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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

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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 régimes

G. C. SMITH† AND STEPHEN HARRIS

Department of Zoology, University of Bristol, Woodland Road, Bristol BS8 1UG, U.K.

CONTENTS

SUMMARY

The threat of rabies being reintroduced into Britain is probably greater now than at any time over the last 60 years. This threat is reviewed with particular regard to the problems that would be posed should rabies be introduced to the high-density fox populations found in many cities in southern England. Computer models can provide a valuable means of understanding the pattern of rabies spread in fox populations and the likely problems of control, so the construction of previous rabies models was reviewed. None were found to be suitable for analysing the particular problems posed by high-density, spatially heterogeneous, urban fox populations. Therefore, a new spatial stochastic simulation model was produced, based on demographic and other data collected during a long-term study on the urban fox population in Bristol, and fox density data collected from a number of cities in southern England.

The simulation model was used to analyse the effects of spatial heterogeneity in the fox population on the pattern of rabies spread. Simulations were then used to evaluate the effects of: (i) varying levels of fox control; (ii) changing the size of the control zone; (iii) the onset of the rabies epizooty at different times of the year; and (iv) delay before the commencement of control on the chances of containing the disease. These simulations were run for four cities (Bournemouth and Poole, Bristol, Leicester and the West Midlands conurbation) with different mean fox population densities. It was found that the variance in the monthly velocity of the rabies front was greater for heterogeneous fox populations. In cities with high fox densities, low or moderate levels of control were unsuccessful in containing the disease, but these urban areas had the highest rates of success with the highest levels of control. A three-month delay in the commencement of a rabies control campaign on average reduced the chance of successfully controlling the disease by 10–20%, although this was higher in lower-density fox populations. Rabies outbreaks in the dispersal period were on average 10% less likely to be contained. Increasing the size of the control zone increased the chances of successfully containing the disease, although this effect was density dependent, so the effect was less in low-density fox populations. These results are discussed in relation to the current rabies contingency plans for British urban areas.

† Present address: Central Science Laboratory, Ministry of Agriculture, Fisheries and Food, Tangley Place, Worplesdon, Guildford, Surrey GU3 3LQ, U.K.

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31-2

1. INTRODUCTION

With the exception of the years 1918–1922, and two isolated cases at Camberley in 1969 and Newmarket in 1970, Britain has been free of rabies since 1902 (Gardner 1983). In Europe, however, rabies has been spreading westward from Poland since the beginning of World War II. The movement of the wave front has averaged 37 km per year, but has varied between almost no movement for short periods of time, to speeds in excess of 80 km per year (Steck & Wandeler 1980). The first cases of rabies in Denmark were recorded in 1964, in Austria, Belgium and Luxembourg in 1966, in Hungary and Switzerland in 1967, and in France in 1968 (Bisseru 1972; Koltai 1986; Sodja & Rödl 1986). The red fox (*Vulpes vulpes*) accounts for between 63% and 90% of all cases of rabies in Europe (Müller 1966; Wandeler *et al.* 1974; Steck & Wandeler 1980; Omatouch & Polák 1982; Dufey & Evrard 1985; Koltai 1986); in the absence of the fox, it is unlikely that the rabies epizooty could be maintained by other wild species either singly or collectively (Lloyd 1977).

The English Channel and quarantine laws should be an effective barrier to the spread of rabies into Britain, although illegally imported mammals could re-introduce the disease. In 1989 the number of legally imported animals was 5915 dogs, 3220 cats and 140327 other mammals, and those known to have been imported illegally were 38, 28 and 93 respectively (Harris & Smith 1990). However, the actual number imported illegally is probably much higher than this, and if one such animal was rabid it could set up a focus of infection (Harris & Smith 1990; Harris *et al.* 1991). As nearly 80% of people in Britain reside in urban areas with a population in excess of 10000, and over 50% in urban areas with a population of over 100000 (Office of Population Censuses and Surveys 1984), it is likely that an illegally imported infected pet would be taken to a large town or city. Hence there is a high chance that an urban area would be the focal point of any rabies epizooty.

An additional, and presently unquantified, potential source of infection is the presence of rabies in some species of European bat, most frequently the serotine (*Eptesicus serotinus*) (Jüdes 1987). The viruses recovered from rabid bats consist of a number of different, closely related antigenic variants that are all different from the classical terrestrial rabies virus (A. King, personal communication). Although aerosol transmission to the red fox has been demonstrated, only a very small number of foxes in North America have been identified with bat-derived rabies virus (Smith & Baer 1988). It seems probable, therefore, that bat viruses will not spread through terrestrial animal populations (King & Davies 1988), and so infected bats are unlikely to be the source of a rabies epizooty in Britain.

In Europe, areas where the fox rabies front has advanced slowly appear to be characterized by a low fox population density (Steck & Wandeler 1980). It has been suggested that there is a threshold host density, below which rabies cannot survive, and Anderson *et al.* (1981) and Anderson (1986) calculated that this critical level is between 0.3 and 0.5 foxes km^{-2}. As fox population densities are difficult to estimate, there are few measures of absolute fox density or the effects of fox density on the pattern of rabies spread. However, fox control on the continent has, until recently, concentrated on reducing the fox population density below this critical level by culling, although national successes from culling operations are few (Smith & Harris 1989).

A second form of rabies control is vaccination. Recent advances in vaccine production have resulted in a number of large-scale field trials to examine their success (Balbo & Rossi 1988; Brochier *et al.* 1988; Johnston *et al.* 1988; Kappeler *et al.* 1988; Schneider & Cox 1988). These trials have begun to involve the co-operation of several countries over very large areas, although they are still a long way from the complete eradication of terrestrial rabies from Europe, even if this goal is actually attainable. The use of vaccination in Britain has not received approval, and current government policy is to stamp out any outbreak by the culling of foxes and control of domestic animals before the disease becomes established (Ministry of Agriculture, Fisheries and Food 1988). Unlike Europe, where rabies is spreading on a wave front 2000 km long, Britain will be dealing with a point source infection, and in such a situation it is probable that a culling campaign may have a greater chance of success than the use of vaccine baits (Harris & Smith 1990; Harris *et al.* 1991).

