The probable assumptions that made bat population control work in a way that can influence the management of the infectious disease are key parts in our study. The first key assumption was a density-dependent transmission mode of HeV among flying foxes. Plowright et al. (2015) have suggested that HeV transmission in flying foxes can be either density dependent or frequency dependent, depending on specific circumstances. In density-dependent transmission, the transmission depends on population size, while in frequency-dependent transmission, the transmission does not depend on population size. In this respect, it is a well-established epidemiological principle that a reduction in population size can reduce density dependence-based transmission, but not transmission that is frequency dependent (McCallum et al. 2001). Accordingly, if frequency-dependent transmission is the predominant mode for the spread of HeV by flying foxes, making changes to the size of bat colonies would have little effect on the extent of virus transmission. Indeed, such an approach would probably be counterproductive, in that, the increased stress caused by culling or colony dispersal may only serve to exacerbate the risk of spillover by disrupting the immune system of these bats due to the stress and poor nutritional state caused by the culling or dispersal processes (Plowright et al. 2008, 2015).

The second key assumption is a close association between the peaks of HeV prevalence and HeV shedding from bats, and thereby the reduction in HeV epidemics in bat populations can facilitate the decrease in the HeV spillover risk. Previously, it was hypothesized that spatiotemporal pulses of virus shedding in bat populations can be explained by "transient epidemics" or by "episodic shedding" (Plowright et al. 2015). Transient epidemic occurs during a relatively short period when the population consisting of a number of susceptible hosts is exposed to infectious hosts, while episodic shedding occurs when the host's immune response fails to suppress persistent infection because of stressors (Plowright et al. 2015). Given that the risk of HeV spillover may be differentially affected depending on virus dynamics, it is necessary that these dynamics are taken into consideration when designing interventions to manipulate bat populations (Plowright et al. 2016). Also, immigration of infectious or susceptible bats between populations can affect the probability of epidemic occurrence (Streicker et al. 2012, Bakker et al. 2019). Transient epidemics are more likely to be influenced by changes in population size and in composition of epidemic status of bats than episodic shedding. From these two key assumptions, we investigate the probability of HeV epidemic occurrence in a metapopulation of flying foxes, when infectious bats are introduced into an infection-free metapopulation. Therefore, the interpretation of our modeling results must take into consideration the assumptions on which the models are based.

The study described herein consisted of two parts. We initially simulated hypothetically designed metapopulation network scenarios to examine the effects of metapopulation-related factors (the number of colonies in a metapopulation, the number of bats in each colony, and the distances among colonies) on the probability of epidemic occurrence. The findings obtained from this analysis not only contribute to our knowledge of metapopulation dynamics but also facilitate interpretation of the results obtained in the second part of the study, in which we assessed the relative effect of various culling and dispersal scenarios on the probability of epidemic occurrence in a metapopulation model that used the real dataset of black flying fox movements. Accordingly, we emphasize the importance of comparing the relative effects of these scenarios on the probability of epidemic occurrence rather than aim to quantitatively predict the risk of HeV spillover.

Methods

Model framework

Based on the assumption that management activities take place on very short timescales, we did not model HeV dynamics while these control measures were in progress. Instead, we modeled transient epidemics associated with the altered metapopulation structures following the completion of culling or colony dispersal. Thus, constant rates of birth and death were applied instead of seasonal birth pulses of flying foxes (Peel et al. 2014). We assumed that only a single colony received infectious hosts as migrants to simulate how different metapopulation structures in various scenarios would facilitate the spread of epidemics within the metapopulation. The number of infectious hosts introduced into the metapopulation (1/700 of the baseline number of bats in a colony) was selected to ensure that appropriate levels of transmission events took place in each scenario, thereby enabling a comparison among scenarios.

The colony, into which infectious bats were introduced, was determined at random and weighted by number of bats in each colony. The pre-existing immunity, the proportion of recovered bats in a colony, was assumed to be 0.5 at the moment of HeV introduction (approximately equivalent to the HeV seroprevalence rates often observed in black flying foxes) (Plowright et al. 2011). At the initiation of each simulation, thus, a certain number of infectious bats were introduced into a stochastically chosen colony within an

infection-free metapopulation, in which 50% of bats were immune. Also, at the beginning of each simulation, the metapopulations already had different structure as a result of culling or colony dispersal.

