

Disease spread models in wild and feral animal populations: application of artificial life models

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Summary

The role that wild and feral animal populations might play in the incursion and spread of important transboundary animal diseases, such as foot and mouth disease (FMD), has received less attention than is warranted by the potential impacts. An artificial life model (Sirca) has been used to investigate this issue in studies based on spatially referenced data sets from southern Texas. An incursion of FMD in which either feral pig or deer populations were infected could result in between 698 and 1,557 infected cattle and affect an area of between 166 km² and 455 km² after a 100-day period. Although outbreak size in deer populations can be predicted by the size of the local deer population initially infected, the resulting outbreaks in feral pig populations are less predictable. Also, in the case of deer, the size of potential outbreaks might depend on the season when the incursion occurs. The impact of various mitigation strategies on disease spread has also been investigated. The approach used in the studies reviewed here explicitly incorporates the spatial distribution and relationships between animal populations, providing a new framework to explore potential impacts, costs, and control strategies.

Keywords

Deer – Feral pig – Foot and mouth disease – Geographic automata – Simulation model – Spatial analysis – Texas – Wildlife.

Introduction

An incursion of foot and mouth disease (FMD) in a country previously free of infection can have severe economic, animal welfare and social impacts (9). The cost of an incursion in the United States has been estimated at US\$14 billion (29). However, this estimate does not account for the potential of non-domesticated animal species to act as reservoir hosts of foot and mouth disease virus (FMDV). If uncontrolled wild and feral animal species were infected – either as the index case or because of spill-over from domesticated species – disease control would be more difficult, the outbreak might take longer to control, and the area affected could be larger. 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 (32, 34). In such a scenario, zoning of disease-free and infected areas would also be difficult to accomplish.

In the 20th Century, FMDV was eradicated from the United States six times, with the last outbreak occurring in 1929 (5). During this phase, the infection of wildlife and feral animal populations complicated disease control efforts. For example, mule deer were infected during the 1924 FMD outbreak in central California. It took two years to eradicate FMDV from the local deer population in one national park, and 22,000 deer were reportedly slaughtered in this park (11, 26). As a second example, the presence of feral pigs on a ranch near Houston, Texas, had to be taken into consideration during the eradication programme implemented following an FMDV incursion in 1924 (11).

Recently, the sizes of white-tailed and mule deer populations in the United States have been estimated at 30 million and 12 million, respectively. Feral pigs are present in at least 44 states. They exist in high densities 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 from Texas: once a population becomes established in a locality, eradication is difficult, time-consuming and expensive. In areas where livestock are extensively grazed (as is the case in most parts of Texas), there is potential for contact between grazing cattle and FMDV-susceptible species such as wild white-tailed deer and feral pigs.

There is both a paucity of information and a lack of experience with FMD in wild and feral animal species in the United States. In such circumstances, simulation modelling is perhaps the only option for exploring the impact of an FMDV incursion and, therefore, for developing response plans and formulating policy (35). Disease outbreaks are spatio-temporal phenomena for which artificial life models such as geographic automata are one useful modelling approach. Geographic automata models treat space and time as discrete units and allow interactions to occur between local neighbours (36). The interaction between each population and its neighbours can be modelled as a set of simple rules. The repetitive application of these rules allows simulation of the complex spatial behaviour of epidemics over time. A geographic automata model has recently been developed to investigate FMDV spread in wild and feral animal populations in Queensland, Australia (6), and in Texas in the United States (39, 40). This paper reviews and summarises the application of this modelling system for developing response plans and formulating policy in anticipation of an FMDV incursion in which wild and feral animal populations might be involved.

The geographic automata model – Sirca: susceptible-infected-recovered cellular automata

By incorporating the conceptual susceptible-latent-infected-recovered (SLIR) framework, the automata modelling approach has been used to investigate the theoretical basis of disease spread phenomena (1, 8, 10, 20). However, application of this class of models to specific disease situations is much less common (4). This approach was first used by Doran and Laffan (6) using a GIS macro script to model infectious diseases in non-domesticated animal populations and the spread of disease from these animals to livestock. Subsequently, a purpose-built geographic automata model was implemented using the

Perl programming language (Sirca: susceptible-infected-recovered cellular automata) and generalised to a geographic automata model.

