BioOne COMPLETE

MODELING CONTROL OF RABIES OUTBREAKS IN RED FOX POPULATIONS TO EVALUATE CULLING, VACCINATION, AND VACCINATION COMBINED WITH FERTILITY CONTROL

Authors: Smith, G. C., and Wilkinson, D.

Source: Journal of Wildlife Diseases, 39(2) : 278-286

Published By: Wildlife Disease Association

URL: https://doi.org/10.7589/0090-3558-39.2.278

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Wildlife-Diseases on 18 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Journal of Wildlife Diseases, 39(2), 2003, pp. 278–286
© Wildlife Disease Association 2003

MODELING CONTROL OF RABIES OUTBREAKS IN RED FOX POPULATIONS TO EVALUATE CULLING, VACCINATION, AND VACCINATION COMBINED WITH FERTILITY CONTROL

G. C. Smith[1,2] **and D. Wilkinson**[1]

[1] Central Science Laboratory, Sand Hutton, York, YO41 1LZ, United Kingdom
[2] Corresponding author (email: g.smith@csl.gov.uk)

ABSTRACT: A predictive model of spread and control of rabies in red fox (*Vulpes vulpes*) populations was used to evaluate efficacy of culling, oral vaccination, and oral vaccination and fertility control (V+FC) as rabies control strategies. In addition, effects of season, fox population density, and a delay in starting control were modeled. At fox densities of 0.5 fox families/km^2 or greater, a single oral vaccination campaign with bait uptake rates of less than 50% resulted in ineffective rabies control. An uptake rate of at least 80% was required to give a better than 80% chance of eliminating rabies. Vaccination was least effective at controlling rabies if applied 1 or 2 mo before the foxes gave birth. Seasonal timing of poison or V+FC had little effect on efficacy, which was always more successful than the oral vaccination alone. The longer the delay between the simulated start of the rabies infection and the application of a single vaccination campaign, the less successful was the control, particularly at the higher fox densities tested. At a fox density of 0.25 families/km^2, all the strategies were equally successful at eliminating rabies. At higher fox densities V+FC was slightly less successful than culling, whereas vaccination-only was considerably less successful. The sole use of vaccination is not considered a viable control method for areas with high fox densities. The model suggests that an area of culling centered on the disease focus, plus an outer ring of vaccine or V+FC, could be the best strategy to control a point-source wildlife rabies outbreak.

Key words: Culling, fertility control, rabies control, red fox, vaccination, *Vulpes vulpes*.

INTRODUCTION

Rabies epizootics can spread over large areas, and the main wildlife vector of rabies in Europe is the red fox (*Vulpes vulpes*). Extensive vaccination programs targeting red foxes have reduced the incidence of rabies across Western Europe, and following discussion (Kennedy et al., 1998) this has resulted in some relaxation of the quarantine and pet movement regulations in the United Kingdom (UK; Statutory Instrument, 1999). However there has recently been a rise in fox populations in certain areas of Western Europe (Chautan et al., 2000), including urban areas (Gloor et al., 2001). The successful European vaccination campaigns may have been the cause of this increase, raising concerns about the risks of larger and more intense rabies epizootics which would be more difficult to eliminate (Chautan et al., 2000).

The recent foot and mouth disease epizootic in the UK in 2001, 34 yr after the previous one in 1967, emphasizes the need to remain vigilant and have contingency plans to deal with such disease outbreaks, even though they may only occur once every 30 to 50 yr. Although the last rabies incidents in dogs imported into the UK were in 1969 and 1970, the risk of a rabies outbreak in the UK warrants maintenance of up-to-date and detailed contingency plans. Following these rabies cases, the Ministry of Agriculture Fisheries and Food (MAFF) set up contingency plans to address a rabies outbreak in the UK, which eventually led to the development of a computer model to simulate disease spread and control strategies (Smith and Harris, 1991; Smith, 1995). The current control policy would involve fox depopulation using poison baits, but allows for the option of oral vaccination.

New control possibilities are now also on the horizon—fertility control with immunocontraception. It is also important to clarify the role that vaccination might play in the control of a wildlife rabies incident in the UK. Smith and Cheeseman (2002)

Downloaded From: https://complete.bioone.org/journals/Journal-of-Wildlife-Diseases on 18 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

used a differential equation model to investigate culling, vaccination, and vaccination combined with fertility control (V+FC) for both rabies and bovine tuberculosis. This model showed that vaccination was less successful than culling, and the lack of success was related to the birth of rabies-susceptible young in spring. In this study we used a spatial stochastic model of fox territories to investigate the effect of fox population density on a rabies epizootic, and to compare the three control strategies in a heterogeneous environment.