The metapopulation modeling of black flying foxes required an estimation of migration frequency between colonies. Based on the overall tendency of movement data of black flying foxes in Sunshine Coast, Queensland, Australia (Towsey 2017), we assumed that bats move between any pair of colonies at a rate that is inversely exponentially proportional to the distance between the two colonies [similar to the assumption made by Plowright et al. (2011)]. Thus, the movement rate (m_{ij}) from one colony to the next was estimated by using the following equation:

$$m_{ij} = e^{\left(-cD_{ij}\right)},$$

where D_{ij} is the distance between the two colonies i and j, and c is a connectivity parameter that controls how the movements of bats between colonies drop off with increasing distance (Plowright et al. 2011). We derived the mean movement rate (1/13.5 per day) and the mean distance among colonies (31.1 km) from the satellite tracking data (Towsey 2017), substituted the values in the equation, and calculated the connectivity parameter ($c = 0.08367$).

The main outcome of the models was the probability of epidemic occurrence. If the number of infectious bats in any colony in a metapopulation exceeded three times the number of infectious bats initially introduced, we considered that an epidemic had occurred in the metapopulation. Generally, there are limited fields and experimental data that can be used to quantify model parameters. In Table 1, we present mean estimates for epidemiological and demographic parameters obtained from the literature. Given the complexity of modeling how the assumed epidemiological and demographic parameter values affect epidemics, we applied a variety of parameter values, while keeping other parameters constant.

Simulation of the model was implemented stochastically using Gillespie's Direct Method (Gillespie 1977), in which all events, with their corresponding change rates, were used to determine the time of the next event and which event would occur (Table 2) (Lu et al. 2013). All models were implemented using the R package "GillespieSSA" (Pineda-Krch 2010), and each scenario was simulated 1000 iterations to generate the outcomes. The time unit of the models was a day, and the models tracked the number of infectious individuals for 150 days. Details of parameters are shown in Supplementary Appendix SA1.

Vial transmission within a metapopulation

We assumed that infectious individuals were introduced into a colony in the metapopulation, and then because of the already decided equation of bat migration among colonies, they may migrate from the initially infected colony to other infection-free colonies to balance the prevalence among the colonies. In this way, infectious individuals are not congregated in a single colony, and no single colony may have a sufficient number of infectious individuals to trigger an epidemic. Moreover, the small numbers of infectious individuals in multiple colonies will lose their infectivity in time without causing an epidemic. Masuda (2010) defined this situation as diffusion. In this study, we defined diffusion as having occurred if there was a decrease in the number of infectious individuals in an initially infected colony and if there was an increase in the sum of the number of infectious individuals in other colonies within a quarter day after the introduction of infectious individuals into a colony. Given that the diffusion effect influences the dynamics as soon as infectious individuals are introduced, we measured the effect during such a short period before the occurrence of a rescue event.

However, even though a virus may be eliminated (i.e., no infection) from a colony, a rescue effect might allow the colony to be re-infected through migration of infectious hosts from other colonies (Grenfell et al. 2001). Thereby, the probability of rescue events occurring depends on the probability of local extinction of infection (Dalziel et al. 2016). In this study, we define rescue as having occurred if the number of infectious individuals in the initially infected colony reached zero at any time point between the introduction of

TABLE 1. MODEL PARAMETERS IN A METAPOPULATION OF BLACK FLYING FOXES
IN THE SUNSHINE COAST, QUEENSLAND, AUSTRALIA

Description	Value	Source
Epidemiological and demographic parameters		
Transmission rate (β)	0.0000476	Plowright et al. (2011)
Recovery rate (γ)	1/7 day	Plowright et al. (2011)
Mortality rate (μ)	1/7 year	McIlwee and Martin (2002)
Birth rate (b)	1/7 year	McIlwee and Martin (2002)
Proportion of immune bats in populations at viral introduction (HI)	0.5	Field (2005)
Initial number of infectious bats (II)	(colony size)/700	
Sunshine Coast metapopulation parameters		
Total colony number	16 colonies	Towsey (2017)
Number of urban colonies	8 colonies	Towsey (2017)
Number of rural colonies	8 colonies	Towsey (2017)
Connectivity parameter (c)	0.08367	From this study
Baseline colony size (N)	10,000 bats	Department of the Environment and Energy (2013)

HI, herd immunity.