In Britain, many cities are known to harbour a moderate- to high-density fox population (Harris 1981; Harris & Rayner 1986*a*; Harris & Smith 1987*a*), a situation rarely encountered in other European or North American cities. In many cases the densities of these urban fox populations are considerably higher than those found in front of the rabies wave in Europe. This combination of high-density fox populations and their close proximity to man and his domestic pets poses particular problems should rabies reach Britain, because not only is it more likely that animal to man transmission will occur than on the continent, but fox control at such high densities has not been attempted before. Therefore some technique was needed to determine how rabies would spread in urban fox populations, its persistence, and any particular problems of controlling the disease in such high-density fox populations.

The most obvious approach was to use a computer simulation to study sylvatic rabies outbreaks in urban areas. In recent years, several other authors have produced a series of models to examine the rate of spread, annual incidence of cases and the periodicity of rabies. These models have been produced for a variety of purposes, and have a varying reliance on the underlying fox biology. However, most suffer from a number of drawbacks for analysing the spread of rabies in urban foxes. Of the 18 such models published since 1973, seven did not consider natural mortality, four ignored reproduction, 14 did not consider fox dispersal separately and nine did not investigate fox control (table 1); 12 of these models utilized a spatial component (which would be vital in the examination of specific urban areas), but only two attempted to

Table 1. *A summary of factors included in the 18 rabies models reviewed in the text*

(Heterogeneous refers to the local distribution of fox density, rabies diffusion is the method of transmission, infectivity is the duration of time for which an animal is infectious, and fox dispersal refers to natural dispersal movements.)

	model																	
factor	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
spatial	y	y	y	—	y	—	—	y	y	y	—	—	y	—	y	y	y	y
heterogeneous	—	y	—	—	—	—	—	—	y	—	—	—	—	—	—	—	—	—
rabies diffusion	p	P	C	k	C	k	k	C	C	p	k	k	k	k	C	p	k	k
incubation period	v	f	f	v	f		v	f		f					v		v	f
infectivity	f	f	f	f	f			i		f					f		v	f
rabies control	—	V	—	b	c	—	b	c	—	c	—	—	—	b	b	c	—	—
fox dispersal	y	—	—	—	y	—	—	—	y	—	—	—	—	—	y	—	—	—
reproduction	y	—	y	y	y	y	y	—	y	—	y	y	y	y	y	y	—	y
natural mortality	—	—	y	y	y	—	y	—	y	—	y	y	y	y	y	y	—	—
stochasticity	y	y	—	—	y	—	—	y	y	—	—	y	—	—	y	—	—	—
continuous time	—	—	—	y	—	—	—	—	—	y	—	—	—	y	—	y	y	—

y, the component is included in the model; —, the component is not included in the model; a blank indicates that it was unclear if this component had been used in the model; k, rabies diffusion uses a constant; p, rabies diffusion uses set probabilities; C, rabies diffusion uses contact rates; P, rabies diffusion uses a Poisson distribution; f, the incubation or infectivity period is fixed; v, the incubation or infectivity period is variable; i, the incubation or infectivity period is instantaneous; c, control with culling has been investigated; V, control with vaccination has been investigated; b, control with both has been investigated.
Models: 1, Preston (1973); 2, Berger (1976); 3, Lambinet *et al.* (1978); 4, Anderson *et al.* (1981); 5, David *et al.* (1982); 6, 7, Bacon (1985*b*); 8, Ball (1985); 9, Garnerin *et al.* (1986); 10, Källén *et al.* (1985); 11, 12, 13, McAllister (1985); 14, Smith (1985); 15, Voigt *et al.* (1985); 16, Murray *et al.* (1986); 17, van den Bosch *et al.* (1990); 18, Gardner *et al.* (1990).

include the spatial heterogeneity of the fox population. Most of these models were designed to reproduce various factors involved in the spread of rabies, rather than to attempt to examine possible means of controlling the disease. In addition, they were mostly concerned with rabies spread at low and fairly homogeneous fox densities, such as those found on the continent, and not with the initial epizootic outbreak of the disease in a high-density, spatially heterogeneous fox population, such as those found in many British cities (Harris & Rayner 1986*b*).

Although many of the 18 models successfully simulated some aspects of the pattern of rabies spread found in Europe or North America, none of the models could easily be applied to studying rabies spread in specific British urban areas. Therefore, to investigate the effects of a rabies outbreak and methods of control in specific urban areas, it was necessary to develop a new model that included spatial and stochastic elements and the relevant aspects of the underlying fox biology. One consequence of such an approach is that the degree of realism required to simulate a rabies outbreak in specific urban areas results in a more complex model, which requires more underlying assumptions, thereby increasing the risk that the results are dependent on the exact assumptions that have been made.

A preliminary investigation into rabies control at high fox population densities, using one of the models already available (Voigt *et al.* 1985), was done by Smith & Harris (1989). With a homogeneous fox density of 1.82 family groups km^{-2}, this model showed that a low level of fox control may actually increase the local duration of the rabies incident without controlling and containing the outbreak. The same model was also used to examine the effects of changing the contact rate between infected and healthy foxes. This was achieved by adjusting the probability of each healthy individual becoming infected by a neighbouring rabid fox. Although there are no data on the level or rate of such contacts in the wild, Smith & Harris (1989) found that an approximation of this parameter was sufficient for many urban areas. However, the model of Voigt *et al.* (1985) could not be used for more detailed simulations because it could not be applied directly to the British situation. In particular, it could neither model spatially heterogeneous high-density fox populations nor measure the level of neighbour to neighbour rabies transmission across the border of the simulation. This latter point was especially important, as the aim of a control operation in Britain would be to contain the disease within the control zone and prevent it becoming established.

This paper is designed to extend the earlier work of Smith & Harris (1989). Here we detail the construction of a simulation model capable of replicating a high degree of spatial heterogeneity and able to measure both forms of rabies transmission (fox dispersal and neighbour to neighbour infection) to outside the simulation area. There was no attempt to model a rabies outbreak for long periods to examine the annual incidence of the disease, speed of propagation or fox population recovery. Instead, the focus was on the outbreak of the disease within an urban area, and its immediate control, because the aim of any control operation will be to eliminate the disease before it becomes enzootic (Harris *et al.* 1991). The effects of fox density heterogeneity were examined to find out how this affected the disease propagation, and a rabies outbreak in actual urban areas was simulated. The

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

relevance of these simulations and their results to rabies control are discussed, as are the limitations of this approach.