Model structure

To model the spread of disease through a population, the authors assume that individuals within this population exist at mutually exclusive locations. Individuals could be individual animals, herds or other functional groups, villages or regions. This modelling approach also assumes homogenous mixing within – but not between – population units. Because of the importance of contact in determining the spread of infectious diseases, matching the scale of analysis to the functional animal grouping (e.g. the herd) is recommended.

For each unit – such as the herd – the minimum requirement for simulating disease spread is knowledge of the location of the unit. Additional information can be included in the model. An important variable for disease spread is often the size or density of the herd. For models of the incursion of infectious disease in a population, it can usually be assumed that each herd is susceptible. In the case of endemic-disease modelling, information about the disease status of each herd would need to be known (for example, via a survey) or assumed.

Using a SLIR framework, the authors assume that population units can pass through four disease states: from susceptible to latent, from latent to infectious, from infectious to recovered and, finally, back to susceptible. These transitions partially determine the dissemination rate of the disease between units.

The first transition depends on contact rates between susceptible and infectious population units, and the probability of disease transmission given contact. When the infected population unit is infectious, disease transmission can occur at any time. Thus, estimates of the disease coefficient of transmission (β) or the basic reproductive rate (R_0) can be used to calculate the transmission rate. Alternatively, the population structure can be used to estimate transmission. For example, transmission can depend on the relative densities or sizes of the susceptible and infectious population units. The strength of the automata modelling system is the implicit incorporation of the spatial structure of the population into the model system. This spatial distribution is incorporated via its influence on contact rates. The modellers can specify distance-dependent contact rates based on either the spatial distance between population units or the neighbourhood arrangements of these units.

In the current version of the Sirca model, the contact between population units (herds) depends on the density

of susceptible animals in each pair of units. This joint probability is adjusted using the inverse distance between the units (expressed as a fraction of a pre-specified bandwidth – for example, 1,000 m – and linearly scaled into the interval [0,1]). Non-linear and discontinuous functional forms can be used when they are supported by known responses. For each animal species, contacts between each neighbour of an infectious population, within an *a priori* specified maximum neighbourhood distance and maximum number of neighbours, are evaluated. Contacts between populations of animal species (e.g. deer–cattle, feral pig–cattle) are assumed to occur with the neighbour nearest to each species-specific infectious population, within the maximum neighbourhood of this infectious population. Within the SLIR framework, the second, third and fourth transitions are generally assumed to depend on species-specific characteristics of the disease – the incubation period, rate of development of immunity, and rate of loss of immunity, respectively. Disease-induced mortality in Sirca is modelled using piecewise linear functions to define the maximum and minimum mortality rates over time.

Animal spatial distributions

Critical factors for modelling the spread of infectious disease include the size and geographical density of susceptible populations and the connectivity of susceptible species distributions (7). These can be efficiently represented by spatial data sets of the susceptible population. Thus, the first step in modelling the spread of disease through wild and feral animal distributions is to develop a spatial representation of those distributions. However, commonly, such information is unavailable for a given study area. There are different geo-statistical methods of deriving such distributions. For example, Doran and Laffan (6) used a feral pig density and distribution map (provided by a government agency – the Australian Bureau of Rural Sciences) in which densities used were low, medium and high, and were based on questionnaires and aerial surveys (41). In most cases, information on feral and wild animal distributions is spatially coarse and must be disaggregated to an appropriate spatial scale for modelling the spread of disease. Finer-scale spatial data can be derived through a range of methods. Doran and Laffan (6) used knowledge of seasonal behaviour and habitat information to derive finer spatial distributions of feral pigs for the purposes of modelling FMD spread. Domestic livestock distributions are generally based on census information, but these might also need to be disaggregated from the measuring unit.