TABLE 2. EVENTS, CHANGES, AND RATES USED
FOR STOCHASTIC SIMULATIONS OF EPIDEMICS
IN A METAPOPULATION OF BLACK FLYING FOXES
IN THE SUNSHINE COAST, QUEENSLAND, AUSTRALIA

Event	Change	Rate
Birth	$S \rightarrow S+1$, $I \rightarrow I+1$, $R \rightarrow R+1$	$b(S+I+R)$
Death	$S \rightarrow S-1$, $I \rightarrow I-1$, $R \rightarrow R-1$	μS, μI, μR
Transmission	$S \rightarrow S-1$, $I \rightarrow I+1$	βSI
Recovery	$I \rightarrow I-1$, $R \rightarrow R+1$	γI
Movement of an infected bat from colony i to colony j	$I_i \rightarrow I_i-1$, $I_j \rightarrow I_j+1$	$\sum_j m_{ij} I_i$

S, I, and R represent susceptible, infectious, and immune, respectively. m_{ij} indicates the movement rate of bats from colony i to colony j. Other abbreviations are found in Table 1.

infectious individuals and the epidemic peak, which was conditional on an epidemic having occurred. We recorded two additional outcomes to the probability of epidemic occurrence, namely, the probability of diffusion and the probability of rescue to explore the effect of metapopulation on epidemic occurrence.

Metapopulation network scenarios

Before simulating various culling and dispersal scenarios for the realistic black flying fox metapopulation, we needed to simulate simpler scenarios to separately examine the effect of metapopulation-related variables (colony number, colony size, and distance among colonies) on the probability of epidemic occurrence. HeV dynamics were initially simulated with the uniform metapopulation network scenarios, in which for each simulation, we assumed (i) equal distances among all colonies, (ii) the same colony number (*i.e.*, number of colonies in a metapopulation), and (iii) the same colony size (*i.e.*, the number of individuals in a colony). Three levels of distance among colonies (1, 20, and 50 km), five levels of colony size (4000, 6000, 8000, 10,000, and 12,000 individuals), and five levels of colony number (2, 4, 8, 12, and 16) were applied in the uniform metapopulation network scenarios. Hereafter, colony number indicates the number of colonies in a metapopulation and colony size indicates the number of bats in each colony.

Sunshine Coast metapopulation

Our model was based on a metapopulation of black flying foxes in the region around the Sunshine Coast, Queensland, Australia, which is one of major regions HeV spillover has occurred and for which bat movement data were available (Fig. 1) (Towsey 2017). We selected black flying foxes (*P. alecto*) as the study species for two reasons. First, spatiotemporal investigations through detection of flying fox pooled urine samples have indicated that black and spectacled flying foxes have been more responsible for the transmission of HeV to horses than have gray-headed and little red flying foxes (Field et al. 2015). Second, the distribution of
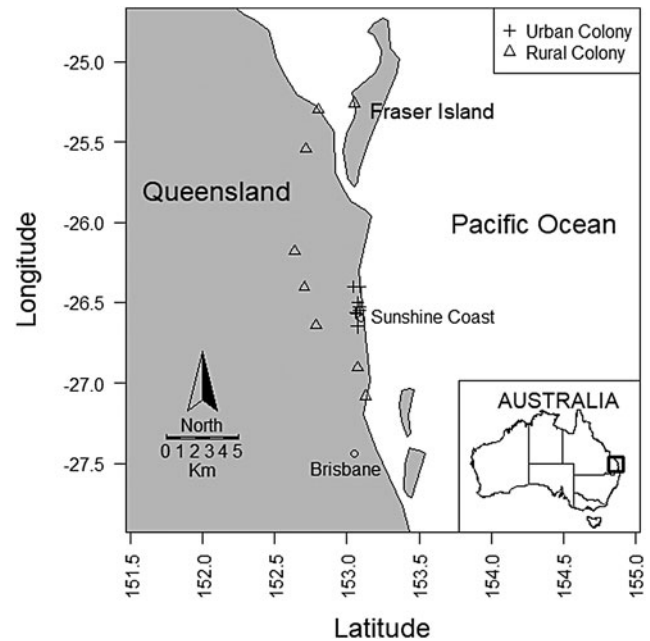

