



# A simple spatiotemporal rabies model for skunk and bat interaction in northeast Texas

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## HIGHLIGHTS

- ▶ A PDE model is formulated for the dynamics of rabies spread among bats and skunks.
- ▶ We incorporate interspecies rabies infection in addition to rabid random movement.
- ▶ We apply this model to the confirmed case data from Texas.
- ▶ Simulations with overlapping reservoir species accurately reproduce the case data.

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## ABSTRACT

We formulate a simple partial differential equation model in an effort to qualitatively reproduce the spread dynamics and spatial pattern of rabies in northeast Texas with overlapping reservoir species (skunks and bats). Most existing models ignore reservoir species or model them with patchy models by ordinary differential equations. In our model, we incorporate interspecies rabies infection in addition to rabid population random movement. We apply this model to the confirmed case data from northeast Texas with most parameter values obtained or computed from the literature. Results of simulations using both our skunk-only model and our skunk and bat model demonstrate that the model with overlapping reservoir species more accurately reproduces the progression of rabies spread in northeast Texas.

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## 1. Introduction

The rabies virus affects the central nervous system of an infected animal, causing abnormal behavior, paralysis, coma, and eventually death. The virus endangers wild animals, domestic animals, farm animals, and humans (Kaplan, 1985). Indeed, it produced one of the earliest recorded instances of human suffering due to infectious disease (Jackson and Wunner, 2002a). When an infected animal bites a susceptible animal, the virus is transmitted through saliva (Jackson and Wunner, 2002b). While fatality due to rabies in humans in the US is rare (1–2/year), viral circulation is maintained in several wildlife reservoir species (Blanton et al., 2009, 2010, 2011). Raccoons, skunks, foxes, and bats are common rabies reservoir species (Rabies, 2011). The increasing interactions of domestic animals with wild ones give rise to the possibility that more and more domestic animals

will be infected by the rabies virus, and hence rabies is a fast growing threat to both humans and domestic animals.

Due to this public health concern, there has been a continuous and growing effort to develop mathematical and computational models to predict the spatial and temporal dynamics of rabies. Many of the existing models dealing with rabies virus spread in Europe are associated with rabies emergence in the red fox which began in Poland in 1939 and spread westward at a rate of 30–60 km per year. Almost all the existing models deal with rabies in a single species (Kallen et al., 1985; Murray et al., 1986; Smith et al., 2002).

The spread of rabies in an area with overlapping reservoir species (those species capable of maintaining the disease in low levels in their population, occasionally cross-infecting other species) is a unique problem. Where rabies has traditionally been modeled – in Europe and the Eastern United States – there has been only one reservoir species, foxes or raccoons, respectively. In areas such as Texas and Arizona, however, overlapping reservoir populations of bats and skunks affect the spread of rabies in unique ways, which have not yet been well studied. The goal of this investigation is to develop a model of interspecies rabies infection between bat and skunk populations, and to apply the

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model to the excellent confirmed case data from the Texas Department of State Health Services (Rabies Maps, 2011).

## 2. Model and method

We focus our discussion on a geographic area of  $(300 \text{ km})^2$  located in northeastern Texas (see Fig. 1). This area is principally located in the Texan biotic province (Blair, 1950), a geographic area with forests to the east and semiarid grasslands to the west. Rabid skunks in Texas, in most cases striped skunks (*Mephitis mephitis*), have been observed to be prevalent mainly in the Texan biotic province (Pool and Hacker, 1982), possibly due to the frequent use of land for agricultural purposes including pasturage, row crops, and wooded acreage. On the other hand, most cases of bat rabies in the  $(300 \text{ km})^2$  area have been distributed with a focus in Dallas, and the dominant bat species is eastern red bat (*Lasiurus borealis*). The area of concern has been known (Pool and Hacker, 1982) and observed to be free of rabies cases in other major mammalian reservoir species, in particular, foxes. Consequently, we can focus our attention on hypothesized interactions between local skunk and bat populations.

The selection of Texas as the state with specified study area is in part due to the availability and quality of the Texas empirical data in comparison with other states' wildlife health resources. Furthermore, bats are a year-round presence in Texas, and there is less variation in the number of continuously active bats and their distribution in Texas than in other states in North America, where bats tend to migrate or hibernate during the winter cold weather to cope with the problem of insufficient food and other energy resources (Schmidly, 1991).