METHODS

Model construction

A spatial stochastic simulation model of rabies in foxes was used as the background component to produce a PC-based user-friendly model which would be used in the event of a real rabies outbreak in the UK (Smith and Harris, 1991). That model was based on an earlier spatial model by Voigt et al. (1985). Modifications of the model also allowed assessments of vaccination (Smith, 1995) and more recently, fertility control. Because a number of significant changes to the model have taken place, an updated description is included below.

The model was constructed to follow the fox-year with a discrete time interval of 1 mo to simulate the rabies incubation period in the red fox (Blancou et al., 1991). The fox population was simulated spatially using a square grid, and the health status of each fox was simulated using three categories: healthy, infected with rabies, and immunized against rabies (vaccinated).

The sequence of the model program is summarized by: 1) creation of spatial grid with fox dens and territories (start of each simulation only); 2) seeding with fox population (start of each simulation only); 3) birth and aging (April only); 4) seeding of rabies (specified month, once only); 5) culling (specified months following start of rabies); 6) vaccination (specified months following start of rabies); 7) vaccination plus fertility control (specified months following start of rabies); 8) natural mortality (every month); 9) spread of rabies and mortality of rabid foxes (every month while rabies present); 10) natural dispersal of foxes (every month between October and March); 11) perturbation of foxes (every month between October and March); and 12) output of population and disease results (end of each month).

The model used a spatial grid of 76×76 squares, each representing 500 m×500 m, to allow a 19 km radius for fox-rabies control as identified in the UK contingency plans. The focus of each fox family was the den. These were distributed at random on the grid at a specified density. The maximum fox population density in the model was four families/km^2—one den/grid square. This grid resolution was considered sufficient as it matched the resolution used for the urban fox surveys in Britain, and yielded a reasonable territory shape for the range of densities tested. Territories were created for each family group by assigning each grid square to the closest den, and the neighbors of each territory were recorded.

Previous versions of this model created territories by examining unallocated squares at random, and allocating each to a random neighboring territory. This had the disadvantage of sometimes producing territories with invaginations projecting some distance between neighboring territories, with the resulting possibility of rabies jumping large distances with neighbor-to-neighbor spread. Tests comparing the two methods of territory formation showed a 10% difference in vaccination control efficacy. Since territory tessellation is considered to be more likely to simulate what happens in the field, it was chosen as the method for this study.

A list of territories at the edge of the grid was compiled to determine if and when rabies reached the edge, since this would denote failure of the control strategy. Relevant spatial barriers to fox movement or contact could be added to the grid, to represent rivers or lakes, although all the simulations in this study were run without any spatial barriers.

In line with the earlier model (Smith and Harris, 1991), each family was seeded at the start of each simulation with one healthy male and one healthy female fox, plus, with a probability of 0.8 and 0.57 respectively, a second male and a second female. Of these each had a 0.47 probability of being juvenile (<1 yr old). The resulting population has been shown to maintain a stable density of animals over the grid in the absence of disease (Smith and Harris, 1991).

At the start of each fox-year (April), each family that had at least one male and one fertile female, produced one litter of cubs. Natural infertility rates were retained from the previous model: 0.23 and 0.34 for adult and juvenile vixens, respectively. If present, an adult fertile female would breed in preference to a juvenile, but if not, a juvenile was allowed to breed. Litter sizes were based on placental scar counts (Harris and Smith, 1987). Cubs were produced stochastically on the basis of an average litter

Downloaded From: https://complete.bioone.org/journals/Journal-of-Wildlife-Diseases on 18 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

size of 4.76 (SD=1.53) for an adult vixen, and 4.53 (SD=1.54) for a juvenile vixen. Cubs were classified as male with a probability of 0.55 (Harris and Smith, 1987). All juveniles from the previous year were considered adults.

Rabies infection was started in the fox population in the first year of each simulation, but the month of infection could be varied to study seasonal effects. Seeding was done by infecting a single fox family at the center of the grid. All the susceptible (non-vaccinated) foxes in that family were changed from the healthy category to the rabies-infected category to ensure that the disease would not die out immediately due to random chance.

Control regimes could be applied to simulate baiting strategies, and could consist of culling and/or vaccination, though in this study such combinations were not tested. In all simulations in this study, control was applied within a circle of 19 km radius around the rabies focal source. Control could be applied in any month(s) from the month of initial rabies infection, to 12 mo later, and the control rates could be varied for each month. In a month with culling, each fox was given an equal probability of being removed. With vaccination, the healthy foxes, but not incubating foxes, were stochastically determined for transfer to the vaccinated category. Such vaccinated foxes were immunized against rabies infection, and there was no vertical transmission of this immunity. The inclusion of immunocontraception in the bait was also modeled to simulate fertility control. Where fertility control was used, vaccinated females were classified as non-breeding. If there was an unvaccinated adult or juvenile female in the family, they were given the chance to breed.