2. DATA BASES

The early data on fox biology are summarized by Lloyd (1980), and more recent data, particularly as they relate to the spread of rabies, in the papers in Bacon (1985*a*). Therefore, in this section, we will only review those studies on urban foxes that are of relevance to the construction of our rabies model. Most work on urban foxes has been in Bristol, where the foxes have been studied continuously since 1977. One of the principal aims of these studies was to understand the demography and behaviour of this urban fox population, and to define the major habitat variables affecting these parameters so that the data could be extrapolated to other urban areas in Britain. Although the mean fox density in Bristol is comparatively high (Harris & Smith 1987*a*), there is a considerable range of fox densities in different parts of Bristol (Harris 1981), and so the data from this city could be used to examine the effects of density on urban fox population demography. Throughout this paper, all foxes are assumed to be born on 1 April each year (in Bristol 66% of all cubs are born before 1 April, 34% soon after), and the term cubs is used to describe animals less than six months old, sub-adults animals six to twelve months old, and adults animals over a year old.

Placental scar counts were used to determine mean litter size (table 2). For Bristol vixens in their first breeding season, litter size was noticeably smaller, and the proportion of non-breeding vixens significantly higher. There was no decrease in litter size with age, although the proportion of non-breeding vixens increased in animals in their fifth or subsequent breeding season. As less than 5% of all vixens reach five years old, for the present analysis only two age categories were recognized (animals in their first breeding season, and older vixens), with the older vixens having a mean litter size (±s.d.) of 4.76±1.53. These results agree with the majority of other studies, which also report a mean litter size of four to five (for example, Fairley 1970; Lloyd 1980; Stubbe 1980; Allen 1984).

Cementum annuli were used to determine age and mortality rates (Harris 1978). Overall annual natural mortality in Bristol was 0.573 for male cubs–sub-adults, 0.544 for female cubs–sub-adults, 0.505 for adult males and 0.468 for adult females (Harris & Smith 1987*b*). There was no evidence for increased mortality levels among the older animals, and so for the present analysis the data were combined into four categories, adults and cubs–sub-adults, males and females. As there were seasonal differences, monthly mortality rates were calculated for each of the four age–sex categories (table 3).

To mark a sample of animals to monitor dispersal, entire litters of cubs were dug out of earths or bolted from cover into long nets (Harris & Trewhella 1988), or caught in baited traps (Harris 1985). Animals were ear-tagged, sexed and released at the point of capture. Dispersal distances from tagging returns for a number of fox populations in a variety of habitats were found to follow a negative exponential curve related to fox population density (Harris & Trewhella 1988; Trewhella & Harris 1988). Fox dispersal occurred mainly from October to March; for Bristol, the probabilities of an individual dispersing for each of these months, and the minimum and maximum distances dispersed in areas of low (less than 1.5 fox family groups km^{-2}), medium (1.5–3.0 fox family groups km^{-2}) and high (greater than 3.0 fox family groups km^{-2}) population density are given in table 4. Minimum dispersal distance is the diameter of the average home range at each density (Trewhella *et al.* 1988), as dispersal, by definition, results in a movement to a different home range, and the maximum dispersal distances used were those of Trewhella & Harris (1988) in their model of fox dispersal. The mean dispersal distance for the Bristol fox population is low in comparison with other studies; this is a consequence of the much higher fox densities found in many British cities (Trewhella *et al.* 1988).

In addition to population parameters it was necessary to determine the number and distribution of foxes, both for Bristol and for any other urban area that may be used in the simulation model. The census method first used in Bristol involved surveying a selected area of a few square kilometres during the spring for litters of fox cubs. As foxes live in family units and breed synchronously once per year, each litter of cubs

Table 2. *Variation of litter size with age for vixens in Bristol, based on placental scar counts; n = 252*

(From Harris & Smith (1987*b*).)

age	mean litter size (±s.d.)	percentage of vixens without placental scars
first breeding season	4.53±1.54	24.4
second breeding season	4.90±1.42	17.1
third breeding season	4.75±1.73	19.1
fourth breeding season	4.73±1.66	2.9
fifth plus breeding season	4.94±1.70	28.0

Table 3. *Monthly mortality rates for male and female, adult and cub–sub-adult foxes in Bristol; n = 1701*

	males		females	
month	adults	cubs–sub-adults	adults	cubs–sub-adults
April	0.035	0.137	0.041	0.129
May	0.039	0.045	0.055	0.052
June	0.020	0.040	0.035	0.067
July	0.028	0.048	0.025	0.037
August	0.014	0.036	0.023	0.042
September	0.039	0.035	0.034	0.037
October	0.036	0.044	0.044	0.044
November	0.046	0.044	0.049	0.032
December	0.041	0.039	0.035	0.039
January	0.121	0.062	0.062	0.025
February	0.069	0.032	0.041	0.034
March	0.029	0.035	0.036	0.030

Table 4. *Probabilities of dispersal in male and female sub-adult foxes in Bristol, and the minimum and maximum distances travelled*

(Calculated from tagging returns from 710 dog foxes and 677 vixens)

	probability of dispersing	
month	male sub-adults	female sub-adults
October	0.068	0.030
November	0.102	0.030
December	0.182	0.136
January	0.159	0.045
February	0.102	0.045
March	0.057	0.030

	dispersal distance/km			
	males		females	
fox density	minimum	maximum	minimum	maximum
< 1.5 family groups km^{-2}	1.2	30.8	1.2	12.6
1.5–3.0 family groups km^{-2}	0.8	12.1	0.8	4.3
> 3.0 family groups km^{-2}	0.6	7.1	0.6	2.4

represents one fox family group. To calculate the number of foxes throughout the rest of the city, school children were asked to record all fox sightings over a period of one month. These sightings were recorded by 500 m × 500 m (25 ha) squares, and the number of sightings per litter in the surveyed area was used to calculate the fox family density in all of the remaining 25 ha squares of the urban area. Despite the simplicity of the approach, continuing work in Bristol over the succeeding ten years has suggested that the survey results were accurate.