Bats are a major source of indigenously acquired human rabies infection in the United States, and more than 2000 rabies-positive bats are collected annually (Blanton et al., 2009, 2010). Since the first bat-related human rabies case was reported in 1951, bats are increasingly popular and important targets of public health programs associated with lyssaviruses, in particular rabies (De Serres et al., 2008). Cross-species transmission cases of rabies from bats to humans, domesticated animals, and terrestrial mammals have been documented. Antigenic typing of rabid carnivores in Arizona from 1996 to 2000 showed rabies virus of bat origin in one domestic dog and two grey foxes (Leslie et al., 2006). Similar transmission occurred in Canada and a variant of the rabies virus seems to have become established in the fox population on Prince Edward Island (Daoust et al., 1996). In 2001,

19 rabid skunks were diagnosed as infected with rabies virus of bat origin in Flagstaff, Arizona (Leslie et al., 2006). Later in 2004 the recurrence of rabid skunks infected with the same rabies virus suggested the probability of independent interspecies transmission (Leslie et al., 2006).

Striped skunks have long been known as a major rabies reservoir species (Jackson and Wunner, 2002c), and population dynamics, experimental as well as field rabies infection of skunks, have been extensively investigated (Weissinger et al., 2009; Pybus, 1988; Chalton et al., 1987; Greenwood, 1997; Pool and Hacker, 1982; Rosatte, 1984). Similar results concerning eastern red bats are rare and historical population information is at best anecdotal. Eastern red bats are migratory, insectivorous, solitary and foliage-roosting bats (Carter et al., 2003). The absence of colonial behavior, such as forming maternity colonies, may have contributed to the lack of information (Carter et al., 2003). They are habitat generalist (Shump and Shump, 1982) and flexible in choosing roosting sites (Downes, 1964). Similar results showed that they have roost fidelity (Mager and Nelson, 2000). Striped skunks and eastern red bats exhibited susceptibility to rabies virus of red bat origin in previous experiments (Constantine and Woodball, 1966).

Although there is evidence that bats and skunks maintain independent rabies enzootic cycles (Pool and Hacker, 1982), clusters of events and experiments documenting cross-species transmission from bats to terrestrial mammalian reservoir species suggest the probability of cross-species transmission of rabies resulting from local interactions between eastern red bat and striped skunk populations in our research. And some recent studies (Streicker et al., 2010; Turmelle et al., 2011) provide further evidence that cross-species transmission of rabies has notable impacts on both establishment and spread of rabies among bats. Eastern red bats usually roost solitarily in open canopy trees and they share some habitat resources with striped skunks. In the daytime skunks may approach bats for food, which could cause unprovoked rabies virus transmission. Furthermore, since both species are nocturnal, it is likely that their overlapping foraging patterns may provoke accidental transmission. There is little evidence to support or exclude continuous dependence of the skunk rabies cycle on that of bats, so in our simple model we assume such a possibility to facilitate discussions.

In addition, since our study serves as a preliminary attempt at modeling the spatiotemporal dynamics of skunk–bat interactions, we choose not to account for any sampling and reporting bias. As a result, due to human involvement in sampling and reporting bias, comments or inferences based on this study cannot be applied to skunk–bat interactions in areas without human population.

For simplicity, we use skunks and bats to represent striped skunks and eastern red bats, respectively. Unlike previous studies on rabies infection that also used SEIR models on a single species (Dimitrov et al., 2007; George et al., 2011), the interspecies rabies infection between bat and skunk populations here can be modeled by a coupled system of nonlinear ordinary (ODE) and partial differential equations (PDE). The infected bats come into contact with both susceptible bats and susceptible skunks. In Fig. 2,



Fig. 1. Region of study and biotic provinces in Texas.

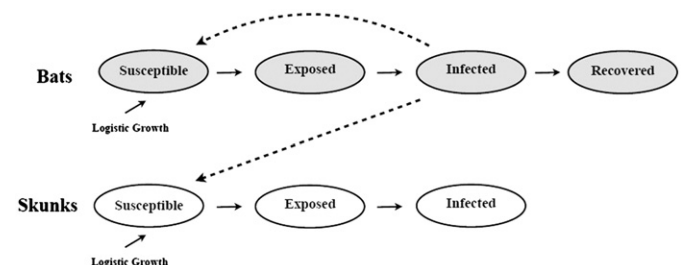


Fig. 2. Coupled SEIR system.

the dotted line represents infection between compartments. The small arrows represent departure from one compartment into another compartment. We assume logistic growth for both populations. The bat system includes a recovered compartment. Unlike skunks, some bats survive rabies infection.