Natural mortality rates were applied each month, dependent on the sex and age class (adult or juvenile) of each fox and were based on rates reported for Bristol, UK (Smith and Harris, 1991).

Following Smith and Harris (1991) and Voigt et al. (1985), infected foxes were converted to infectious (rabid) foxes with a probability of 0.42 and each rabid animal was then allowed to infect healthy foxes according to specified contact probabilities (Table 1). These probabilities were dependent on type of contact, time of year, and size of the rabid fox's territory to produce density-dependent values. At high density, contact probabilities between members of the same family, and between males and females of neighboring territories in winter, were set close to unity. At low density, contact probabilities were set much lower, particularly between neighboring territories in spring. We assumed 100% mortality of rabid animals, so infectious foxes were removed from the population.

TABLE 1. Monthly rabies contact probabilities, as calculated for a density of four families/km^2, as used in Smith (1995).

Contact	Probability
Within-group contacts	0.999[a]
Neighbors in spring	0.122[a]
Neighboring juveniles in spring/summer	0.329[a]
Other neighbors in summer	0.499[a]
Neighbors in autumn	0.255[a]
Males to females in winter	0.912[b]
Other neighbors	0.514[a]

[a] These probabilities are assumed to be linearly density dependent, passing through the origin.

[b] Mating-contact probabilities are assumed to be linearly density dependent, but with a minimum value of 0.2, following White et al. (1995).

Each month from October to March inclusive, juvenile foxes were allowed to disperse according to probabilities dependent on sex and time of year. The dispersal probabilities and distances were based on results from a Bristol study (Smith and Harris, 1991). The dispersal distances were calculated separately for low, medium, and high fox density. The direction for dispersal was determined randomly. Since infected foxes could disperse, this is a mode by which rabies infection can spread at a rate of more than one territory per month.

Following each dispersal routine, additional fox movements into adjacent territories were permitted to fill vacant territories or those that contained only foxes of the opposite sex. This dispersed non-breeding foxes resulting in paired males and females before the next breeding season, thus increasing productivity. As expected, the number of perturbation movements was highest following culling.

At the end of each month, a summary of the fox population and its health status was produced. After each simulation, the program determined whether rabies had been successfully eliminated by the control regime applied, or in the case of no control, whether the disease became epizootic, or disappeared. A rabies case in an edge territory at any time during a simulation was classed as a control failure, as was a rabies-infected fox dispersing beyond the simulation grid. For any given control scenario, the probability of rabies being eliminated was calculated from a minimum of 50 simulations, and used as a standard measure of control success. The average duration of the rabies epizootics was also determined.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Wildlife-Diseases on 18 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Fox densities were simulated by randomly adding a variable number of fox family dens to the spatial grid. Lower fox densities (i.e., 0.15–0.5 fox families/km^2) are typical of rural scenarios, although density may reach 0.9 families/km^2. Higher densities (i.e., 1.0–2.5 fox families/km^2) are more typical of some urban areas in the UK (Smith, 1989).

The following assumptions are explicit in the model: 1) foxes live in family groups of between two and three and a half adult foxes, 2) family groups are contiguous with each other and minimize their boundary with neighbors, 3) home range size can be adequately described in terms of 25 ha units, 4) the minimum rabies incubation period in wild foxes approximates 1 mo, 5) the infectious period is instantaneous compared to the timescale of 1 mo, 6) rabies is always fatal to foxes, 7) contact rates among foxes can be approximated by linear density dependence, 8) seasonal births can be adequately approximated by instantaneous birthing on 31 March each year, and 9) neither culling, nor the effect of rabies depopulation, produces extra-territorial movements to non-neighboring territories.

The model can be summarized by the following finite rate difference equations to describe the numbers of adults and juvenile foxes of each sex. The number of healthy adult males at a particular spatial location, z, at time t, was denoted by N_{tz}. After one monthly step of the model, the number of healthy adult males was described by:

$$N_{(t+1)z} = N_{tz}((1 - m_t)(1 - c_t)(1 - i_{tz})), \quad (1)$$

where m_t was the monthly natural mortality rate at time t for adult males, c_t was the proportion culled at time t, and i_{tz} the proportion which became infected at time t at location z.

The number of infected adult males at time $t+1$ at location z was denoted by:

$$I_{(t+1)z} = I_{tz}((1-m_t)(1-c_t)(1-p)) + i_{tz}N_{tz}, \quad (2)$$

where p was the proportion of infected animals that became infectious and died.