FIG. 1. Colonies ($n = 16$) of black flying foxes (*Pteropus alecto*) in the Sunshine Coast, Queensland, Australia.

black flying foxes includes South East Queensland and northeast New South Wales, where most HeV spillover events have occurred historically, whereas the distribution of spectacled flying foxes is limited to north Queensland (Hall and Richards 2000). The division of colonies into urban and rural ones is because people want bats to decrease in densely populated regions and in sparsely populated regions bats are relatively tolerable (see Supplementary Appendix SA2 for more details of Sunshine Coast metapopulation structure).

Culling scenarios

Culling can be implemented in numerous ways, and for the purposes of simulation, we selected two fundamental parameters that show the significance of changes in the population size of urban and rural colonies: (i) whether colonies were culled in urban areas or rural areas and (ii) whether the colony number or colony size was reduced. Taking these two basic parameters into consideration, we modeled culling scenarios 1 to 3, in which colony number was reduced, and modeled culling scenarios 4 to 6 in which colony size was reduced. Colonies were removed in a random order (scenario 1), successively close to each other (scenario 2), and as far away as possible from each other (scenario 3). Bats were culled both in urban and in rural colonies (scenario 4), only in urban colonies (scenario 5), and only in rural colonies (scenario 6). Each of these scenarios was implemented with five different degrees of intensity. Numerical details of these scenarios are presented in Table 3.

Dispersal scenarios

Compared with culling, induced bat colony dispersal has been proposed as a less radical strategy for mitigating the human–wildlife conflict caused by flying foxes (Eby and Lunney 2002). Given the increased urban presence of flying

TABLE 3. DESCRIPTION OF CULLING AND DISPERSAL SCENARIOS OF A METAPOPULATION
OF BLACK FLYING FOXES IN THE SUNSHINE COAST, QUEENSLAND, AUSTRALIA

Scenario	Control strategy	Location of colonies	Intensity of action				
			1	2	3	4	5
Culling							
			Remaining colony number after culling				
1	Reduction of colony number	All	16	12	8	4	2
2	(differences in the order	All	16	12	8	4	2
3	of colonies removed)	All	16	12	8	4	2
			Remaining proportion of bats in colonies after culling				
4	Reduction of colony size	Urban	1	0.825	0.75	0.625	0.5
		Rural	1	0.825	0.75	0.625	0.5
5		Urban	1	0.75	0.5	0.25	0
		Rural	1	1	1	1	1
6		Urban	1	1	1	1	1
		Rural	1	0.75	0.5	0.25	0
Dispersal							
1	Increasing connectivity		Connectivity parameter (c)				
		All	$c/1$	$c/2$	$c/3$	$c/5$	$c/10$
2	Removal of urban colonies		Remaining colony number after dispersal				
	and establishment of new	Urban	8	6	4	2	0
	colonies in rural areas	Rural	8	10	12	14	16
3	Joining of dispersed urban		Remaining colony number after dispersal				
	bats to existing colonies	Urban	8	6	4	2	0
		Rural	8	8	8	8	8

The first level of actions in all scenarios (baseline model) is identical for all scenarios. The baseline model includes eight urban colonies and eight rural colonies. The number of bats in each colony is identically 10,000 in the baseline model. In dispersal scenario 1, the connectivity among colonies is inversely proportional to the connectivity parameter.

foxes in urban habitat (Edson et al. 2015), we considered only urban colonies in our dispersal scenarios. We assumed that all bats in the selected colony were permanently dispersed: that is, the colony was eliminated from the metapopulation, as would be accomplished by removal of vegetation in the roost site. After dispersal, the dispersed bats could either form new colonies or merge with existing colonies, and these colonies could be in either rural or urban areas. In addition, we considered that, where possible, dispersed flying foxes did not move far from the sites of their original colonies, and that they would maintain efforts to re-colonize these sites (Roberts and Eby 2013, unpublished report). Considering these characteristics and their response, we modeled three scenarios of bat behavior following colony dispersal (Table 3).