The skunk population is modeled by the following coupled set of nonlinear ODEs/PDEs:

$$\frac{\partial S_s}{\partial t} = r_s S_s \left(1 - \frac{N_s}{K_s}\right) - \beta_s S_s I_s - \gamma S_s I_b + d_{ss} \nabla^2 S_s \tag{1}$$

$$\frac{\partial E_s}{\partial t} = \beta_s S_s I_s - (\sigma_s + m_s) E_s + \gamma S_s I_b + d_{es} \nabla^2 E_s \tag{2}$$

$$\frac{\partial I_s}{\partial t} = \sigma_s E_s - m_{rs} I_s + d_{is} \nabla^2 I_s \tag{3}$$

while the bat population is modeled by a similar set of coupled nonlinear ODEs/PDEs

$$\frac{\partial S_b}{\partial t} = r_b S_b \left(1 - \frac{N_b}{K_b}\right) - \beta_b S_b I_b \tag{4}$$

$$\frac{\partial E_b}{\partial t} = \beta_b S_b I_b - (\sigma_b + m_b) E_b \tag{5}$$

$$\frac{\partial I_b}{\partial t} = \sigma_b E_b - m_{rb} I_b - \rho_b I_b + d_b \nabla^2 I_b \tag{6}$$

$$\frac{\partial R_b}{\partial t} = \rho_b I_b - m_{wb} R_b \tag{7}$$

where  $S_s$  is the susceptible skunks,  $E_s$  is the exposed skunks,  $I_s$  is the infected skunks, and the total number of skunks is  $N_s = S_s + E_s + I_s$ ; and  $S_b$  is the susceptible bats,  $E_b$  is the exposed bats,  $I_b$  is the infected bats,  $R_b$  is the recovered bats, and the total number of bats is  $N_b = S_b + E_b + I_b + R_b$ . Logistic growth is introduced in each susceptible compartment with the appropriate birth rates ( $r_s$  and  $r_b$ ) and carrying capacities ( $K_s$  and  $K_b$ ).

**Infection and incubation.** Skunks are susceptible to infection from skunks and bats. The term  $\beta_s S_s I_s$  represents infected skunks

produced per year resulting from contact between infected and susceptible skunks at a transmission rate  $\beta_s$ . Susceptible skunks progress into the exposed compartment after being inoculated with rabies virus due to the contact with infected skunks. The transmission function  $\gamma S_s I_b$  represents skunk infection resulting from contact with infected bats. The term  $\beta_b S_b I_b$  represents the infection of susceptible bats by infected bats at a bat transmission rate  $\beta_b$ . After an average incubation period of  $1/\sigma_b$ , exposed individuals move into the infected compartment. The incubation period for skunks is  $\sigma_s^{-1}$ .

**Fertility.** We assume that only susceptible individuals are capable of reproduction and that the total population production follows the logistic growth equation.

**Mortality.** In the exposed compartments, individuals die from background mortality (terms  $m_s E_s$  and  $m_b E_b$ ). In the infected compartments, individuals die at a much higher rate that accounts for disease related mortality (terms  $m_{rs} I_s$  and  $m_{rb} I_b$ ). Recovered bat mortality is expressed by  $m_{wb} R_b$ .

**Diffusion and recovery.** Diffusion terms ( $d_{ss} \nabla^2 S_s$ ,  $d_{es} \nabla^2 E_s$ ,  $d_{is} \nabla^2 I_s$ , and  $d_b \nabla^2 I_b$ ) have been added to the infected compartments. Although symptoms of (furious) rabies include disregard for territorial boundaries and a general increase in movement, diffusion rates  $d_{ss}$  and  $d_{es}$  for susceptible and exposed skunks were assumed to be the same as  $d_{is}$ , as results of field study suggest practically no difference between characteristics of dispersal and home ranges between members of healthy and rabid skunk populations (Greenwood, 1997). Some bats survive rabies infection. These bats are accounted for by the advancement of  $\rho I_b$  from the infected bat compartment into the recovered bat compartment.

### 3. Parameter values for the model

The skunk and bat parameter values are summarized in Tables 1 and 2, respectively.

The skunk birth rate,  $r_s$ , is set to 4 (per individual per year) in our study. Each fertile female skunk gives birth to 3–9 skunks.

