Modelling spread of foot-and-mouth disease in wild white-tailed deer and feral pig populations using a geographic-automata model and animal distributions[☆]

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ABSTRACT

We investigated how the size and distribution of wild deer and feral pigs – species that might act as potential foot-and-mouth disease (FMD) virus maintenance hosts – might affect the persistence and spread of FMD. We used a susceptible-latent-infected-recovered geographic-automata model and spatially referenced data from southern Texas, USA. Within this study area, 100 locations were randomly selected and FMD virus spread was simulated (50 simulations each) at each location. As expected, the predicted sizes (km^2) of the wild deer outbreaks were highly correlated ($r_{SP} > 0.95$) with the number of deer at incursion locations, the total number of deer within 2 km of incursion locations, and the minimum and maximum deer herd size within 2 km of incursion locations. However, the predicted sizes of the feral pig outbreaks were only moderately correlated (r_{SP} 0.63–0.67) with the total, maximum and variance of the number of feral pigs within 2 km of incursion locations. Lack of continuity within the feral pig herd distribution across the landscape makes predicting disease spread more difficult than for deer, a more homogenously distributed species. When assessing the potential of wild and feral animal species at a locality to act as maintenance hosts of FMD virus, estimates of the population size and distribution might serve as a useful indicator of potential outbreaks in some circumstances.

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1. Introduction

Foot-and-mouth disease (FMD), a highly contagious disease of cloven-hoof animals, can cause economically devastating outbreaks when incursions occur in countries previously free of infection (Ferguson et al., 2001). For example, an incursion in the United States might cost $14 billion (Paarlberg et al., 2002). However, this cost estimate does not include the potential for non-domesticated animal species to act as maintenance hosts of FMD virus.

Infection of uncontrolled wild and feral animal species would greatly complicate disease control measures. It is conceivable that in the presence of such infected populations, eradication would be unsuccessful in the short-term and the disease could become endemic (Pinto, 2004; Sutmoller et al., 2000).

In the 20th century, FMD virus was eradicated from the United States six times, the last outbreak occurring in 1929 (Bierer, 1939). During this phase of surveillance and stamping out, wildlife and feral animal disease maintenance populations presented a barrier to successful disease control. For example, during the 1924 outbreak of FMD in California, mule deer in the central portion of the state were infected. It took 2 years to eradicate FMD virus from the local deer population in one national park, and 22,000 deer were slaughtered. About 10% of deer

slaughtered in this outbreak showed lesions typical of FMD (McVicar et al., 1974; Fletcher, 2004). The presence of a feral pig population complicated FMD control measures during a 1924–1925 outbreak on a ranch near Houston, Texas (Fletcher, 2004).

Recently, the sizes of white-tailed and mule deer populations in the United States have been estimated at 30 and 12 million, respectively. Feral pigs are present in at least 44 states. High densities exist in parts of Texas, where the population size has recently been estimated at 1.5 million. It is unlikely that feral pigs will ever be eradicated: once a population becomes established in a locality, eradication is difficult, time consuming, and expensive. The home range of feral pigs may be as large as 50 km^2 for males during the breeding season. In areas of the United States where livestock are extensively grazed (such as in most parts of Texas), there is potential for interaction between cattle and FMD virus susceptible species such as wild white-tailed deer and feral pigs.

The conditions under which wild and feral animal species might become maintenance hosts of FMD virus, following an incursion into a country free of disease, are unknown. However, several factors – including population density and distribution, habitat requirements, social organization, age structure, home range, and barriers to dispersal – are likely to be important. The most recent outbreaks of FMD in the United States, which coincidently involved wild (deer) and feral (pigs) animal species, occurred in the 1920s.

Because of the paucity of information and experience with FMD in wild and feral animal species, simulation modeling is perhaps the only option for exploring the impact of an FMD virus incursion and therefore developing response plans and formulating policy (Taylor, 2003). Artificial life models, such as geographic-automata, treat space and time as discrete units and allow interactions to occur between local neighbors (Torrens and Benenson, 2005). The interaction between each population and its neighbors is based on a set of rules and states at earlier time steps. The repetitive application of transmission rules within this local neighborhood allows the replication of complex spatial behavior, such as disease outbreaks. Geographic-automata models can deal with complex initial conditions and geographical boundaries, are conceptually simple, and can model a variety of spatial interactions. A geographic-automata model has recently been developed to investigate FMD virus spread in wild and feral animal populations in Queensland, Australia (Doran and Laffan, 2005) and in Texas, United States (Ward et al., 2007).