For healthy juvenile males, we used the equation:

$$M_{(t+1)z} = M_{tz}((1 - m_t)(1 - c_t)(1 - i_{tz}) \times (1 - d_{tz})) + F_{tz}, \quad (3)$$

where d_{tz} was the proportion of animals dispersing from location z, and F_{tz} the number of immigrant healthy juvenile males.

For infected juvenile males, we used the equation:

$$J_{(t+1)z} = J_{tz}((1 - m_t)(1 - c_t)(1 - p) \times (1 - d_{tz})) + i_{tz}M_{tz} + G_{tz}, \quad (4)$$

where d_{tz} was the proportion of animals dispersing from location z, and G_{tz} the number of immigrant infected juvenile males.

At the beginning of each year, after month twelve and before month one, all juvenile foxes became adults, and females were given the opportunity to breed. At this point in time we used the equations:

$$N_{tz} = N_{tz} + M_{tz}, \quad (5)$$

$$I_{tz} = I_{tz} + J_{tz}, \quad (6)$$

$$M_{tz} = lr, \quad \text{and} \quad (7)$$

$$J_{tz} = 0, \quad (8)$$

where l was the litter size of any resident breeding female, and r the proportion of the litter that was male. Equations (1)–(8) were also used to describe the female populations.

Fox control

In an actual control campaign, poison, vaccine, or immunocontraceptive would be given in baits, and hence the rate of control would be directly dependent on the rate of bait uptake. In rural areas the proportion of the population that take baits is likely to be around 70–80% (Masson et al., 1999), whereas only about 40% bait uptake is reported in urban areas of the UK (Trewhella et al., 1991; Baker et al., 2001). Therefore we simulated a range of vaccination rates to study the effects of bait uptake on rabies control. We assume, for simplicity, that only one baiting campaign is undertaken, and the effect of multiple campaigns performed sequentially is equivalent to a single campaign of greater magnitude. Throughout, we define the term bait uptake to mean the proportion of the population that consume and are affected by the baits (i.e., become immune, or die).

In the UK rabies control would be initiated immediately after rabies is confirmed, so we looked at the effects of rabies introduction in different months, using a scenario with a fox density of 0.5 fox families/km^2 and a control rate of 80% (single campaign). Poison, vaccination, and V+FC were evaluated, with control being applied 1 mo after the start of the rabies infection. Only a single control event was simulated, to allow comparison of the strategies.

It is possible that an initial outbreak of rabies would go undetected for several months (Bacon, 1981), so we investigated the effect of a

Downloaded From: https://complete.bioone.org/journals/Journal-of-Wildlife-Diseases on 18 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

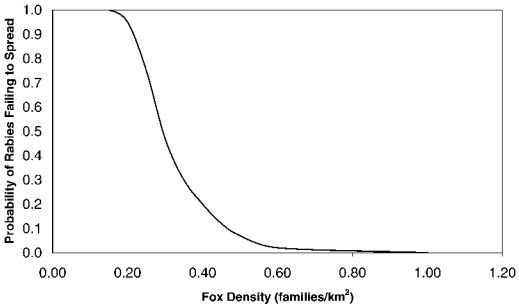


FIGURE 1. Effect of fox density on the probability of rabies failing to spread in a rural environment in the absence of control.

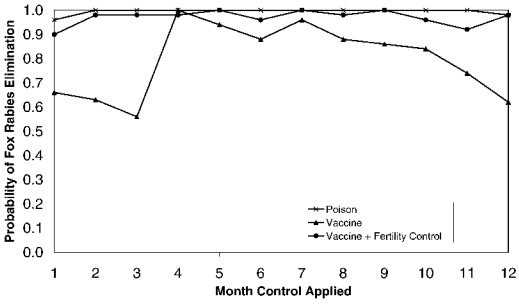


FIGURE 3. Seasonal effect on the success of three different control regimes at a fox density of 0.5 families/km^2 in a rural environment. Each regime was simulated for a single application at a rate of 80%, 1 mo after the rabies started.

delay of up to 12 mo using three different fox densities: 0.25, 0.5, and 1.0 fox families/km^2.

The efficacy of poison, vaccination, and V+FC was modeled for two different levels of control (50% and 80%), and the duration of each successful control was also determined to ascertain the speed of control.