**Table 1**  
Skunk parameter set.

Parameter	Value	Information	Reference
$K_s$	20	Density 0.7–18.5 individuals per km <sup>2</sup>	Wade-Smith and Verts (1982)
$\beta_s$	2.5	Unknown	Ad hoc
$r_s$	4	Litter size 3–9	Schmidly (1994)
$m_s^{-1}$	2.5	Lifespan 2–3 years	Pybus (1988)
$m_{rs}^{-1}$	0.0274	Years (10 days)	Chalton et al. (1987)
$\sigma^{-1}$	0.164	Years (60 days), range 21–117 days	Chalton et al. (1987)
$d_{ss}$	10	km <sup>2</sup> per year	Greenwood (1997)
$d_{es}$	10	km <sup>2</sup> per year	Greenwood (1997)
$d_{is}$	10	km <sup>2</sup> per year	Greenwood (1997)

**Table 2**  
Bat parameter set.

Parameters	Value	Information	Reference
$K_b$	250	Individuals per km <sup>2</sup> , 1 red bat per acre	Schwartz and Schwartz (2002)
$\beta_b$	0.12	Estimated by Dimitrov et al.	Dimitrov and King (2008)
$r_b$	0.4	80% Chance of birth per female per year, litter size 1–4	Dimitrov and King (2008); Schwartz and Schwartz (2002)
$m_b^{-1}$	10	Years, life span may be 12 years	Saunders (1988)
$m_{rb}^{-1}$	0.0384	Years (14 days)	Constantine and Woodball (1966)
$m_{wb}^{-1}$	10	Years, assumed as same as $m_b^{-1}$	Ad hoc
$\sigma_b^{-1}$	0.0384	Years (14 days)	Constantine and Woodball (1966)
$\rho_b^{-1}$	0.5	Years	Turmelle et al. (2010)
$\gamma$	0.05	Unknown, but orders of magnitude lower than $\beta_s$	Ad hoc
$d_b$	300	km <sup>2</sup> per year, 46% of successive roosts < 25 m apart	Mager and Nelson (2000)

The skunk population is assumed to have an equal number of males and females. Not all female skunks are capable of having a litter. The skunk carrying capacity,  $K_s$ , is estimated to be 20 individuals per  $\text{km}^2$ , slightly higher than 18.5, the maximum striped skunk population density observed. The transmission rate between susceptible skunks and infected skunks,  $\beta_s$ , is unknown. A high transmission rate is assumed and  $\beta_s$  is set to 2.5. The skunk incubation period  $\sigma^{-1}$  is set to 60 days. A striped skunk's rabies incubation period ranges from 21 to 117 days (Chalton et al., 1987). The healthy skunk has a life span,  $m_s^{-1}$ , which is set to 2.5 years. The life span for striped skunks is between 2 and 3 years (Pybus, 1988). As the infected skunk dies about 10 days after development of the disease (Chalton et al., 1987),  $m_{rs}^{-1}$  is set to 10 days. No skunks survive rabies infection (Weissinger et al., 2009). The infected skunk diffusion coefficient,  $d_{is}$ , is estimated to be  $10 \text{ km}^2$  per year, based on the home range data provided in Greenwood (1997). Both the susceptible and exposed skunk diffusion coefficients,  $d_{ss}$  and  $d_{es}$ , are set at the same value as  $d_{is}$ .

The bat birth rate,  $r_b$ , is set to 0.4. The sex ratio of male bats to female bats is approximately 1:1. Each female bat has an 80% chance of giving birth each year (Dimitrov and King, 2008). The litter size of a typical red bat is 1–4 young (Schwartz and Schwartz, 2002). The bat carrying capacity,  $K_b$ , is estimated to be 250 individuals per  $\text{km}^2$ , about 1 individual per acre, which is given in Schwartz and Schwartz (2002). The transmission rate between susceptible bats and infected bats is set to 0.12 based on the available literature (Dimitrov and King, 2008). The bat incubation period,  $\sigma_b^{-1}$ , is set to 14 days. The eastern red bat life span,  $m_b^{-1}$ , is set to 10 years, slightly shorter than the 12 years estimated by Saunders (1988) as the longest life span of a typical eastern red bat.