Previous studies (Doran and Laffan, 2005; Ward et al., 2007) using the geographic-automata model have described the broad, potential spatial distribution of FMD infection in wild and feral animal populations in the event of an incursion. In contrast, our objective in this study was to use the previously developed geographic-automata model and spatial data describing population density distribution to identify some local population characteristics helpful for predicting localities where wild and feral animal species might form maintenance populations of FMD virus, should an incursion occur. In this study, we focused on the potential spread of FMD virus in wild and feral animal populations during the earlier phases of an incursion, prior to the likely detection of FMD in domestic livestock.

2. Materials and methods

2.1. The geographic-automata model

A previously developed geographic-automata model was used to simulate the spread of FMD virus infection through populations of wild deer and feral pigs (Ward et al., 2007). The population consists of groups of susceptible animals that form behavioral groups (herds). The herd is the unit of analysis, and disease spread is modeled via the interaction between these herds.

In this geographic-automata model (Ward et al., 2007), herds can pass sequentially through four model states: susceptible, latent, infectious and immune. The probability of FMD virus transmission from one herd to another is the product of the relative animal densities of the two herds, modified by the distance (km) by which they are separated. Within an *a priori* specified maximum neighborhood distance and up to a maximum number of neighbors, interactions between each infectious herd and its neighbors are evaluated. The conceptual model of disease transmission is shown in Appendix A.

Once a herd is infectious the second, third, and fourth transitions in the model depend on the specified length of the latent, infectious and immune periods. To incorporate chance into the model, interactions between an infectious herd and a susceptible neighbor occur when a value from a pseudo-random number generator is below their joint probability threshold (Appendix A).

2.2. Study site and animal distribution variables

The study site selected to simulate incursions of FMD virus is an area of southern Texas, USA, bordering Mexico, consisting of 9 counties (Fig. 1). The annual rainfall ranges between 750 and 1200 mm and the land area is approximately 24,000 km^2. Approximately 134,000 feral pigs (5.6/km^2) and 395,000 deer (16.4/km^2) are estimated to be present in this region. It is predominantly rangeland characterized by plains of thorny shrubs and trees, and scattered patches of palms and subtropical woodlands. The primary vegetation includes species such as mesquite, acacia, and prickly pear mixed with areas of grasses. Seasonal variation is characterized by hot, dry summers and mild, moist winters. Livestock production is predominantly extensive beef cattle grazing.