RESULTS

As fox family density decreases, a critical threshold density (approximately 0.2) occurs below which rabies fails to become epizootic (Fig. 1). For oral vaccination, higher rates of bait uptake increase the probability of disease elimination (Fig. 2). However, there was a clear effect of density on control success rate. At low density (0.25 fox families/km^2), a modest 20% uptake is likely to control the disease outbreak. At high density (1.0 fox families/km^2), 80% uptake is required to achieve the same success. An uptake of 50% had no effect at the higher density. The above simulations were performed for rabies introduction in April, and control applied in May. There was a strong seasonal trend in the ability to control rabies by vaccination, as demonstrated for a density of 0.5 fox families/km^2 and an uptake rate of 80% (Fig. 3). Control with poison and V+FC, had high probabilities of disease elimination throughout the year with no seasonal trend. The efficacy of vaccination alone showed a cyclical pattern, with the best results just after the foxes gave birth. The poorest results occurred when control was performed 1 mo before birthing. The size of this pre-birthing dip in effectiveness is density related (Fig. 4), with fox densities above 0.4 families/km^2 resulting in a noticeable decline in the effectiveness of vaccination.

Low numbers of infected animals dur-

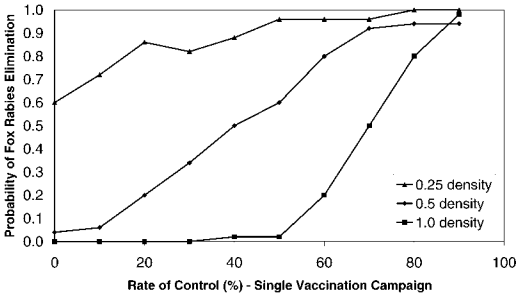


FIGURE 2. Effects of fox density and control rate on the efficacy of a single vaccination campaign in eliminating fox-rabies in a rural environment. Rabies was started in April and vaccine given in May.

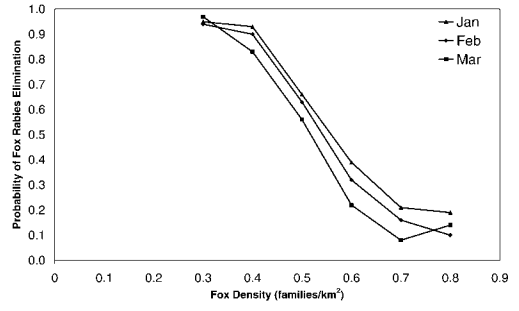


FIGURE 4. Effect of fox density on the success of oral vaccination applied in January, February, or March 1 mo after rabies started. The vaccine regime comprised a single application at a rate of 80%.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Wildlife-Diseases on 18 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

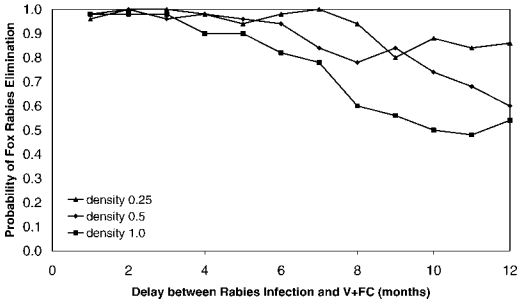


FIGURE 5. Effect of the length of delay between rabies starting and V+FC being applied on control success. Rabies was started in April.

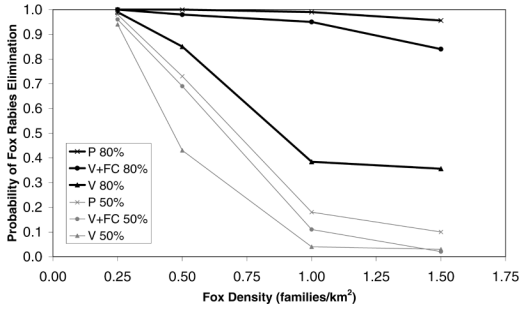


FIGURE 6. Probability of eliminating fox-rabies at varying fox densities and control rates of 50% and 80%, for poison, vaccination, and V+FC. Rabies was started in August and control was applied in September.

ing the start of an epizootic could delay detection and thus the implementation of control. For V+FC control at a rate of 80%, a delay of up to 4 mo following rabies introduction in April had little effect on the overall success rate (Fig. 5). Above this time limit there is an increasing density dependent effect. For poisoning (not illustrated), there was no noticeable drop in success rate until a delay of at least 6 mo. In both these cases the decline in success became steeper during the main dispersal period (November to January). For vaccination the effect of any delay was compounded by the seasonal effectiveness of control.