The methods used to disaggregate spatial animal data – particularly those on feral and wild animal species – can have a substantial effect on the disease modelling process and the conclusions drawn. For example, in a study using

the Sirca model and the spread of FMD through wild white-tailed deer in south Texas, Highfield *et al.* (17) examined the influence of 15 geo-statistical methods applied to the data available – county-level estimates of the number of deer per reporting sampling unit and per county (25). The estimated number of deer in the study region, based on the geo-statistical estimation procedure used, ranged from 386,000 to 768,000. The predicted magnitude of the FMD outbreaks ranged from approximately 1,500 to 9,000 deer infected and 50 km² to 450 km² affected. How animal populations are represented must be considered in all spatial disease spread models.

Model parameterisation

In the Sirca model, contact between population units is based on distance. For feral and wild animal species, the home range is critical for defining the potential contacts that must be evaluated for each day simulated. For example, Highfield *et al.* (17, 18, 19), in their studies, assumed the home ranges of deer in the study area were 2 km and that no interactions took place beyond this distance. Ward *et al.* (39) examined the influence of the assumed home range of feral pigs and wild deer on FMD spread, using the Sirca model. Increasing the potential number of neighbouring populations increased the size of the outbreak. This increase was greatest between first- and second-order neighbour interactions. In the study area, the effect was more pronounced in feral pig populations, because of the more heterogeneous distribution of this species.

To incorporate stochasticity into the model, interactions between a susceptible location and an infectious neighbour occur when a random number from a pseudo-random number generator (PRNG) is below the assigned probability threshold of disease transmission for that pair of susceptible and infectious units being considered. The randomness of sequences generated using PRNGs is crucial to model results; however, the quality of these algorithms varies significantly and many display serial correlations and suffer from other issues of non-randomness (37). To reduce these effects, the Mersenne Twister mt19937 algorithm (27) is used, which has a large period length before the sequence of random values repeats ($2^{19937}-1$) and good spectral properties. In addition, correlation structures within the random number sequence are very small.

Once a population unit is infectious, the second, third, and fourth transitions in the model depend on the length of the latent, infectious and immune periods. In feral and wild animal species, these parameters are uncertain and must often be extrapolated from relevant studies on corresponding domestic animal species. For example, Ward *et al.* (39) used values for white-tailed deer

populations from two experimental studies (12, 15). In the Sirca model, values are assigned randomly within the corresponding parameter ranges using a uniform distribution.

The potential FMD-induced mortality in feral pigs and wild deer populations is, likewise, uncertain. Within the Sirca model, a sensitivity analysis has been conducted by varying the minimum and maximum FMD-induced mortality from nil to 1.5% per day during the period of infection, and by setting maximum mortality to occur at 25%, 50% (mid-point) or 75% of the infection period. Model results were found to be insensitive to these assumptions (39).