Herds of wild deer and feral pigs were the input data used to model the spread of FMD in this study. Herd distributions were created using geostatistical methods, land-use data and estimated ecological site carrying capacity, as previously described (Ward et al., 2007; Highfield et al., 2008). Briefly, data on the estimated total number of wild deer and feral pigs within the study area were obtained and disaggregated. Suitable land-use types were selected from the 1992 National Land Cover Dataset (NLCD), a raster with square cells of 1 km × 1 km resolution. The number of pixels per suitable land use type was multiplied by carrying capacity, as a weighting factor. The
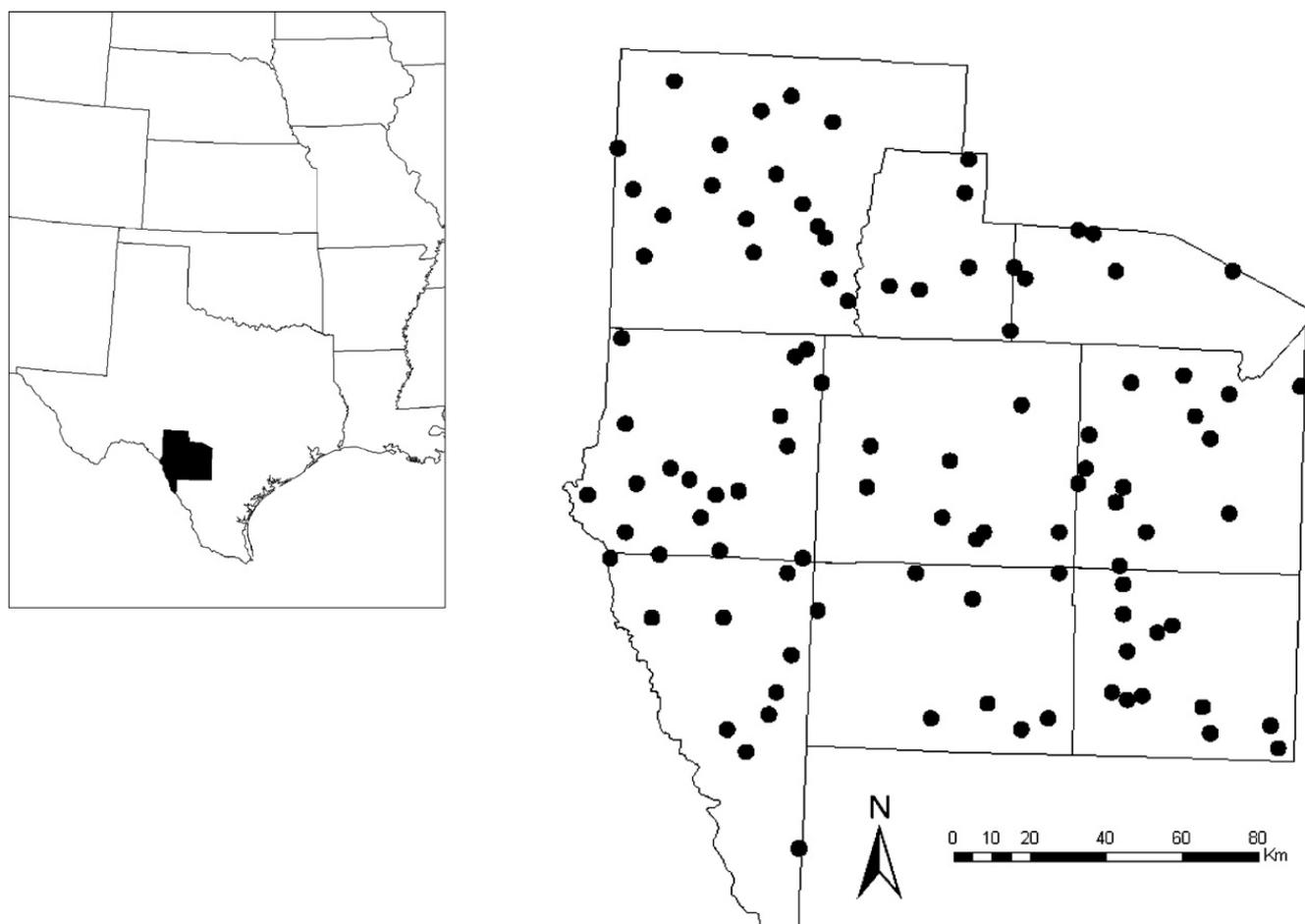
Fig. 1. One hundred locations randomly selected to investigate population characteristics that might predict the formation of maintenance populations of wild and feral animal species for FMD virus, should FMD virus be introduced. The location of the study area in Texas, USA, is shown as an inset.

estimated numbers of wild deer and feral pigs in the study area were then proportionally disaggregated. Thus, animal distributions were represented as number of animals per unit area (km^2), stored as raster density surfaces. Animals within each unit area represented a social group ("herd"). By using estimated population data sets, population density distribution and habitat requirements within the study area were explicitly incorporated in the model.

2.3. Simulations

We used a purpose-built geographic-automata model implemented using the Perl programming language. We used the same set of baseline model parameters as Ward et al. (2007). The assumed period of latency (minimum, maximum) for deer and feral pigs were 3–5 and 7–13 days, respectively, and the assumed duration of infectiousness (minimum, maximum) were 3–14 and 14–17 days, respectively. The duration of resistance to re-infection (minimum, maximum) was assumed to be 90–180 days for both species. We modeled FMD-induced mortality for herds in the infectious state using piecewise linear functions to specify the minimum and maximum fraction dead at each simulated time step (day). Values were drawn from a random distribution: in this study a constant value of zero was used for the minimum, and the maximum rate was drawn from a triangular (two piece linear) distribution with

zero at the first and last time steps and a peak at a specified time step. We assumed that the peak maximum FMD-induced mortality was 1.5%, with this peak occurring at the midpoint of the infection period for each herd that was infected. Using these parameters, the total FMD-induced mortality in simulations – for both wild deer and feral pigs – was approximately 5%. Within the geographic-automata model, the maximum distance at which neighboring herds could interact with each infected herd (equivalent to a home range) was assumed to be 2 km. The transmission of disease between an infected herd and a susceptible herd was assumed to depend on both the distance separating the herds (modeling by a spatial kernel) and the relative density of animals in the herd. A density scaling parameter of 30/km^2 for deer and 40/km^2 for feral pigs was used to represent high density locations where disease transmission would almost certainly occur because of the number of animals present. These scaling parameters were arbitrarily set, based on the frequency distributions of deer and feral pig populations within the study area.