There is a clear relationship between method of control, fox density, and success rate (Fig. 6). Vaccination is consistently less effective than either poisoning or V+FC, but this difference is most marked at higher densities and levels of control. At a density of 0.25 families/km^2, all control scenarios had a greater than 90% chance of eliminating the disease. As density increased, the probability of rabies elimination decreased for all controls. Since the results for a control rate of 50% are lower than those for the 80% control, control rate is a more important factor than the type of control. Notwithstanding this, if we compare the results for 80% control, culling is consistently the most effective at eliminating rabies, followed by V+FC. The vaccination-only control was very sensitive to fox density, with rabies elimination occurring in less than 40% of the simulations at a fox density of 1.0 or higher.

For those simulations where rabies was eliminated, the time between the application of control and the extinction of disease varied with both fox density and control method (Fig. 7). Culling is consistently quicker at eliminating rabies than the V+FC. However, the vaccination-only control method appears not to be as density dependent, in terms of duration, as the other two controls. In fact at a density of 1.5 families/km^2, when vaccination did eliminate rabies, it took no longer on average than at a density of 1.0 families/km^2. Individual simulations at the 1.5 density revealed that if rabies was still present by the following April (month 12) when the

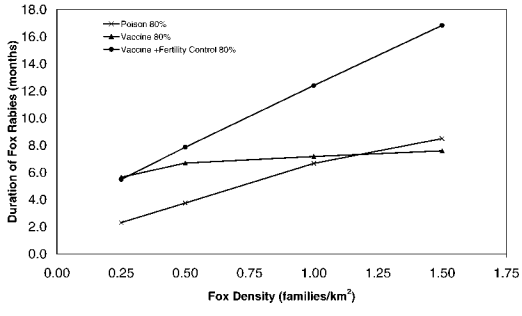


FIGURE 7. Average duration of rabies epizootics at varying fox densities and a control rate of 80% for poison, vaccination, and V+FC. Rabies was started in August and control was applied in September. Only those rabies epizootics that were eliminated within 48 mo were used to calculate the average.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Wildlife-Diseases on 18 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

foxes gave birth, rabies was eliminated in only 8% of simulations with vaccination alone. Culling resulted in a 20% chance of immediate disease elimination at this density by severe reduction or complete removal of infected foxes. Thus, where vaccination works, it would eliminate rabies before new cubs appeared. The arrival of new cubs represents a large addition of non-vaccinated and susceptible animals. Conversely, with the culling and V+FC, there are many cases (32% and 59% respectively) where rabies lasted beyond the arrival of the next batch of cubs, yet rabies was eliminated. The average duration for the vaccination-only control is thus biased downwards, particularly at the higher densities, and must be interpreted with caution.

DISCUSSION

A spatially explicit fox population model is described which can include heterogeneity in territorial size and evaluate different control strategies. This model is incorporated into wildlife rabies control contingency planning for the UK. Outbreaks would result from a point-source infection, since rabies is not enzootic in the UK. The model demonstrated a critical threshold density of 0.2 fox families/km^2. This is equivalent to 0.4–0.7 foxes/km^2, which is within the commonly reported range of 0.25–1.0 foxes/km^2 (Anderson et al., 1981). Therefore the individual based simulation model produced results consistent with simple non-spatial models.

As expected, the existence of a critical threshold density means that as fox density increases it becomes harder to control the disease. The low bait uptake in urban foxes (40%) indicates that multiple control campaigns would be required in areas supporting higher fox population densities.

The model also suggested that the success of vaccination had a strong seasonal and density component, with greatest success (similar to that of poisoning or V+FC) immediately after the cubs were born. In April, the optimum time of year for simulated control, vaccination rates of 70–80% are unlikely to eliminate rabies if the fox density exceeds 1.0 families/km^2 (Fig. 2). In March, the least optimal time for simulated control, disease elimination becomes unlikely at densities above 0.5 families/km^2 (Fig. 4). In the field, bait uptake by juvenile foxes is less than adults, although it can be increased by targeting dens (Vuillaume et al., 1998). However, our model assumed no change in the uptake rate. The reason for this difference between March and April is the birth of cubs, which in the model always occurred on 31 March. However, the birthing period in the field may last over a month (Lloyd and Englund, 1973), which would smooth out this transition. Recent evidence also indicates that oral vaccination of young cubs of vaccinated mothers may result in an impaired immune response (Müller et al., 2001). This would result in a lower peak in April with multiple campaigns. The inclusion of an anti-fertility agent removed this seasonal effect, but the impaired immune response of young cubs would suggest a small decrease in effectiveness between birthing and about eight weeks of age (early March to late May). Overall, this suggests that vaccination at low densities could occur at any time of year, whereas when fox density exceeds 0.5 families/km^2, vaccination around the birthing period should be avoided.