Eastern red bats infected with rabies were observed to have short life expectancy, with approximately 14 days estimated as the duration between development of the disease and death (Constantine and Woodball, 1966). Hence,  $m_{rb}^{-1}$  is set to 14 days. The rabid bat recovery rate,  $\rho_b$ , was set to 2, since, according to Turmelle et al. (2010), rabies antibody titers were observed to drop below the detection level at least half a year after infection in those bats that survived previous rabies infections. The recovered bat mortality rate,  $m_{wb}$ , is assumed to be the same as  $m_b$ . Little evidence exists suggests that recovered bats have a longer or shorter life expectancy than bats that never experience any rabies infection. The bat diffusion coefficient,  $d_b$ , was set to  $300 \text{ km}^2$  per year. This parameter value is estimated based on the fact that successive roosts for eastern red bats were likely (46% of the time) to be less than 25 m apart (Mager and Nelson, 2000).

The contact rate between skunks and bats,  $\gamma$ , is unknown.  $\gamma$  is expected to be much smaller than the transmission rate  $\beta_s$  within the skunk population, since generally bat–skunk contacts are rare compared to skunk–skunk contacts. By repeated comparison of the simulation results to data, this parameter is adjusted to be 0.05.

#### 4. Confirmed case data and simulations

Bats and skunks account for the majority of rabies cases in our research area (Rabies Maps, 2011). The influence of bats on the spatial distribution and rabies dynamics of skunks became apparent after we processed the Texas map data of confirmed rabies cases (Rabies Maps, 2011). We altered the maps from 2003 to 2010 to have a uniform size and orientation. We also plotted skunk and bat cases for each year in a uniform format.

We compiled these images in a slideshow that displays year-to-year changes in the distribution of confirmed cases. There appears to be a two to three year period in which initial dispersal is followed by a resurgence of infected individuals. This pattern is indicative of the

skunks' role as a reservoir species for rabies. The study was focused on a  $(300 \text{ km})^2$  region in northeast Texas (see Fig. 1).

The coupled ODEs/PDEs in Eqs. (1)–(7) were solved in MATLAB using the adaptive timestep fourth/fifth order Runge–Kutta solver, after discretizing the diffusion PDE terms with second-order accurate central differences. Homogeneous Neumann boundary conditions were imposed on the diffusion equations.

Simulations using both the original model (skunks only) and the new model (skunks and bats) are shown in Fig. 3. Gaussian distributions were used to instantiate the infected compartments with an approximation of the 2007 confirmed case data, as shown in Fig. 4. We assumed that the initial distribution of exposed skunks could be approximated by decreasing the density of infected individuals, and that the initial distribution of exposed bats could be approximated by increasing the density of infected individuals. We also assumed that the initial distribution of recovered bats could be approximated by decreasing the density of infected individuals. The susceptible skunk compartment was initialized by subtracting the number of exposed and infected individuals from the skunk carrying capacity. Similarly, the susceptible bat compartment was initialized by subtracting the number of exposed and infected individuals from the bat carrying capacity.

Dallas is located towards the center of the  $(300 \text{ km})^2$  region of study. The city's location and highway system likely affect rabies propagation. The old model includes spatial effects of diffusion, but treats only skunks. The new model which includes bat infection represents the confirmed rabies case data better. Higher concentrations of infected individuals are represented in the 2008 aerial view simulation which uses the new model. This observation is mirrored by the 2008 confirmed case data. A more even distribution of infected individuals is represented in the 2009 aerial view simulation which uses the new model. This observation is mirrored by the 2009 confirmed case data.

The number of infected bats does not fluctuate greatly. For the simulation to accurately reflect the confirmed case data, there should be a pocket of space in the center where there are no infected skunks. This may be due to a geographic barrier or the lack of suitable habitat for skunks in the urban settings. Bats, however, can adapt well to the urban area by foraging on the abundance of insects near lamp posts at night. Indeed, historical records demonstrate that three major focal areas with high concentrations of bat rabies cases are all clustered around big cities (Pool and Hacker, 1982). More accurate initialization of infected individuals and boundary conditions may be needed.