In scenario 1, bats dispersed from urban colonies established new colonies near their original sites, resulting in a small change in the metapopulation structure. However, dispersed bats may move more frequently than before because of their attempts to return to their original sites. We applied a range of increased connectivity parameters to model this behavior. In scenario 2, bats dispersed from urban colonies established new colonies in rural areas. The distances between newly formed rural colonies and other colonies were determined by randomly selecting distances from a rural colony to other urban or rural colonies. Urban colonies to be dispersed were randomly selected. In scenario 3, bats dispersed from urban colonies did not form new colonies and instead merged with any colony in urban or rural area. The number of bats moving into each unaffected colony was inversely exponentially proportional to the distances between a dispersed colony and unaffected colonies.

Results

Uniform metapopulation network scenarios

The simulations of uniform metapopulation network scenarios showed that the probability of epidemic occurrence was proportional to colony size (Fig. 2A). Given a density-dependent transmission scenario, it was predictable that larger colonies would provide more infectious (initially introduced) bats with a higher likelihood of infecting a sufficient number of susceptible individuals to trigger an epidemic. In addition, the probability of epidemic occurrence was shown to be inversely proportional to colony number. As the models assumed that the same number of infectious bats was introduced into a single colony in the metapopulation regardless of the colony number, the increase in colony number facilitated the migration of newly introduced infectious bats to other colonies. Accordingly, this migration served to prevent the occurrence of an epidemic in the initially infected colony by leaving too few infectious hosts to trigger an epidemic.