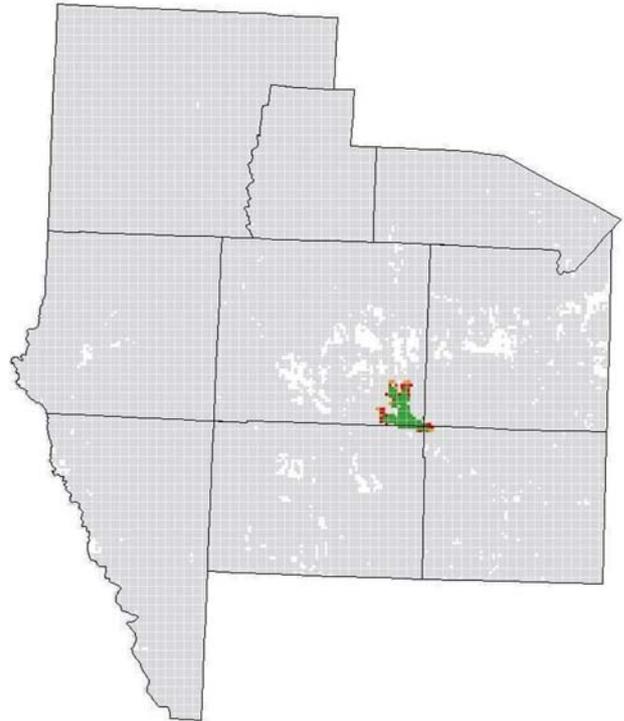
Applications

The authors have used the Sirca model to examine the potential spread – and policy control implications – of an incursion of FMDV that might involve either feral pigs or white-tailed deer in south Texas (17, 18, 19, 39, 40). Their studies focused on an area consisting of nine counties in southern Texas, bordering Mexico. Within this area there are estimated to be approximately 85,000 domestic cattle (3.5/km²), 134,000 feral pigs (5.6/km²) and 395,000 white-tailed deer (16.4/km²). The spatial distributions of feral pigs and deer were derived using land-use data and information on the estimated carrying capacity of the ecological site, as described above. All animal information was converted to raster surfaces in which a raster pixel (1 km²) was assumed to represent a functional unit, that is, a herd of cattle, feral pigs or deer. Examples (a single model simulation) of the predicted spread of FMD from a single incursion site in feral pigs 100 days and 365 days post incursion are shown in Figure 1. Figure 2 shows the predicted spread of FMD in cattle herds from multiple incursions in feral pigs 100 days and 365 days post incursion.

Some of the important findings from the studies included:

- an uncontrolled FMD outbreak initiated in feral pigs and in wild deer might infect up to 698 (90% prediction interval [PI], 181–1,387) and 1,557 (90% PI, 823–2118) cattle and affect an area of 166 km² (90% PI, 53–306) and 455 km² (90% PI, 301–588), respectively
- the predicted spread of FMDV infection is most sensitive to the assumed number of neighbourhood interactions between herds. In simulated FMD outbreaks in deer, the Sirca model is also sensitive to the assumed latent period. How these parameters are estimated is likely to be critical in studies on the impact of FMD spread in situations in which wildlife reservoirs might potentially exist

a) 100 days post introduction



b) 365 days post introduction

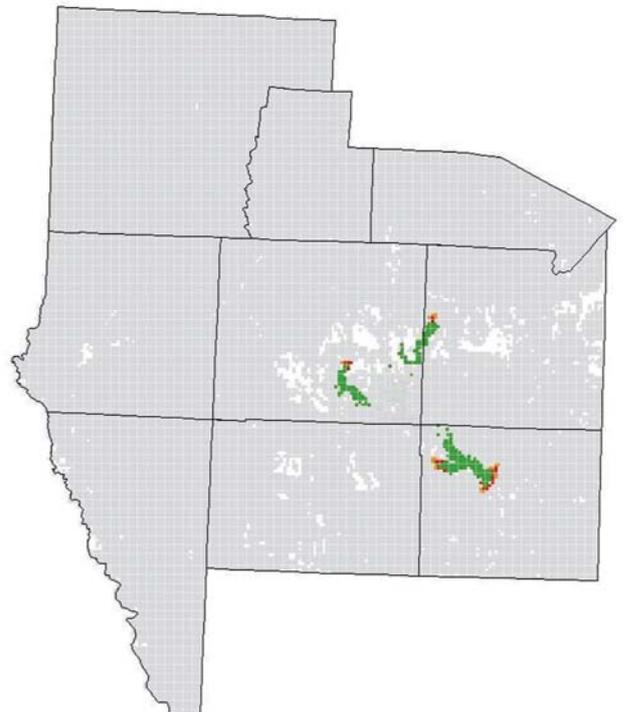
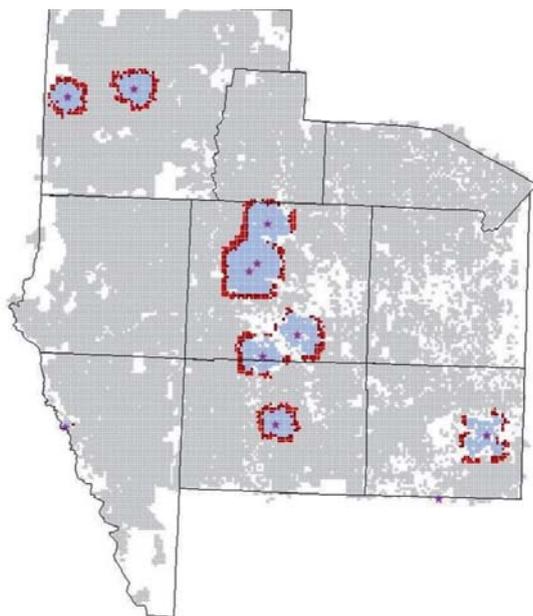
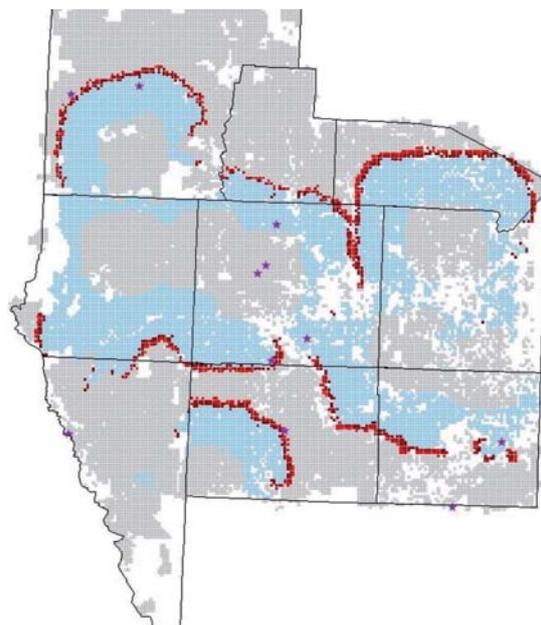