The model showed that a delay of up to 4 mo in starting control should have no major effect on the ability to eliminate rabies. If rabies were introduced in autumn and the infection was not discovered for several months, considerable spread could occur. Simulations suggest that trying to control an outbreak of rabies in late winter or early spring with vaccination alone is a risky strategy if the disease has been around for a few months.

The model has shown that culling is more effective than vaccination for the control of rabies. This is in agreement with a generic non-spatial model for wildlife diseases (Barlow, 1996). Although some

Downloaded From: https://complete.bioone.org/journals/Journal-of-Wildlife-Diseases on 18 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

models conclude that culling is less effective at disease control than vaccination (Murray et al., 1986), this conclusion is generally based on the fact that vaccination rates exceed culling rates. However, our approach assumes that both techniques rely on baits and reach the same proportion of the fox population.

Comparison of the three types of control indicated promising results for V+FC, particularly at higher fox population densities. However, the results emphasized the importance of maximizing bait uptake; even the most successful culling regime was poor at the lower control rate for a high fox density.

For simulations where there was a high chance of rabies being eliminated, the epizootic duration was shortest for culling, followed by vaccination and V+FC. Within the constraints of our model we have demonstrated that failure of vaccination at high densities is due to the birth of susceptible young, which resulted in densities well above the critical threshold. When vaccinated animals were not allowed to reproduce, the success rate approached that of culling. Culling produced shorter epizootics than V+FC by killing all, or nearly all, of the infected animals in simulations. Even at high density, poisoning immediately eliminated rabies in 20% of the simulations; whereas V+FC was never able to achieve this, thus increasing the mean duration. This latter point may be less important when addressing an established rabies epizootic front, but is important when the disease is localized to a focal source. One reason for not using culling to control density-dependent wildlife diseases is the expected increase in the animal movements as space becomes available. In order to combat this, culling integrated with a ring of vaccination was effective in rabies models (Smith, 1995). In addition, it is being evaluated in Ontario, Canada for raccoon (*Procyon lotor*) rabies foci with early promise of success (Rosatte et al., 2001). Raccoon culling and vaccination are being performed by trapping, thus the efficacy of both is similar. Since the rate of control is very important, it is not possible to compare culling and vaccination if they are performed by different means. Culling of foxes has only controlled rabies spread where disease was localized, and effort was intense and persistent, (e.g., Denmark, Müller, 1971; and Italy, Irsara et al., 1982). Inconsistent effort probably resulted in the spread of fox rabies in some parts of France (Aubert, 1994), as predicted by modeling (Smith and Harris, 1989). Subsequent vaccination was more efficient and successful.

We do not suggest that culling takes precedence over vaccination as a wildlife disease control strategy, but efficient culling was more effective at high density, without seasonal disadvantages. However, we recognize that social acceptability and non-target species complications associated with poisons frequently hamper the use of poisons on a broad scale. If the goal is to eliminate an isolated focal outbreak as quickly as possible, then culling should be considered. It should be noted that in these simulations, failure to control disease occurred if the disease persisted for 4 yr or if it spread outside the simulation grid. For long-term control of enzootic rabies this definition of failure would not be relevant. Where contraceptives are available, their inclusion in vaccine bait should be further investigated.

ACKNOWLEDGMENTS

This work was funded by the Department for Environment, Food and Rural Affairs, UK. We thank the reviewers and editors for their useful suggestions.

LITERATURE CITED

ANDERSON, R. M., H. C. JACKSON, R. M. MAY, AND A. D. M. SMITH. 1981. Population dynamics of fox rabies in Europe. Nature 289: 765–771.

AUBERT, M. 1994. Control of rabies in foxes: What are the appropriate measures? Veterinary Record 134: 55–59.

BACON, P. J. 1981. The consequences of unreported fox rabies. Journal of Environmental Management 13: 195–200.

BAKER, P. J., S. HARRIS, C. P. J. ROBERTSON, G. SAUN-

Downloaded From: https://complete.bioone.org/journals/Journal-of-Wildlife-Diseases on 18 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

DERS, AND P. C. L. WHITE. 2001. Differences in the capture rate of cage-trapped red foxes *Vulpes vulpes* and an evaluation of rabies control measures in Britain. Journal of Applied Ecology 38: 823–835.

BARLOW, N. D. 1996. The ecology of wildlife disease control: Simple models revisited. Journal of Applied Ecology 33: 303–314.

BLANCOU, J., M. F. A. AUBERT, AND M. ARTOIS. 1991. Fox rabies. *In* The natural history of rabies. G. M. Baer (ed.). CRC Press, Boston, pp. 257–290.

CHAUTAN, M., D. PONTIER, AND M. ARTOIS. 2000. Role of rabies in recent demographic changes in red fox (*Vulpes vulpes*) populations in Europe. Mammalia 64: 391–410.