In larger colony sizes, the probability of epidemic occurrence was proportional to the distance among colonies, while in smaller colony sizes, the probability was inversely proportional to the distance. This is because diffusion effect was predominant in larger colony sizes, but rescue effect was critical in smaller colony sizes (Fig. 2B, C). Given that the initially introduced number of infectious bats was proportional to the colony size, in the large colonies, the number of infectious bats was likely to be enough to trigger an epidemic unless the frequent movement of bats among shortly distanced colonies (1 km). On the contrary, in small colony sizes, the initially introduced infectious bats are unlikely to
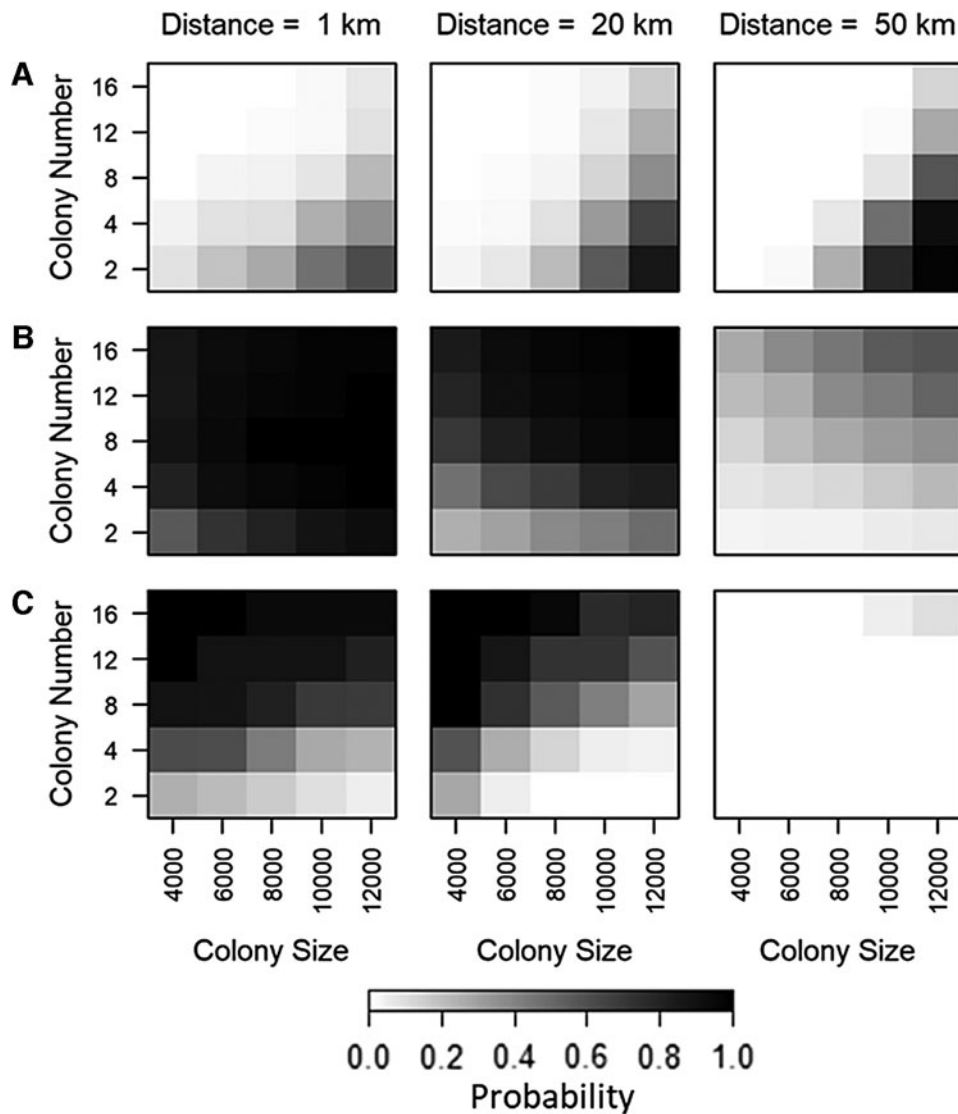
FIG. 2. Simulation outputs in the scenarios of uniform metapopulation network. **(A)** The probability of epidemic occurrence in the stochastic simulations. **(B)** The probability of diffusion. **(C)** The probability of rescue. Three different distances (1, 20, and 50 km apart, from *left* to *right columns*) were used to model with differing colony numbers, and differing colony sizes.

trigger an epidemic. Instead, the infectious bats that moved other colonies might have a chance to initiate epidemics, and thereby higher colony numbers and colonies with 1 km of distance, which could produce more movements of bats among colonies, caused the higher probability of rescue effect.

Culling scenarios

A reduction in colony number (scenarios 1–3) was found to be counterproductive in terms of reducing the probability of epidemic occurrence, and in most cases significantly increased the probability of epidemics occurring (Fig. 3A). Regarding no management action, the culling of colonies that were closest to each other (scenario 2) resulted in the most pronounced increase in the probability of an epidemic and this effect increased with an increase in the number of culled colonies. Culling colonies in a random order (scenario 1) showed a similar trend to scenario 2, whereas in contrast, initially, culling colonies that were furthest apart (scenario 3) had little impact on the probability of epidemic outbreak when only distant colonies were culled (culling levels 1, 2,

and 3), although a significant increase in the probability was observed when closer colonies were culled (culling levels 4 and 5).

In the scenarios in which the number of colonies remained unaltered, the probability of an epidemic occurring decreased when colony sizes were reduced (scenarios 4–6). This effect was less marked when the size of urban colonies was reduced (scenario 5) compared with a reduction in the size of rural colonies (scenario 6).

The probability of epidemics arising from the culling of colonies in random order (scenario 1) was found to be intermediate between the probabilities predicted for scenarios 2 and 3, whereas the probability of epidemics arising from a reduction in colony size in both urban and rural colonies (scenario 4) was lower than the average of the probabilities predicted for scenarios 5 and 6.