The potential spread of FMD virus infection through the landscape was modeled separately for wild deer and feral pig populations. Within the study area, 120 locations were randomly selected by using a random number generator (Microsoft® Office Excel. Microsoft Corporation, Redmond WA, 2003) to generate x (longitude) and y (latitude) coordinates within the range of 98.8–100.8°W and 28.2–

30.3°S, respectively. Projecting these locations using a shape file of the 9-county region (GCS North American Datum 1983) within a GIS (ArcMap^{TM} version 9.0, ESRI® Inc., Redlands CA, 2004), the first 100 locations that lay within the study area were selected (Fig. 1). For each animal species, the spread of FMD virus infection at each site was simulated. The model was simulated 50-times for each location for each animal species, so that a total of 10,000 model runs were performed. We simulated the model to represent a time period of 100 days.

2.4. Data analysis

The outcomes of interest were the sizes (area infected, km^2) of wild deer and feral pig outbreaks in each of the 100 simulated incursions. Since deer and feral pig distributions were represented as 1 km^2 rasters (projected using a GCS North American Datum 1983 shape file of the study area), the outcome was simply measured as a count of the number of grid cells in which the animal population status was 'infected' at any time during the 100 day simulated period. We were interested in predicting outbreak size from animal distribution characteristics within the vicinity of each simulated incursion. Potential predictors of outbreak size investigated were the animal distribution variables described previously (deer per km^2 and feral pigs per km^2 at incursion locations), together with additional variables created from these animal distribution variables: the total animal population size within 2 km of each incursion, and the minimum, maximum and variance of herd sizes within 2 km of each incursion. For the latter, we created a 2 km radius buffer around each incursion location (Analysis Tools. ArcMap^{TM} version 9. ESRI® Inc., Redlands CA, 2004). Projected animal distributions were clipped using this buffer (Analysis Tools. ArcMap^{TM} version 9. ESRI® Inc., Redlands CA, 2004) and statistics describing the populations within 2 km of each incursion were calculated (ArcMap^{TM} version 9. ESRI® Inc., Redlands CA, 2004). These statistics were the total size of the population within 2 km of each incursion ('total'), the size of the smallest (minimum) and largest (maximum) individual herd within 2 km of each incursion, and the variance of the herd sizes within 2 km of each incursion (Appendix B).

In addition, the spatial distribution of wild deer and feral pigs within 2 km of each outbreak location was described by a geographically local Moran's spatial autocorrelation statistic, I (Anselin, 1995). This statistic is a measure of the attribute similarity of spatial locations. A value of zero indicates an unstructured ("random") spatial distribution with respect to the attribute of interest. A positive I value results when each location tends to be surrounded by similar values ("clustering"), whereas a negative I value results when each location tends to be surrounded by dissimilar values ("overdispersion"). In this study, we were interested in the spatial distribution of wild deer and feral pig herd sizes. Thus, I was calculated for both wild deer and feral pig herds within 2 km of each outbreak location (a local calculation, $n = 12$), using herd size as the weighting (attribute) factor (Spatial Statistics. ArcMap^{TM} version 9. ESRI® Inc., Redlands CA, 2004).

For each of the 100 incursion locations, the 50 simulations performed for each species were summarized by calculating means. The median and interquartile range of these summary statistics were then calculated. The association between the outcome of interest – the size of wild deer or feral pig outbreaks – and potential predictor variables was estimated using Spearman's rank correlation (Statistix 7.0. Analytical Software, Tallahassee FL, 2000).

3. Results

A description of outbreak size and potential predictors of outbreak size, for simulated spread of FMD in wild deer and feral pig populations within the study area, is shown in Table 1. The median predicted outbreak size (km^2) for deer was approximately 3-times greater than for feral pigs, and considerably more variable.

The size of simulated FMD outbreaks in deer populations was highly correlated with the size of the deer population at incursion locations (r_{SP} 0.976, $P < 0.0001$; Fig. 2), the total deer population within 2 km of incursion locations (r_{SP} 0.994, $P < 0.0001$; Fig. 3), and the minimum (r_{SP} 0.976, $P < 0.0001$) and maximum (r_{SP} 0.964, $P < 0.0001$) size of deer herds within 2 km of incursion locations. The correlation between the size of simulated FMD outbreaks and variance of deer herds within 2 km of incursions was 0.694 ($P < 0.0001$). The correlation (r_{SP} −0.029) between the size of outbreaks and the spatial distribution of deer herds within 2 km of outbreak locations was not statistically significant ($P = 0.7764$).

The size of simulated FMD outbreaks in feral pig populations was moderately correlated with the total feral pig population within 2 km of incursion locations (r_{SP} 0.674, $P < 0.0001$; Fig. 3), the maximum (r_{SP} 0.634, $P < 0.0001$) size of feral pig herds within 2 km of incursion

Table 1

The predicted size (km^2) of outbreaks of foot-and-mouth disease in populations of wild deer and feral pigs in southern Texas, and population size and distribution explanatory variables.