The same technique was subsequently applied to a number of cities throughout southern England (Harris & Rayner 1986*b*), and the results used to produce regression models to predict fox density for other urban areas (Harris & Rayner 1986*c*; Harris & Smith 1987*a*). Evidence to support these estimates came from the results of three independent urban fox surveys, all of which fell within the confidence limits of the original predictions. Page (1981) calculated the mean fox density of the London Borough of Hillingdon at 1.0 fox family groups km^{-2}. Page's survey area corresponded to Ruislip–Northwood and Uxbridge in the analysis of Harris & Smith (1987*a*), and the mean estimate for these two areas was 1.1 fox family groups km^{-2}. A more recent survey of Uxbridge, using the survey method of Harris (1981), revealed a density of 1.1 fox family groups km^{-2} (N. Shennan, personal communication). Finally, a survey of Reading Borough showed a fox density of 0.63 family groups km^{-2} (P. Cox, personal communication), which falls within the 95% confidence limits of Harris & Smith (1987*a*) of up to 0.7 family groups km^{-2}.

In a rabies event, it will be necessary to produce local fox population estimates quickly. The model of Harris & Rayner (1986*c*) used data that had to be extracted from large-scale maps, and was therefore time consuming to apply, and could be open to subjective treatment. To avoid these problems, the mean fox density in each electoral ward of 14 cities surveyed between 1979 and 1986 was calculated and combined with data from the 1981 Census (Smith 1989). These data were then used to produce a predictive regression model, which had an explained variation of just over 60%, slightly less than the model of Harris & Rayner (1986*c*). However, because it did not rely on habitat data derived from maps, it can produce predictions quickly by electoral wards for every urban area in England and Wales. There are no comparable data on the density of rural foxes, but a crude estimate of rural fox density can be produced by using the figures of Macdonald *et al.* (1981). These authors estimated the number of adult foxes per 10 km^2 for each of 32 land classes found in Britain. Their figures are less reliable than the predictive estimates for urban areas, but will suffice until more exact rural data are available.

3. THE MODEL

The major limitation of previous models, when trying to simulate the pattern of rabies spread in a specific fox population, was their inability to reproduce the differing home range sizes found at different fox densities. In Bristol the minimum and maximum surveyed fox densities are 0.3 and 4.8 fox families km^{-2}, respectively (Harris 1981). Although home range sizes have not been measured for this range of population densities, an estimate was made using the equation of Trewhella *et al.* (1988). This gave a home range area varying between 2.7 km^2 (at the lowest densities) and 0.3 km^2 (at the highest densities), almost a tenfold change in size. At high population densities, it would appear that there is an increase in the amount of overlap between neighbouring home ranges, with a minimum threshold range size (Trewhella *et al.* 1988). To accommodate the variation in range sizes, the simulation area was mapped with a grid square size of

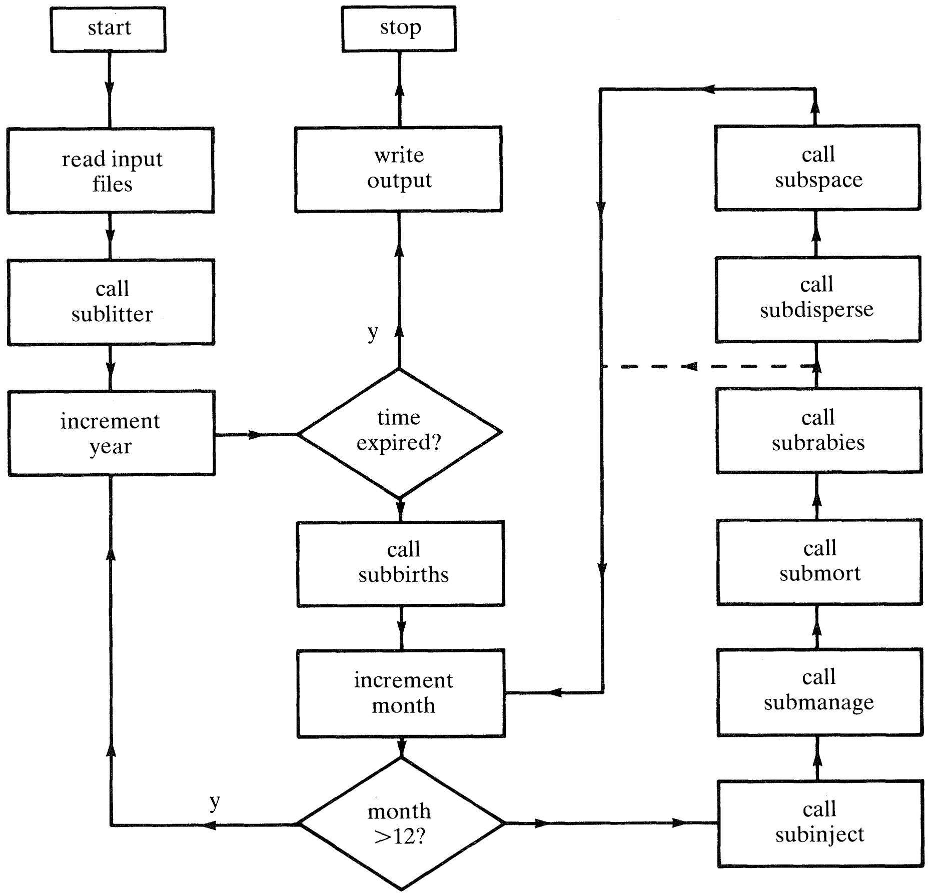

Figure 1. Flowchart showing the operation of the Bristol rabies model. The broken line is followed in months 1–6 (April–September) of the fox year.

25 ha. This was chosen because it corresponded with the grid size used for the fox surveys, was found to be satisfactory for urban fox dispersal simulations (Trewhella & Harris 1988), and also permitted a maximum density of four fox family groups km^{-2}. The areas of greater fox density within most cities are very small; in Bristol for instance, a high-density city, the total such area is about 2.5 km^2 (2.2 %), so this upper limit on population density was unlikely to pose a problem. To produce larger home range sizes, each fox home range was programmed to consist of one or more 25 ha squares. Each home range area was static during a single simulation. The objective was to simulate an actual rabies outbreak, and so the grid had to be large enough to accommodate a control zone of radius 19 km, the size designated in the Ministry of Agriculture, Fisheries and Food's rabies contingency plans (C. L. Cheeseman, personal communication). Hence the maximum grid size was set at 99×99 squares (49.5 km $\times$ 49.5 km).