For uniform metapopulation network scenarios, when metapopulations consisted of small colonies, the probability of epidemic occurrence was higher when the distances between colonies were shorter than when the distances were longer. However, with respect to culling scenarios, we found

FIG. 3. (A) Probability of epidemic occurrence in six different culling scenarios and five levels of intensity (refer to Table 3). Scenarios 1 to 3 refer to colony number variations; scenarios 4 to 6 refer to colony size variations. **(B)** Probability of epidemic occurrence in three different dispersal scenarios and five levels of intensity (refer to Table 3). The first levels of culling and dispersal refer to no action and each colony has equally 10,000 bats.
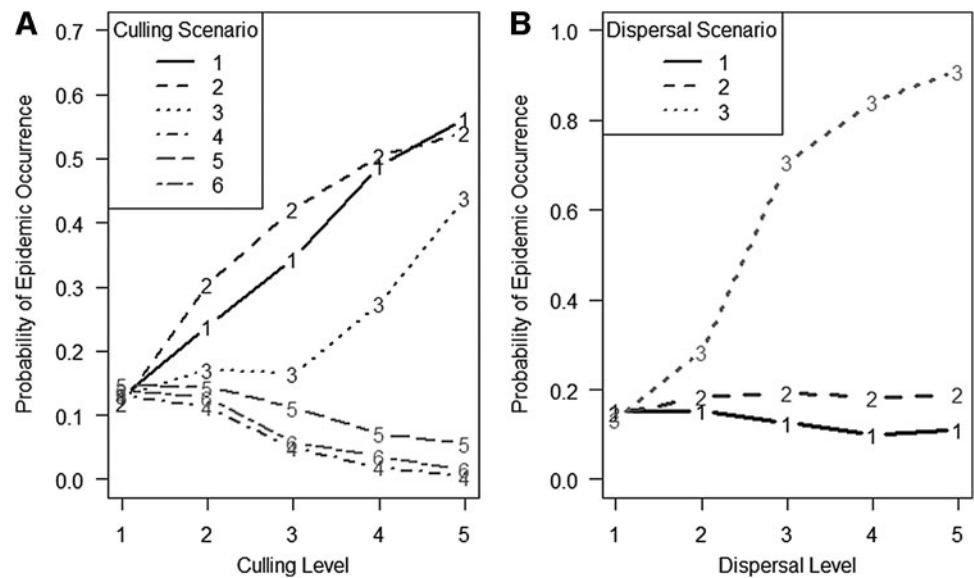
that in metapopulations consisting of small colonies, the probability of epidemic occurrence was lower when there was an overall higher connectivity among colonies (scenarios 3 and 6) than when there was an overall lower connectivity (scenarios 2 and 5). Nevertheless, the higher connectivity among colonies in scenarios 3 and 6 was not deemed to be very influential and colonies in the Sunshine Coast metapopulations were still located further apart compared with the 1-km distance among colonies in the uniform metapopulation network scenarios. Moreover, differences in the probabilities of epidemic occurrence based on changes in the connectivity among colonies decreased concomitantly with a decrease in colony size.

Dispersal scenarios

We found that for the Sunshine Coast metapopulation, a change in colony number or colony size had a considerably more pronounced influence on the likelihood of epidemic occurrence than did a change in the connectivity among colonies (Fig. 3B). In dispersal scenario 3, increased colony size and decreased colony number resulted in a substantial increase in the probability of epidemic occurrence, whereas in contrast, changes in connectivity (scenario 1) and changes in colony location (scenario 2) had only a marginal effect. In dispersal scenario 1, the increased movements of bats among colonies resulted in a higher diffusion effect, leading to a decrease in the probability of epidemic occurrence. In dispersal scenario 2, the removal of urban colonies and new establishment of rural colonies were observed to result in a decrease in the overall movement of bats among colonies in the metapopulation, thereby reducing the diffusion effect.