Variable	Wild deer	Feral pig
Median predicted outbreak size, km^2	46.3 (15.4–87.1)[a]	14.3 (14.0–14.7)
Median number of animals at incursion locations	11 (5–24)	1 (1–2)
Median total number of animals <2 km of incursion locations	466.5 (70–1967)	33.5 (14–108)
Minimum total number of animals <2 km of incursion locations	8 (4–17)	1 (1–1)
Maximum total number of animals <2 km of incursion locations	12 (5–31)	12 (2–34)
Variance of animal herd sizes <2 km of incursion locations	1.3 (0.2–4.6)	11.6 (0–124)
Number of locations at <2 km was uniform	3	27
Median autocorrelation statistic <2 km	0.01 (−0.06 to 0.14)	0.01 (−0.03 to 0.07)

[a] Interquartile range.

$r_{SP} = 0.976$

$r_{SP}\ 0.232$
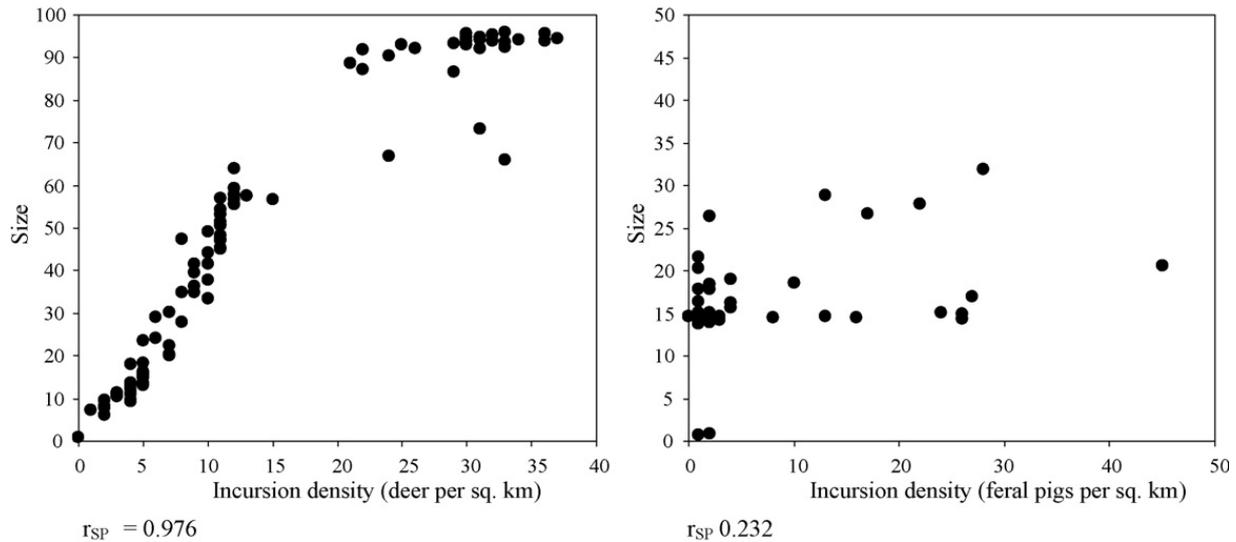
Fig. 2. Scatterplots of the size (km²) of predicted FMD outbreaks at 100 locations in southern Texas, versus density of animal populations (km²) at the 100 FMD virus incursion locations for wild deer (left) and feral pigs (right). Spearman rank correlation statistics are shown.