In addition to being able to reproduce the exact fox density pattern found within, and surrounding, a city, the model had to be capable of simulating the effects of large topographical barriers to fox movement. As foxes in Bristol have been radio-tracked crossing the tidal reaches of the River Avon (Harris 1986), only those bodies of water greater than 500 m across were considered as barriers to movement. For the model, when a dispersing fox met a topographical barrier it continued the remaining dispersal distance in a new direction chosen at random.

The simulation model was written in FORTRAN 77 and constructed to follow the fox year. As the average incubation time for rabies in the red fox is about 28 days (Sikes 1962; Parker & Wilsnack 1966; Tierkel 1966; Black & Lawson 1970), a discrete time simulation model with monthly steps was used. This approach has also been used successfully by Preston (1973), David *et al.* (1982), Bacon (1985*b*) and Ball (1985) to simulate the patterns of rabies spread. The following assumptions were inherent within the program: (i) foxes live in family groups; (ii) family groups are mostly contiguous with each other; (iii) local fox density is known with some degree of accuracy; (iv) home range size can be adequately described in terms of 25 ha units; (v) the minimum incubation period of rabies approximates to one month; (vi) the infectious period is more or less instantaneous compared with a timescale of one month; and (vii) rabies is invariably fatal to foxes. The latter assumption is known to have been violated, although less than 3 % of foxes inoculated with rabies virus survive to become immune (Steck & Wandeler 1980; Voigt *et al.* 1985), so this violation can be effectively ignored in the short term.

At the start of each simulation, foxes were allocated to home ranges as follows: one male and one female plus, with a probability of 0.80 or 0.58 respectively, a second male or female. Of these foxes, 0.47 were sub-

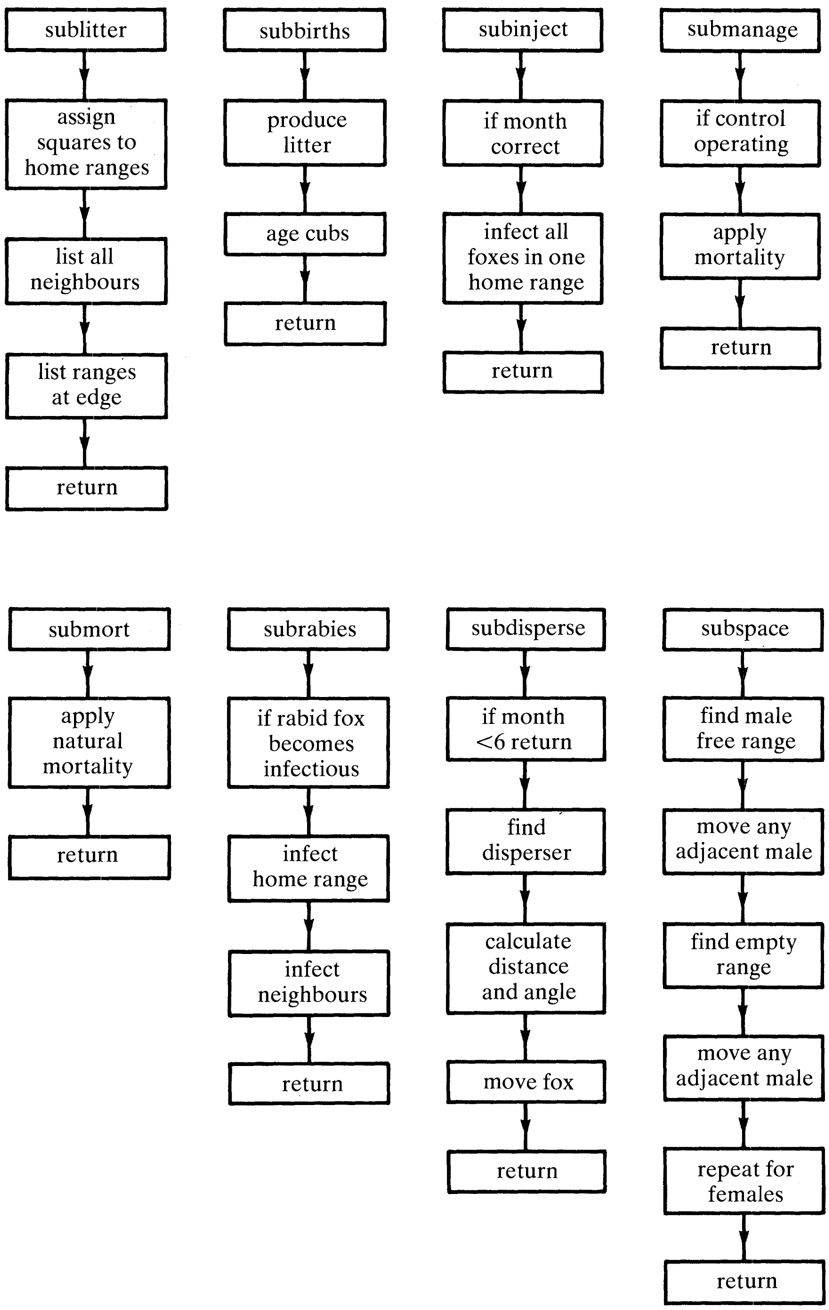

Figure 2. Subroutines used in the Bristol rabies model.

adults. These figures were designed to represent the total number of foxes spatially, but not necessarily socially, attached to each fox family group (Harris & Smith 1987*b*). At the start of each year, all sub-adult foxes became adults, and all female foxes, which were not randomly determined as non-breeding, produced a litter of cubs, with a limitation of one litter per home range. As some home ranges were occupied by more than one vixen, this meant that some vixens in a fox family group would not be given the opportunity to reproduce. To compensate for this, the proportion of non-breeding vixens used in the model was reduced in proportion to the number of these non-breeding vixens in the original population. This gave a level of productivity equal to that observed amongst the Bristol vixens at the start of the simulation, and, as vixens were killed by rabies or culled, the overall productivity increased slightly, as a result of a reduction in the number of family groups with a second vixen present.

A flowchart is shown in figure 1, and the subroutines in the program in figure 2. Rabies was introduced by infecting all foxes within a specified, central, home range at the beginning of any month. If fox control was undertaken during that month this was performed next, giving each fox an equal probability of being culled. Natural mortality, at specific levels for males and females, adults and cubs–sub-adults, occurred next, and was followed by the rabies subroutine. This utilized five variables which enabled infectious rabid foxes to: (i) infect other foxes within the same home range; (ii) infect neighbouring cubs in spring and summer; (iii) if male, to infect adjacent females during winter; and (iv) for any fox to infect any neighbouring fox other than those above. In addition, there was a set

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

probability of an infected fox becoming infectious after each monthly step. These routes of infection were similar to those used by Voigt *et al.* (1985), and the monthly probability of becoming rabid, 0.42, was taken from their model.