GLOOR, S., F. BONTADINA, D. HEGGLIN, P. DEPLAZES, AND U. BREITENMOSER. 2001. The rise of urban fox populations in Switzerland. Mammalian Biology 66: 155–164.

HARRIS, S., AND G. C. SMITH. 1987. Demography of two urban fox (*Vulpes vulpes*) populations. Journal of Applied Ecology 24: 75–86.

IRSARA, A., A. RUATTI, G. GAGLIARDI, Z. ORFEI, L. BELLANI, AND A. MANTOUANI. 1982. Control of wildlife rabies in north-eastern Italy. Comparative Immunology, Microbiology and Infectious Diseases 5: 327–335.

KENNEDY, I., M. AUBERT, B. BANNISTER, P. DEVILE, C. DYE, A. HIGGINS, O. JARRETT, H. SEWELL, AND J. SMITH. 1998. Quarantine & Rabies: A reappraisal. MAFF Publications, London, UK, 316 pp.

LLOYD, H. G., AND J. ENGLUND. 1973. The reproductive cycle of the red fox in Europe. Journal of Reproduction and Fertility Supplement 19: 119–130.

MASSON, E., V. BRUYERE-MASSON, P. VUILLAUME, S. LEMOYNE, AND M. AUBERT. 1999. Rabies oral vaccination of foxes during the summer with the VRG vaccine bait. Veterinary Research 30: 595–605.

MÜLLER, J. 1971. The effect of fox reduction on the occurrence of rabies. Observations from two outbreaks of rabies in Denmark. Bulletin l'Office International des Épizooties 75: 7673–7776.

MÜLLER, T. F., P. SCHUSTER, T. SELHORST, U. D. WENZEL, AND A. M. NEUBERT. 2001. Effect of maternal immunity on the immune response to oral vaccination against rabies in young foxes. American Journal of Veterinary Research 62: 1154–1158.

MURRAY, J. D., E. A. STANLEY, AND D. L. BROWN. 1986. On the spatial spread of rabies among foxes. Proceedings of the Royal Society of London B 229: 111–150.

ROSATTE, R. C., D. DONOVAN, M. ALLAN, L. A. HOWES, A. SILVER, K. BENNETT, C. MACINNES, C. DAVIES, A. WANDLER, AND D. B. RADFORD. 2001. Emergency response to raccoon rabies introduction into Ontario. Journal of Wildlife Diseases 37: 265–279.

SMITH, G. C. 1989. Urban foxes (*Vulpes vulpes*) and rabies control. PhD Dissertation, University of Bristol, Bristol, UK, 229 pp.

———. 1995. Modelling rabies control in the U.K.: The inclusion of vaccination. Mammalia 59: 629–637.

———, AND S. HARRIS. 1989. The control of rabies in urban fox populations. *In* Mammals as pests. R. J. Putman (ed.). Chapman & Hall, London, UK, pp. 209–224.

———, AND ———. 1991. Rabies in urban foxes (*Vulpes vulpes*) in Britain: The use of a spatial stochastic simulation model to examine the pattern of spread and evaluate the efficacy of different control regimes. Philosophical Transactions of the Royal Society of London B 334: 459–479.

———, AND C. L. CHEESEMAN. 2002. The control of diseases in wildlife populations: Culling, vaccine and fertility control. Ecological Modelling 150: 45–53.

STATUTORY INSTRUMENT. 1999. The Pet Travel Scheme (Pilot Arrangements), England Order 1999.

TREWHELLA, W. J., S. HARRIS, G. C. SMITH, AND A. K. NADIAN. 1991. A field trial evaluating bait uptake by an urban fox (*Vulpes vulpes*) population. Journal of Applied Ecology 28: 454–466.

VOIGT, D. R., R. R. TINLINE, AND L. H. BROEKHOVEN. 1985. A spatial simulation model for rabies control. *In* Population dynamics of rabies in wildlife. P. J. Bacon (ed.). Academic Press, London, UK, pp. 311–349.

VUILLAUME, P., V. BRUYERE, AND M. AUBERT. 1998. Comparison of the effectiveness of two protocols of antirabies bait distribution for foxes (*Vulpes vulpes*). Veterinary Research (Paris) 29: 537–546.

WHITE, P. C. L., S. HARRIS, AND G. C. SMITH. 1995. Fox contact behaviour and rabies spread: A model for the estimation of contact probabilities between urban foxes at different densities and its implication for rabies control in Britain. Journal of Applied Ecology 32: 693–706.

Received for publication 25 January 2002.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Wildlife-Diseases on 18 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use