$r_{SP} = 0.994$

$r_{SP}\ 0.510$
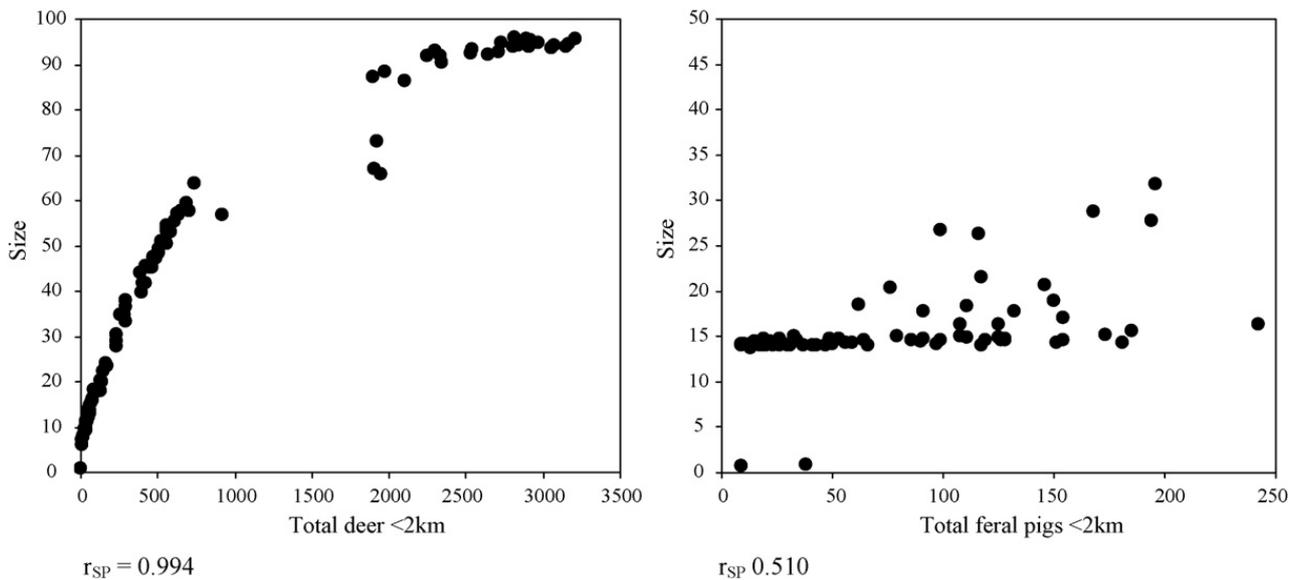
Fig. 3. Scatterplots of the size (km²) of predicted FMD outbreaks at 100 locations in southern Texas, versus density of animal populations within a 2 km radius of the 100 FMD virus incursion locations for wild deer (left) and feral pigs (right). Spearman rank correlation statistics are shown.

locations, and the variance of feral pig herds within 2 km of incursion was (r_{SP} 0.626, $P < 0.0001$). The correlation between the size of outbreaks and the size of feral pig herds at incursion locations (r_{SP} 0.382, $P = 0.0009$; Fig. 2), the minimum size of feral pig herds within 2 km of incursion locations (r_{SP} 0.363, $P = 0.0017$), and the spatial distribution of feral pig herds within 2 km of outbreak locations (r_{SP} 0.116, $P = 0.3279$) was poor.

4. Discussion

The initial size of simulated outbreaks of FMD in deer increased as the deer density at the incursion location, and measures of density within 2 km, increased. The size of the outbreaks also increased as the deer density within 2 km became more variable, but was not related to the spatial distribution of herds. For simulated outbreaks in feral pigs,

the relationship between the size of outbreaks and population characteristics was more complex: although larger outbreaks occurred with more dense and more variable populations within 2 km of incursion locations, the size of outbreaks was poorly correlated with the size of feral pig herds at incursion locations.

FMD virus spread was simulated in this study using a geographic-automata model in which the probability of FMD virus transmission from one herd to another is the product of the scaled relative size of the two herds, modified by the distance by which they are separated (Appendix A). Thus, it is not surprising that in both wild deer and feral pigs, a metric of the density of animals within the vicinity of an incursion is important in determining the size of the outbreak.

Although the size of simulated FMD outbreaks in deer populations was highly correlated with the size of the deer

population at incursion locations (r_{SP} 0.976), the size of outbreaks in feral pig populations in comparison was only poorly correlated (r_{SP} 0.382) with size of feral pig herds at incursion locations. Furthermore, the correlation between outbreak size and the variance in herd sizes within 2 km of outbreak locations was similar (r_{SP} approximately 0.6–0.7) in both species models. Although measures of spatial dispersion of animal distributions within 2 km of outbreak locations (Moran's autocorrelation statistic) were not strongly correlated with the size of outbreaks, for pigs this variable was relatively more important (r_{SP} 0.116, versus 0.674 for the total feral pig population within 2 km of incursion locations) than for deer (r_{SP} −0.029, versus 0.994 for the total feral pig population within 2 km of incursion locations).

At a fine scale, the estimated distribution of deer in this study area is relatively uniform (herd size standard deviation < mean herd size; coefficient of variation, 0.83), with population densities changing gradually over large spatial distances. Disease spread over space is both scale- and pattern-dependent. At the fine scale, a tendency towards a relatively unstructured mix of dense and sparse animal populations might facilitate disease spread. However, at a greater scale the stronger the structured pattern of the population distribution (areas of high population density separated by areas of low density), the greater is the barrier to disease spread. In the latter case, we would expect localized outbreaks of disease that are unconnected to other outbreaks within the region. For example, at a fine spatial scale the distribution of feral pig populations in the study area is highly unstructured (herd size standard deviation > mean herd size; coefficient of variation, 1.93). There are substantial areas between highly dense feral pig localities (generally areas in which water features such as creeks and ponds can be found) where feral pig populations are estimated to be low (only 1–2 pigs per km²). Thus, if the population distribution is unstructured, this might present a barrier to establishment of the infection in a population at a larger spatial scale. This is in agreement with some theoretical conclusions regarding the effect of local spatial heterogeneity on disease invasion and spread (Keeling, 1999). Also, in some other simulation studies, it has been found that increased spatial variation in the local density of hosts decreased the proportion of the host population infected during an epidemic (Caraco et al., 2001).