There were two additional subroutines called during months seven to twelve (October to March). Male and female sub-adult foxes were given set probabilities of dispersing in each month, and dispersal distances followed a negative exponential curve where the minimum and maximum distances were dependent upon fox density (table 4). This subroutine was that used by Trewhella & Harris (1988) in their dispersal simulations. The dispersal subroutine was followed by a spacing subroutine to allow empty home ranges, or home ranges devoid of one sex, to be filled by foxes from adjacent home ranges. This routine spaced out excess foxes, and paired males and females before the next breeding season. As a consequence, the spacing routine increased between home-range movements of individuals when the population was culled.

The model can be summarized by the following finite rate difference equations to describe the numbers of adult and juvenile male and female foxes. 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 which became infectious and died.

For healthy juvenile males, the equation:

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

was used. The term $(1-d_{tz})$ represented animals dispering from location z, and N_{tz} the number of immigrant healthy juvenile males.

For infected juvenile males, the equation:

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

was used, where the terms $1-d_{tz}$ and N_{tz} represented dispersal of 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, the equations used were:

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

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

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

and

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

The litter size of any resident breeding female was l and the sex ratio r. Equations (1)–(6) and (8) were also used to describe the female populations, and equation (7) was replaced with:

$$M_{tz} = l(1-r). \quad (9)$$

A full sensitivity analysis of a difference equation model of this form is difficult, because of the number of factors and interaction effects that are possible. However, the construction of the model was based on the approach of Voigt *et al.* (1985), for which a thorough sensitivity testing was performed. In addition, the model of Voigt *et al.* (1985) was adapted for a preliminary investigation into the spread of urban rabies (Smith & Harris 1989), and the two models show a similar level of sensitivity to the input parameters for which variance is required. The output of the model shows a high level of sensitivity to very low probabilities of infection, below those used in the analysis, and to very low fox densities, again lower than any which have been simulated. The latter appears to be a result of the scaling of the model, and is not a limitation under the conditions for which the model has been constructed.

For this model, a change in fox density would have no effect on the spread of rabies per se, and so it was necessary to adjust the contact probabilities by some function of fox density. As there were no reliable data from which to produce such a function, a simplifying assumption that the relation is both monotonic and linear was made. The contact probabilities used in the input file were assumed to be for a fox density of four family groups km^{-2}, and they could be proportionately reduced in a linear manner by a direct relation with the area which the home range encompassed. Stubbe (1980) calculated a fox family density of 0.8 km^{-2} for a rabies endemic area of the Hakel, and by measuring the home ranges of rabid foxes studied by Andral *et al.* (1982), an approximate density of 0.4 km^{-2} was obtained. The simulation model of Voigt *et al.* (1985), which used the same forms of fox contact as the present model, produced endemic rabies when these probabilities of contact approximated 0.2. The simplest linear model to give a contact probability of 0.2 for the above home range areas is:

$$P = 2/\text{home range area}; \quad \text{maximum} = 1.0, \quad (10)$$

where P is the proportion of the contact probability to be used, and the home range area is measured as the number of 25 ha squares. As rabies outbreaks can occur in areas of relatively low fox density, at a density of 4.0 fox family groups km^{-2}, the probability of contact between a healthy fox and an infectious one within the same social group must be close to unity. The following contact probabilities were used in the model: within-group infection 0.900; with neighbouring cubs during summer 0.300; between males and females during winter 0.900; and any other neighbour to neighbour infection 0.600. Small changes in these contact figures had little overall effect when the fox density was as high as that found in Bristol (Smith & Harris 1989).

Two other input files were used; these were both numeric maps of the simulation area. The first identified squares into which foxes could neither move nor reside, and also identified squares which lay outside the control area. The second file identified the location of fox family groups. When simulations were run for actual geographic locations, a grid was prepared onto which the urban boundary was drawn. Coastlines and all bodies of water over 500 m wide were mapped onto the grid from Ordnance Survey maps. Any areas where fox control would not occur were then mapped onto the grid, and the final grid was then copied to the computer. A second grid showing the urban boundaries was produced. Fox family groups were then located within the urban boundaries as designated by the fox density predictions (Smith 1989) or the results of an actual survey (Harris & Smith 1987*a*). For rural areas, the remainder of the grid map was divided into sub-areas. Within each sub-area, a sample of 1 km squares were identified to a particular land class and fox density (in family groups km^{-2}), estimated by using the figures of Macdonald *et al.* (1981), with the assumption of two adult foxes per family group.

During an outbreak of rabies in Britain, fox control would be instigated at two-month intervals (Lloyd 1976). Baiting experiments in the city of Bristol showed that less than 30% of the fox population might be reached in any one control operation (Trewhella *et al.* 1991). These experiments took place without dogs and cats being restricted, as would occur in a real rabies event. Such controls on pets, plus an increase in the number of baits laid per unit area, may increase the rate of bait uptake by foxes. Therefore, for these simulations, a 40% level of fox control was applied every two months as necessary. Hence the total proportion of the fox population removed would be 40%, 64%, 78%, 87% and 92% for up to five control campaigns.

Although, in a real event, fox control would commence within 14 days of notification (C. L. Cheeseman, personal communication), it is possible that the original rabies introduction will pass unnoticed, and a delay of a few months may occur (Harris *et al.* 1991). Bacon (1981) suggested that a delay of some two to six months is possible because of the expected low reporting rate of any individual infected fox. Pech & Hone (1991) estimated that in this time rabies may have spread 5–35 km from the point of initial infection before detection, giving a maximum distance between infected foxes of twice this distance. To look at the consequences of a delay in reporting, and the effects of rabies introduction at different times of the year, rabies was introduced in the simulation in both summer and autumn, both with and without a delay in implementing control operations.

Output from the model consisted of monthly numerical summaries showing the total number of foxes, the number of infected foxes, and counts of the numbers and health of all foxes which either occupied peripheral home ranges or emigrated from the simulation area, and a graphical output showing the number of healthy and infected foxes in each home range for each month of the simulation.