Discussion

In this study, we examined HeV dynamics for a range of modeled bat metapopulation structures when infectious hosts were introduced in an infection-free metapopulation, based on the assumption that changes in population size may have an effect. Having initially determined the effects of colony number, colony size, and distance among colonies on the probability of epidemic occurrence, we showed how the predictions obtained from the hypothetical scenarios could be used to interpret the simulation results of more realistic culling and dispersal scenarios. Although HeV infection prevalence in flying foxes is a critical factor in determining the infection in horses, the spatiotemporal variations of HeV infection are so vast that it is not relevant of modeling their patterns (Field et al. 2015). Thus, we focused in this study on the changes in probability of epidemic occurrence associated with different population structures, in contrast to most of the previous models that have been generated to provide information relevant to the prevalence management of wildlife diseases (McCallum 2016).

We found that the culling and colony dispersal scenarios often resulted in counterproductive outcomes with respect to virus transmission, even with the assumptions that might facilitate the reduction of HeV transmission. From the theoretical perspective of disease ecology, population size is a critical factor in determining the probability of epidemic occurrence, given density-dependent transmission. This finding is consistent with the principle that culling wild animals can help control wildlife diseases. However, under our assumed conditions, it would appear that the management of HeV epidemics based on the control of flying fox populations is an unrealistic strategy. Even though the culling scenarios 4, 5, and 6, which generated reduced probability of epidemic occurrence, were supposed, massive culling of bats should be to acquire a significant reduction in the probability. Such a marked reduction in bat numbers would predictably have detrimental knock-on effects, given the important ecosystem services, such as pollination, provided by bats (Páez et al. 2018).

The frequent movement of bats between colonies within the metapopulation has greatly increased the degree of reduction in population size to have a tangible effect in controlling epidemic outbreaks (Roberts et al. 2012). The frequent movement also took a role in increasing rescue effect higher with smaller colony size. Given density-dependent transmission, population sizes should be larger than a threshold for infection persistence (Lloyd-Smith et al. 2005). Likewise, population sizes that are larger than a threshold are important

for an epidemic to occur. However, the frequent movement compensated this unfavorable condition of small population size for epidemic occurrence by spreading the probability of initiating epidemics to various colonies.

Understanding the behavioral characteristics of flying foxes is essential to manage their populations. Moreover, culling would need to be conducted on an annual basis to compensate for potential population recovery through increased recruitment or replenishment due to the long distance and frequent movements of flying foxes (Roberts et al. 2012). Our study is in line with previous studies that showed unsuccessful trials of wildlife culling for the purpose of controlling zoonotic diseases (Donnelly et al. 2003, Streicker et al. 2012, Bakker et al. 2019). In addition to culling, colony dispersal may not appear to be an appropriate alternative to culling in terms of reducing the risk of HeV epidemics, given that we found the scenarios of colony dispersal did not predict a reduced probability of epidemics. Rather, scenario 3, which simulated a decrease in colony number and an increase in colony size, predicted a substantially enhanced probability of epidemic occurrence. Thus, these findings would tend to indicate that an altered metapopulation structure in response to colony dispersal may be conducive to the development of HeV epidemics in bats.

From a metapopulation dynamics perspective, the effect of a high rate of movement on the spread of epidemics can be correlated with the rate of metapopulation recovery (Cross et al. 2005). If the recovery rate vastly exceeds the movement rate, infectious individuals would have few opportunities to spread the infection to other colonies. The potential high recovery rate (1/7 per day, *i.e.*, a short infectious period) of HeV in flying foxes (Plowright et al. 2011) limits the likelihood that an epidemic would spread across a metapopulation. Nevertheless, our Sunshine Coast metapopulation model predicted high temporal synchrony among epidemics in individual colonies, and a notably efficient spread of epidemics across the metapopulation (Supplementary Appendix SA3). This pattern can be attributed to the fact that the movement rate, which was calculated with the movement data of black flying foxes in east Australia (Towsey 2017), was sufficiently high to offset the effect of the short infectious period, thereby facilitating epidemic spread, which could even occur synchronously. Nevertheless, the fact that the spread of epidemics is highly dependent on the infectious period emphasizes that more accurate estimates of the infectious period would be necessary to enhance our predictions of the extent of epidemic spread.

Author Disclosure Statement

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Funding Information

Supplementary Material

Supplementary Appendix SA1
Supplementary Appendix SA2
Supplementary Appendix SA3

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