In both wild deer and feral pig models, the maximum size of animal herds within 2 km of incursion locations were correlated with the size of simulated FMD outbreaks. In aspatial mathematical models of infectious disease spread, disease extinction is a recognized phenomenon: without a sufficiently large population of susceptible individuals, infectious diseases tend to fade-out because of a reduction in the effective reproductive number below the threshold value of 1. This theory has been used to explain some observations of the natural history of diseases such as measles in island or isolated communities, based on the "critical community size" (Keeling and Grenfell, 1997). The same principles may apply in the case of disease spread across the landscape: if insufficient connectivity is present in a population (represented by at least one 'large'

population within the local neighborhood), then disease extinction might occur. This has important implications for disease control and eradication when an uncontrolled host species, such as feral pigs or wild deer, are infected with a foreign animal disease. In this case, the host density and the spatial distribution and structure of the population need to be considered before mitigation strategies are implemented.

The geographic-automata model is particularly suited to simulating disease spread in feral- and wild-animal populations: geographic variations can be explicitly included by developing appropriate animal population distributions. However, further model development is needed to address the temporal variations in wild- and feral-animal populations, and assumptions regarding home range. In a previous study (Ward et al., 2007), simulated outbreaks of FMD failed to develop in some model runs. If susceptible animal population densities are low then FMD virus might become extinct within specific localities before it is able to infect a critical number of animals (Durand and Mahul, 2000). The conditions (including population density, season and landscape) that might lead to such extinction of FMD need to be better defined.

In the absence of significant airborne infection and following imposition of movement restrictions, FMD spread in domestic livestock populations is presumed to occur from neighbor-to-neighbor according to a constant transmission probability on a fixed lattice (Kao, 2001). In these situations, there is a critical transmission probability above which spread will continue indefinitely, and below which it will die out. A similar self-limiting effect occurs when the number of neighbors falls below a critical value. In simulation studies, Kao (2001) suggested that a higher connectivity of farms (greater nearest neighbor index) enhanced FMD transmission and epidemic propagation. The regional variation in "local disease spread" (within a neighborhood of up to 3 km) in the 2001 United Kingdom outbreak (Gibbens et al., 2001) may be a reflection of this spatial heterogeneity. Although it is difficult to make direct comparisons between the potential spread of FMD virus in wildlife populations and FMD virus spread between domestic herds of livestock, uniformity (overdispersion) of wildlife populations is the equivalent to the phenomenon of higher connectivity within livestock distributions. Although patches of high wildlife density are likely to lead to initial rapid spread of disease, without a broader connectivity of the populations, disease spread might be suppressed over the longer term.

The relationship between outbreak size and size of the animal populations within 2 km of the incursion location (Fig. 3) suggests that a threshold phenomenon may exist. For deer, above average (47.8 km²) outbreaks corresponded to locations in which >500 deer were estimated to exist within a 2 km radius, a density of about 40 deer per km² (1 per 2.5 ha). For feral pigs, above average (15.2 km²) outbreaks corresponded to locations in which >50 feral pigs were estimated to exist within a 2 km radius, a density of about 4 feral pigs per km² (1 per 25 ha). This information could be used to identify areas at-risk of FMD spread in wild and feral animal populations, in anticipation of potential FMD virus incursions. Such risk maps could also

be useful during the control phases of an FMD outbreak. For example, areas in which wild deer and feral pig populations within a 2 km radius exceed 500 and 50, respectively, could be targeted with surveillance so that infection of these potential FMD virus maintenance populations can be detected earlier. Alternatively, a greater level of surveillance of domesticated animal species might be incorporated into surveillance programs to increase the effectiveness of control. This might prevent the disease becoming endemic in the susceptible animal populations.

In this study, the issue of edge effect was ignored. Edge effect is a form of spatial censoring (Lawson, 2001), in which spatially correlated data within the study area (in this case, the 9-county area) are related to unobserved data outside the study area (bordering Texas counties and Mexican states). Locations at which FMD incursions were simulated in this study were randomly selected. There were 8 locations that were within 2 km of the border of the study area. The measured outbreak size of these locations were likely underestimated, but so too probably were predictors of outbreak size. Given the focus on initial disease spread, edge effect is unlikely to have biased results in this study.