Fig. 1
Predicted spread of foot and mouth disease within feral pig populations in an area of southern Texas, United States, using a susceptible-infected-recovered cellular automata model (Sirca)
 Green cells represent recovered populations, whereas orange and red cells represent latently-infected and infectious populations

a) 100 days post introduction in feral pigs



b) 365 days post introduction in feral pigs

**Fig. 2**

Predicted spread of foot and mouth disease within cattle herds in an area of southern Texas, United States, after multiple incursions in feral pig populations, using a susceptible-infected-recovered cellular automata model (Sirca)

Purple stars indicate the incursion sites ($n = 10$), blue cells represent recovered populations, and orange and red cells represent latently-infected and infectious populations

- the size of simulated FMD outbreaks in deer populations is highly correlated with the size of the deer herd initially infected, the size of the total deer population and the minimum and maximum size of deer herds within 2 km of the initially infected herd
- the size of simulated FMD outbreaks in feral pig populations is moderately correlated with the total feral pig population, the maximum size of herds, and the variance of herd sizes within 2 km of the initially infected herd
- the predicted spread of FMD might also depend on animal density and seasonal conditions; for example, within simulations, outbreaks in higher-density deer populations were 1.15 times larger in winter than in summer, and outbreaks in lower-density populations were 1.35 times larger in summer and autumn than in winter
- the Sirca model has been used to evaluate how pre-emptive mitigation strategies (targeted cull, random cull, and targeted depopulation buffer) applied to white-tailed deer populations might impact the predicted magnitude and distribution of outbreaks following FMDV incursion. Within simulations, the creation of a targeted depopulation buffer was found to be most effective, reducing the predicted number of deer infected by up to 52%, and the area affected by up to 31%.

Discussion and conclusions

A range of models have been developed that address the issue of disease spread through populations of domestic animal species (3, 13, 14, 16, 24, 28, 33); many are reported in this current volume. In general, these models have ignored the potential involvement of feral and wild animal species. However, in some situations, spill-over of infection from domestic herds and flocks into such uncontrolled populations – or initiation of disease spread within these wild and feral animal populations – must be considered when developing disease control policy and response strategies. The application of artificial life models, such as geographic automata, is an approach which offers many advantages, including explicit incorporation of spatial and ecological relationships and conceptual and computational simplicity (6). Based on general disease ecology principles, several factors – including population density and distribution, habitat requirements, social organisation, age structure, home range, and barriers to dispersal – might determine whether an infection will be maintained within feral or wild animal populations. These factors must be incorporated into models. The need to use spatially explicit models to simulate the spread of FMDV has been recognised (9, 22). Capturing spatial heterogeneity is probably the major challenge in

realistically representing FMDV spread through a landscape (9). In the Sirca model, geographic variations are explicitly included within the modelling framework in a simple manner, rather than needing exhaustive animal-census data (which is often unavailable or unreliable for wild or feral species). However, the methods used to estimate these animal distributions, from often very limited data, require further investigation (6, 17).