4. RESULTS

(*a*) *The effects of fox population heterogeneity on rabies spread*

Two simulation areas were constructed to examine the mean and variance of the monthly velocity of the rabies front. Both were 99 squares long by 12 squares wide. In the first simulation area, fox family groups

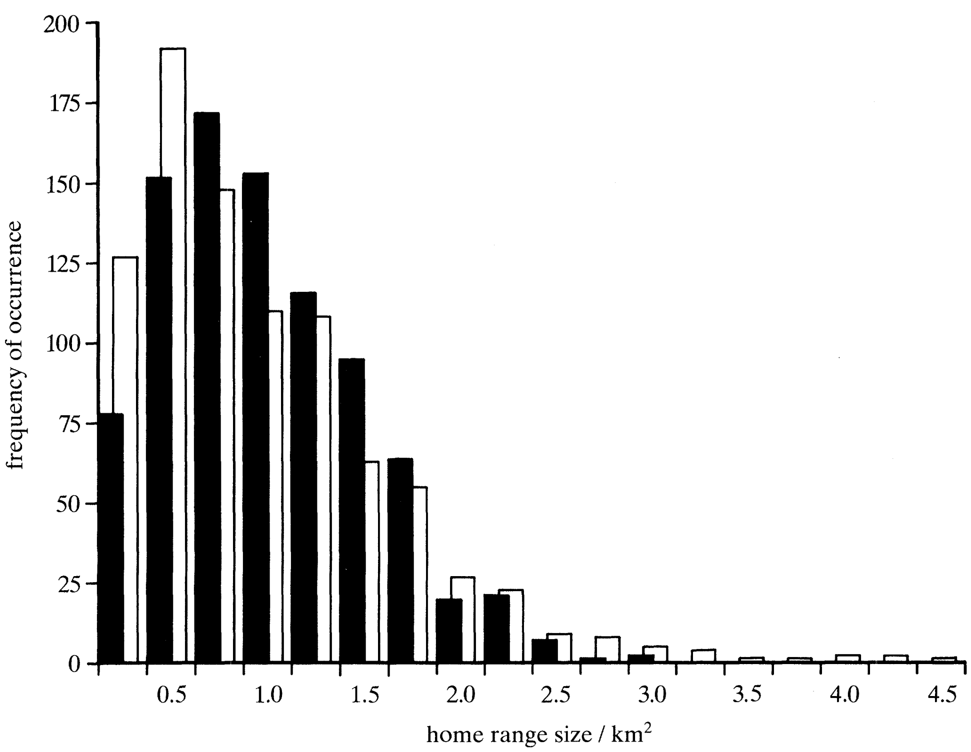

Figure 3. Frequency distribution of home range sizes for both the homogeneous (solid columns) and heterogeneous (open columns) fox densities used to study the effects of spatial heterogeneity on the pattern of rabies spread.

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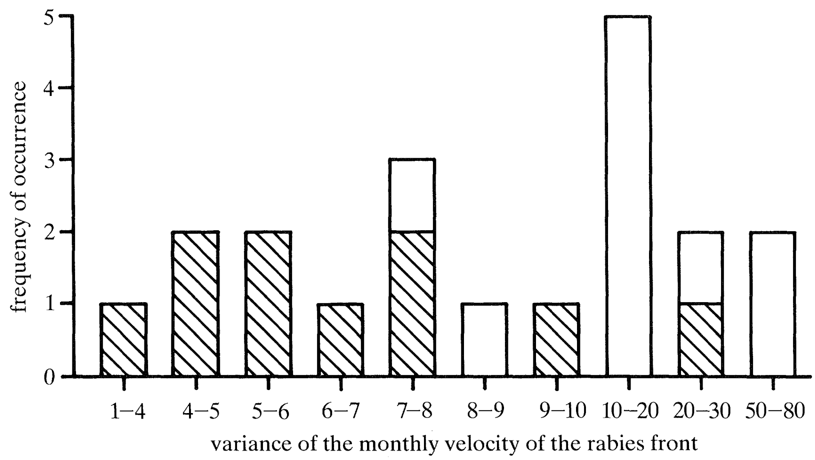

Figure 4. Variance of the monthly velocity of the rabies front for both homogeneous (hatched) and heterogeneous (open) fox densities. The variance is measured in units of 25 ha to correspond with the scale of the simulation model.

were evenly spaced (mean fox family density 1.00 km^{-2}, s.d. 0.52 km^{-2}), but in the second they were clumped (mean fox family density 1.00 km^{-2}, s.d. 0.67 km^{-2}) (figure 3). A total of 10 runs were done with each of the homogeneous and heterogeneous densities. Analysis of variance was done on the mean monthly velocity of the rabies front; no differences were found between homogeneous and heterogeneous fox densities (mean velocity 1.2 km per month, $F = 0.02$, $p > 0.900$). Although the annual velocity of the rabies front in these simulations (14.4 km) was low when compared with continental rates of spread, this was a feature of the high fox population density used in the simulations. Fox densities similar to those found in Europe had a rate of rabies spread similar to that found in Europe.

The range in the variance of the monthly velocity (in 25 ha squares) for each run is compared in figure 4; the variance in the monthly velocity of the rabies front was greater for the heterogeneous fox population. Small pockets of infection preceding the rabies front were more common in the heterogeneous fox population. The exact variances were compared by using a Wilcoxon Rank Test; the difference in variance was very significant ($z = -2.87$, $p < 0.005$), suggesting that the monthly velocity is more changeable, and therefore less predictable, for the spatially heterogeneous fox population.

(*b*) *The success of rabies control in specific urban areas*

The urban areas of Bournemouth and Poole, Bristol, Leicester and the West Midlands conurbation were chosen to give a range of fox population densities. Fox surveys had been done in these cities, and the distribution and density of foxes in each city is shown in figure 5. The mean urban fox densities and the overall mean fox densities for each size of simulation area are shown in table 5. The Bournemouth and Poole simulation included a total urban area of 83 km^2, and part of the coast of the English Channel. The Bristol simulation included the urban area of Bath, a total of 137 km^2 of urban land, two large reservoirs and part of the Severn Estuary. Leicester had a total urban area of 89 km^2, and the West Midlands conurbation covered the contiguous urban areas of Birmingham, Dudley, Sandwell, Solihull, Walsall and Wolverhampton, a total of 589 km^2. Each city was placed centrally in the simulation area, and rabies was introduced into the fox family group that included the centre square within its home range.