The spatial distribution of herds within 2 km of outbreak locations were characterized using Moran's autocorrelation statistic, I. The statistic does not differentiate between situations in which the spatial distribution of the attribute (herd density) is uniformly high or uniformly low. In the case of simulated FMD spread modeled using the geographic-automata model, locations in which the animal density distribution is uniformly high would be expected to produce the large outbreaks. Other metrics might be more appropriate for characterizing the patchy distribution of animal density that are expected to influence the spread of FMD across a landscape.

The rank correlation statistic was used in this study as a measure of association between simulated outbreak size and animal population predictors. Our ability to detect important associations between feral pig outbreak sizes and predictors might have been reduced by the distribution of the data: 90% of predicted deer outbreaks ranged in size from 8 to 95 km², whereas 90% of predicted feral pig outbreaks ranged in size from 14 to 22 km².

The focus of this study was on the predicted spread of FMD during the early phase of an incursion. Other factors – such as disease-induced mortality, and the assumed periods of infectiousness and immunity – are likely to become more important in determining the longer-term outcome of an incursion in the absence of disease mitigation strategies. The values of such disease parameters are highly uncertain, presenting a challenge to modeling longer-term disease spread.

5. Conclusions

The number of animals present at the site of incursion of a disease such as FMD, and within the immediate vicinity, is important in determining the outcome of such an incursion in the case of a disease whose spread is density-dependent. However, the outcome of a disease incursion might also vary, depending on the spatial distribution of the species affected. These landscape characteristics should be considered when designing and implementing disease mitigation strategies for foreign animal disease such as FMD, if involvement of a wild or feral animal species is anticipated.

Conflict of interest

None declared.

Appendix A

A conceptual framework for modeling disease transmission using a geographic-automata model, for a case where the population is represented as a square lattice. Assume that each cell represents a herd, with the numbers representing the number of animals within the herd (1A).

0	3	0	1	1							0		
3	2	1	1	3						0.016	0.008	0.008	
9	4	7	2	1		→		0.070	0.031		0.016	0.008
8	5	6	1	1					0.039	0.047	0.008	
6	4	2	1	2						0.016		
			1A									1B

If the center herd is assumed to be infected (bold outline) and infectious, the probability of an interaction between herds, and thus transmission of the disease, is the product of the scaled herd densities modified by a spatial kernel calculated as a bandwidth divided by the distance between the herds. The kernel also has a maximal distance beyond which it has a value of zero. For example, if these represent deer herds placed within 1 km × 1 km cells, herd-to-herd contact is assumed to occur over a maximum distance of 2 km, a scaling density of 30 is used, and the bandwidth is set at 1 km (Ward et al., 2007), then the following 12 potential transmissions would be evaluated (before adjusting by the spatial kernel): $[(7 \div 30) \times (0 \div 30)] = [7 \times 0] \div 30^2; [7 \times 2] \div 30^2; [7 \times 1] \div 30^2; [7 \times 1] \div 30^2; [7 \times 9] \div 30^2; [7 \times 4] \div 30^2; [7 \times 2] \div 30^2;$ $[7 \times 1] \div 30^2; [7 \times 5] \div 30^2; [7 \times 6] \div 30^2; [7 \times 1] \div 30^2;$ and $[7 \times 2] \div 30^2$, so that the base transmission probabilities shown in 1B result. On this basis, the herd shown with darkest shading in 1B is the most likely to become infected (probability = 0.07). However, when adjusting for distance using the spatial kernel, it is the herd shown with darkest shading in 1C that is most likely to become infected (probability = 0.047).

0	3	0	1	1					0		
3	2	1	1	3				0.011	0.008	0.006	
9	4	7	2	1		→		0.035	0.031		0.016	0.004
8	5	6	1	1				0.027	0.047	0.006	
6	4	2	1	2					0.009		
				1A							1D

Appendix B

An example of how predictors of outbreak size were calculated in a simulation study of the potential spread of foot-and-mouth disease in wild and feral animal populations using a geographic-automata model. If the center cell was the incursion site, the herd size at the incursion site, the total animal population size within 2 km of each incursion, and the minimum, maximum and variance of herd sizes within 2 km of each incursion would be 7, 41, 0, 9 and 7.81. Moran's autocorrelation (I) for this distribution, weighting by inverse-distance squared, is 0.08 (clustered).

0	3	0	1	1
3	2	1	1	3
9	4	7	2	1
8	5	6	1	1
6	4	2	1	2

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