#### 5. Discussion

This investigation demonstrates the use of a simple spatio-temporal model to make inferences about drivers of local rabies epizootics and related wildlife rabies control measures. While other spatially explicit models have been developed to study the spatial distribution of rabies cases and evaluate the efficacy of public health control measures, they mainly focus on a single species (Broadfoot et al., 2001; Recuenco et al., 2011). In this study, a spatial model couples two reservoir host species with different manifestations of rabies infection, based on experimental evidence that bats, unlike skunks, are sometimes able to survive infection (Turmelle et al., 2010). Compared with a non-coupled spatial model for skunks, the coupled model demonstrates a closer fit with the actual spatial distribution map of skunk rabies occurrences. Thus this result provides insights into and supports the probability of spillover transmission of bat rabies virus to skunks, and the subsequent change in the spatial distribution of skunk rabies cases. Indeed, there is evidence that the south central skunk rabies virus variant that is prevalent in



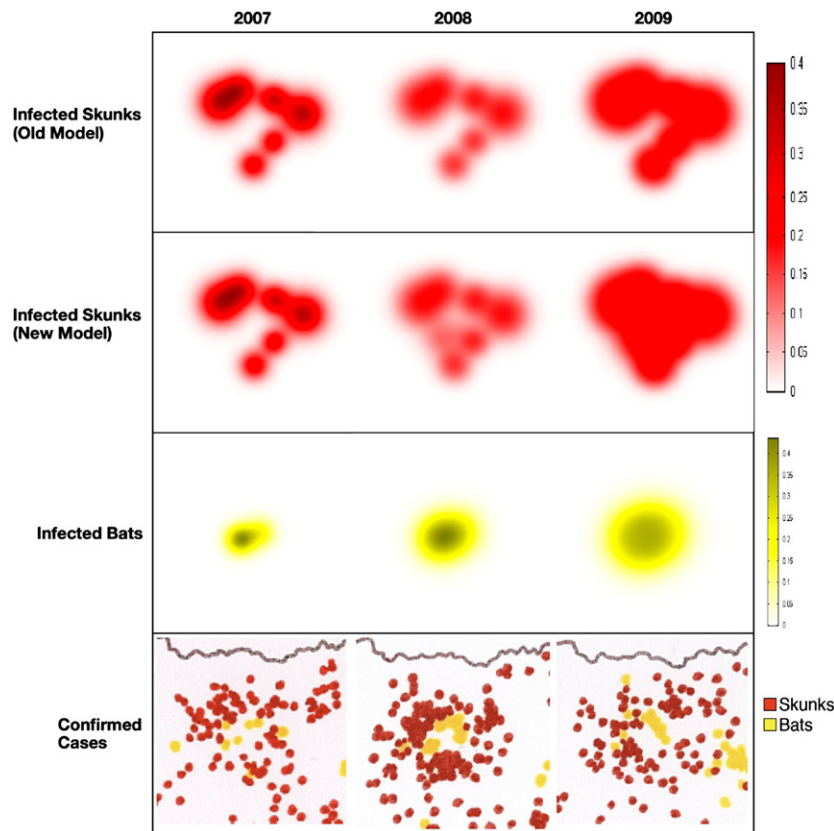


Fig. 3. Simulations and confirmed case data.

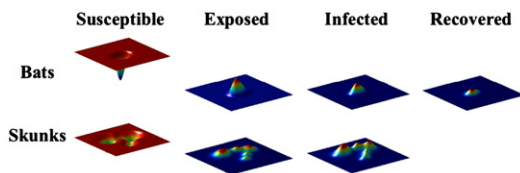


Fig. 4. Initialization of compartments.

Texas is significantly associated with the bat rabies virus variant, possibly resulting from fundamental bat–carnivore interactions (Rupprecht et al., 2011; Blanton et al., 2009, 2010). Although little evidence exists that corroborates continuous dependence of skunk rabies epizootic cycles on those of bats (Pool and Hacker, 1982), the continuous dependency in this model is assumed to be weak and still produces expected spatial effects of coupling.

Sampling and reporting bias serves as an important factor in surveillance, control, and studies of zoonotic diseases. Since available data on rabies cases are obtained from public sightings and individual encounters, as well as surveillance results from laboratory facilities, the initialization abundance of rabies occurrences varies strongly with public awareness, human population densities, and the availability of qualified reporting and processing infrastructures. With the coupling of two targeted reservoir species, the effect of reporting bias on study results can only be magnified. Consequently, any suggestions or observations obtained from this study should be considered preliminary. This simple model, however, is not designed to account for the impact of sampling and reporting bias due to its deterministic nature. Instead, this work sets the time frame as 2007–2009 and assumes that errors caused by sampling and reporting bias have not changed much during that period. Thus, in not seeking long-term prediction and evaluation, we can apply this model to

approximate the short-term spatial distribution of rabies, without making unwarranted extrapolations.