Connectivity of populations is known to be important for persistence of infectious diseases within communities (21, 23). The authors have noted that in some scenarios, simulated outbreaks of FMD failed to develop (see Fig. 2). If susceptible animal population densities are low then FMDV might become extinct within specific localities before it is able to infect a critical number of animals (7). The conditions (including population density, season and landscape) that might lead to such extinction of FMD need to be better defined.

It is important to realise the limitation of the Sirca model: the authors have found that such a model is best-suited to simulating the spread of disease through wild and feral animal species in relatively small study areas in which ecological transmission – rather than human-mediated transportation and indirect contacts – plays an important role. Integrating this type of ecological modelling approach with the more traditional models used to simulate disease spread through domestic livestock populations is a worthwhile pursuit. An initial attempt at such integration is described by Ward *et al.* (38). The further integration of disease spread models with livestock transportation, carcass disposal and economic models to create a scalable and generic decision support system is a goal.

The current version of Sirca assumes that groups of animals interact based on their relative size, density and distance. This is reasonable, since the most important factors determining the propagation and maintenance of FMDV between susceptible populations (so-called ‘inter-herd’ spread) are their geographical density, connectivity and size (7). However, the studies discussed here did not take the social organisation of the study populations into account, because of a lack of information with which to parameterise the model. Further work is needed to estimate such parameters and to determine the importance of social organisation and interactions on predicted disease spread. The computing issues, with respect to integrating this information into the Sirca model, are relatively minor. Likewise, in the studies described here, the distribution of the population at risk is assumed to be constant during any given model simulation, with only a local home range included. Allowing for greater, systematic changes in the animal population distribution (for example, a directional trend in population distribution from north to south because of changing seasonal conditions) is another refinement that should be investigated.

A critical issue in modelling the spread of a disease, such as FMD, through wild and feral animal species is the likelihood of transmission between these populations and populations of domestic animals. Contact rates between domestic and wild animals are, in most cases, uncertain. Thus, parameterisation of any model is very difficult. Even the nature of the contact needed – direct contact within a range of about one metre or indirect contact via contaminated environments such as watering and feeding points – is unknown. In their studies the authors have assumed that, if infected feral pigs or white-tailed deer are present, domestic cattle will become infected. This assumption is reasonable when susceptible species share the same habitat (2, 31), because feral pigs and wild deer are likely to come into contact with livestock at water and feed sources. The transmission of *Mycobacterium bovis* between deer and cattle in Michigan (30) demonstrates that such a disease spread pathway can exist. Also, the apparent spread of FMD between livestock and wild deer and feral pigs was documented in the United States during outbreaks in the 1920s. However, such an assumption is likely to represent a worst-case scenario. The actual interactions between feral and wild animal species and domesticated livestock – and therefore the potential for the infection to spread between these populations – are likely to vary substantially between regions, species and seasons.

Finally, the development of a user-friendly version of the Sirca model is a priority. To enhance more general access to this model, a user-interface that is accessible for all those working in disease control, not just modelling experts, is necessary. An example is shown in Figure 3. Use of the model to explore potential disease control response strategies could provide substantial benefit to many disease control authorities around the world.