Sampling and reporting bias may arise naturally in virtually all scientific fields even when researchers are aware of it, simply because of the desire to report useful findings. This situation is far from ideal, but it does not undermine the reliability of the surveillance data. Therefore, the empirical data are usually adjusted for reporting bias before being used in modeling or other research practices. However, when comparing results obtained from our deterministic model with the rabies case distribution from empirical data, we did not adjust the data to account for the reporting bias, which is mainly due to the lack of knowledge about specific factors influencing the reporting bias, such as the distribution of reporting facilities and concentration of human population, and the extent to which these factors impact the efficacy of reported data. Hence, the absence of adjustment for sampling and reporting bias originating from human observations limits the application of our results to areas populated by humans. Consequently, our study and results cannot be applied to make inferences about interactions between skunks and bats in natural settings free of human influences. Additionally, since our simple model aims to provide preliminary insights into potential coupling of and interactions between two rabies reservoir populations, we opt not to implement any statistical tools in our study. As a result any inference based on our results without further adjusting the data for reporting bias will be limited by an incomplete statistical justification.

A relatively positive fit with real data is obtained from this study. However, this result does not preclude the possibility that other spatial models with characteristic designs exist that can produce qualitatively similar or better fits to the data. The implicit assumption of identical individuals often pervades simplistic and even sophisticated models of population dynamics. This tradition is reflected in the current model, despite the

possible age and sex differences in all kinds of model parameter values. Furthermore, seasonality plays a critical role in epizootiological processes and zoonotic disease emergence (Turmelle and Olival, 2009), but is also absent in this study. As additional data becomes available, the current study can be expanded to capture seasonal variation in gregarious behaviors such as migration and hibernation. Additionally, ring-like dispersal characterizes the results of the current model, unlike the usually observed wave-like dispersal of rabid animals and rabies cases (Guerra et al., 2003; Gordon et al., 2004). With the development of more complicated models, a framework can be constructed to include all of these effects and to conduct a statistical evaluation to select the most important new effects, with the goal of applying specific rabies control measures (Beyer et al., 2010).

This study also provides a means for selecting appropriate areas of research for target animals. Mesocarnivores, such as skunks, foxes, and raccoons, exhibit distinct preferences for habitat resources. Different geographical regions in Texas feature characteristic habitat resource abundances, generating varying degrees of population densities for skunks, foxes, and raccoons (Pool and Hacker, 1982). These geographical regions are known to be partitioned into biotic provinces associated with the prevalence of certain terrestrial mammals. Based on these results, areas with skunks as the predominant terrestrial mammals could be singled out, and the one with overlapping occurrences of bat rabies cases becomes the designated research area.

Our results show it is likely that spillover infection of bat rabies virus to skunks occurred. If laboratory analyses confirm this suggestion by isolating rabies of bat origin from rabid skunks in this area, our study will have practical implications for wildlife rabies control measures. Although the current model is simple and might not be able to offer specific and realistic guidelines for rabies control in wildlife, the possibility of additional skunk rabies dynamics resulting from bat–skunk interactions offers a way to optimize deployment of limited intervention resources. For free-ranging wildlife animals, intervention measures to control rabies epizootics are limited. Population reduction and trap–vaccinate–release (TVR) have been practised for a long time and were effectively adopted quite recently (Pybus, 1988). Oral vaccines have been successfully developed for gray foxes, raccoons, and skunks (Lyles and Rupprecht, 2007). Raboral V-RG is the only oral rabies vaccine licensed in the United States, and is known to produce insufficient levels of population immunity in skunks (Slate et al., 2005). For terrestrial animals, such as skunks, these vaccines are usually contained in bait which is scattered in foraging areas. Vaccination of bats via oral vaccine programs is generally not considered promising, due in part to bats' virtually unlimited access to refuge in houses and other dwellings (Slate et al., 2005), though other rabies control strategies such as topical anticoagulants have been used in hematophagous bats in Latin America with temporary success, exploiting their mutual grooming behavior at the roost (Flores-Crespo and Arellano-Sota, 1991; Streicker et al., 2012). Therefore, to control rabies in local skunk populations, a suggestion can be made from our study to employ a combination of population suppression, TVR, and oral vaccination surrounding the area where bat rabies have been frequently documented, in order to create a vaccination buffer zone, thus decreasing the chances of spreading rabies infections from bat–skunk interactions.

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