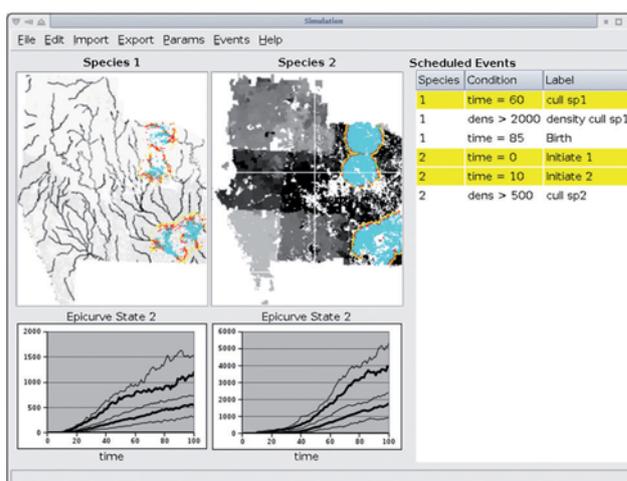


Fig. 3
An example of a potential user interface to enhance access to a susceptible-infected-recovered cellular automata model (Sirca), for investigation of the potential spread of foot and mouth disease

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Modèles de propagation des maladies animales chez les animaux sauvages et marrons : une application de la modélisation artificielle du vivant

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Résumé

Les populations d'animaux sauvages ou marrons ne reçoivent pas l'attention qu'exige l'influence exercée par ces populations sur les incursions et sur la propagation de maladies animales transfrontalières majeures comme la fièvre aphteuse. Un modèle de vie artificielle (Sirca) a permis de mener une étude sur cette question, à partir d'une série de données recueillies au sud du Texas et accompagnées de leur référencement spatial. L'étude a permis de montrer que l'incursion de la fièvre aphteuse dans une population de porcs marrons, ou de cervidés, pouvait entraîner, dans un délai de 100 jours, l'infection d'un nombre de bovins compris entre 698 et 1 557 animaux et affecter une surface totale comprise entre 166 km² et 455 km². S'il est possible d'estimer la taille d'un foyer affectant des cervidés à partir de la taille de la population locale initialement infectée, il est beaucoup plus difficile d'anticiper les caractéristiques des foyers qui affecteront ensuite les populations de porcs marrons. En outre, s'agissant des cervidés, la saison à laquelle apparaît le foyer peut influencer sur sa taille potentielle. L'étude a également porté sur les effets de diverses stratégies visant à atténuer la propagation de la maladie. L'approche suivie dans ces études incorpore explicitement la distribution spatiale ainsi que les relations entre les différentes populations animales, ce qui fournit un cadre innovant permettant d'analyser les conséquences potentielles, les coûts et les stratégies de lutte.

Mots-clés

Analyse spatiale – Automate géographique – Cervidé – Faune sauvage – Fièvre aphteuse – Modèle de simulation – Porc marron – Texas.



Modelos de propagación de enfermedades en poblaciones de animales salvajes o asilvestrados: aplicación de modelos de vida artificial

M.P. Ward, S.W. Laffan & L.D. Highfield

Resumen

La función que las poblaciones de animales salvajes o asilvestrados podrían desempeñar en la penetración y propagación de importantes enfermedades animales transfronterizas, como la fiebre aftosa, viene recibiendo menos atención de la que merecería por sus eventuales repercusiones. Para investigar la cuestión se aplicó un modelo de vida artificial (Sirca) al estudio de series de datos espacialmente referenciados correspondientes al sur de Texas. Un caso de penetración de fiebre aftosa en el que resultaran infectadas poblaciones de cerdos asilvestrados o de cérvidos podría acarrear el contagio de entre 698 y 1.557 bovinos y afectar una zona de entre 166 km² y 455 km² tras un periodo de 100 días. Aunque es posible predecir el tamaño de un brote en poblaciones de ciervos atendiendo al tamaño de la población local inicialmente infectada, menos previsible resultan los consiguientes brotes en poblaciones de cerdos asilvestrados. Por otro lado, en el caso de los ciervos, el tamaño de un brote podría depender de la estación en que tenga lugar la penetración. También se estudiaron los efectos de diversas estrategias de mitigación sobre la propagación de la enfermedad. El método utilizado en los estudios que aquí describen los autores integra explícitamente la distribución espacial de las poblaciones animales y los vínculos entre ellas, sentando así nuevas bases para examinar posibles consecuencias, costos y estrategias de lucha.

Palabras clave

Análisis espacial – Autómata geográfico – Cerdo asilvestrado – Ciervo – Fauna salvaje – Fiebre aftosa – Modelo de simulación – Texas.



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