Table 5. *Overall fox population densities (family groups* km^{-2}*) used in each simulation area*

location	urban area only	size of control area (km) 15 × 15	17 × 17	19 × 19	23 × 23
Bournemouth–Poole	1.73	0.73	0.71	0.70	0.67
Bristol	1.82	0.84	0.80	0.77	0.74
Leicester	0.43	0.62	0.63	0.64	0.64
West Midlands	1.16	1.03	0.96	0.91	0.85

Figures 6–8 show the spread of rabies in Bristol, Leicester and the West Midlands with no control, two bouts of 40% fox population reduction and four bouts of 40% population reduction. The control zones had a radius of 19 km. In these examples, rabies was introduced in month 6 (September) and followed until month 48 (March). Table 6 summarizes the numerical results from these simulations. From the initial point of infection, rabies cases spread outward by neighbour to neighbour transmission, resulting in a radial pattern where the total number of cases per unit area was a factor of the local fox population density and time of year. When no control was done, dispersal resulted in small groups of rabies cases ahead of the radial front wave. With fox control, these were either the result of fox dispersal or neighbour to neighbour transmission followed by successful culling of the intervening foxes. As the front wave spread through the susceptible fox population, a central area with very few surviving foxes was left. With increasing levels of fox control, the rate of spread became slower and less regular. Finally, with 87% fox control, which successfully eradicated rabies in all instances, there were only small pockets of infected animals and no radial spread.

As table 6 shows, where no control was instigated the disease wave moved out of the simulation area entirely in 35–37 months for all four cities, whereas with a 64%

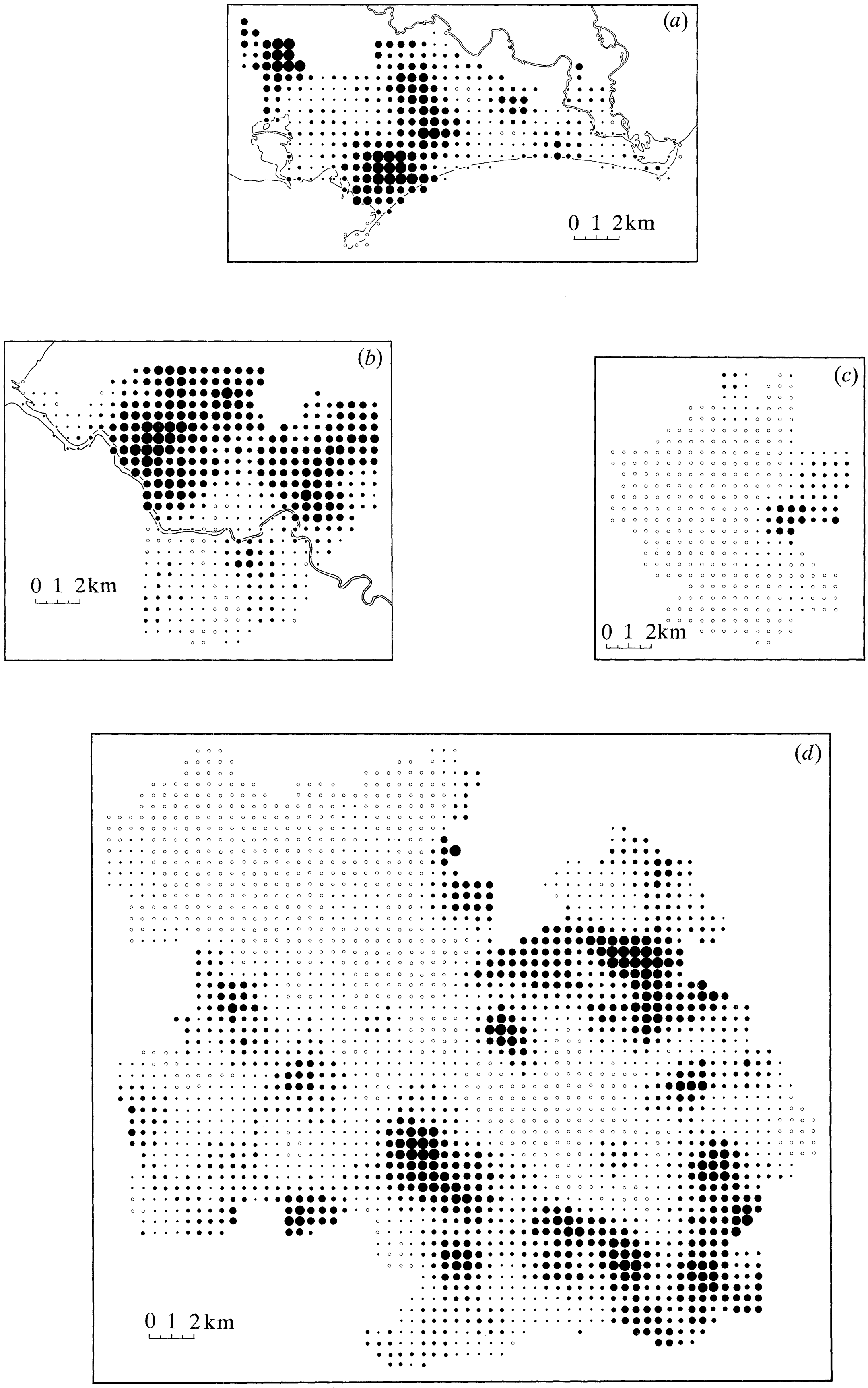

Figure 5. Fox distribution and density for the four urban areas for which the pattern of rabies spread was analysed in detail. Each symbol denotes the density calculated for that particular 25 ha square. The symbols, open circles and increasingly large closed circles, denote: < 0.5; 0.5–1.0; 1.0–1.5; 1.5–2.0; 2.0–3.0; 3.0–4.0; and 4.0–5.0 fox family groups km^{-2}, respectively. (*a*) Bournemouth and Poole, surveyed in 1981 (from Harris & Rayner (1986*b*)). (*b*) Bristol, surveyed in 1979–1980 (from Harris (1981)). (*c*) Leicester, surveyed in 1984. (*d*) the West Midlands conurbation, surveyed in 1982 (from Harris & Rayner (1986*b*)).

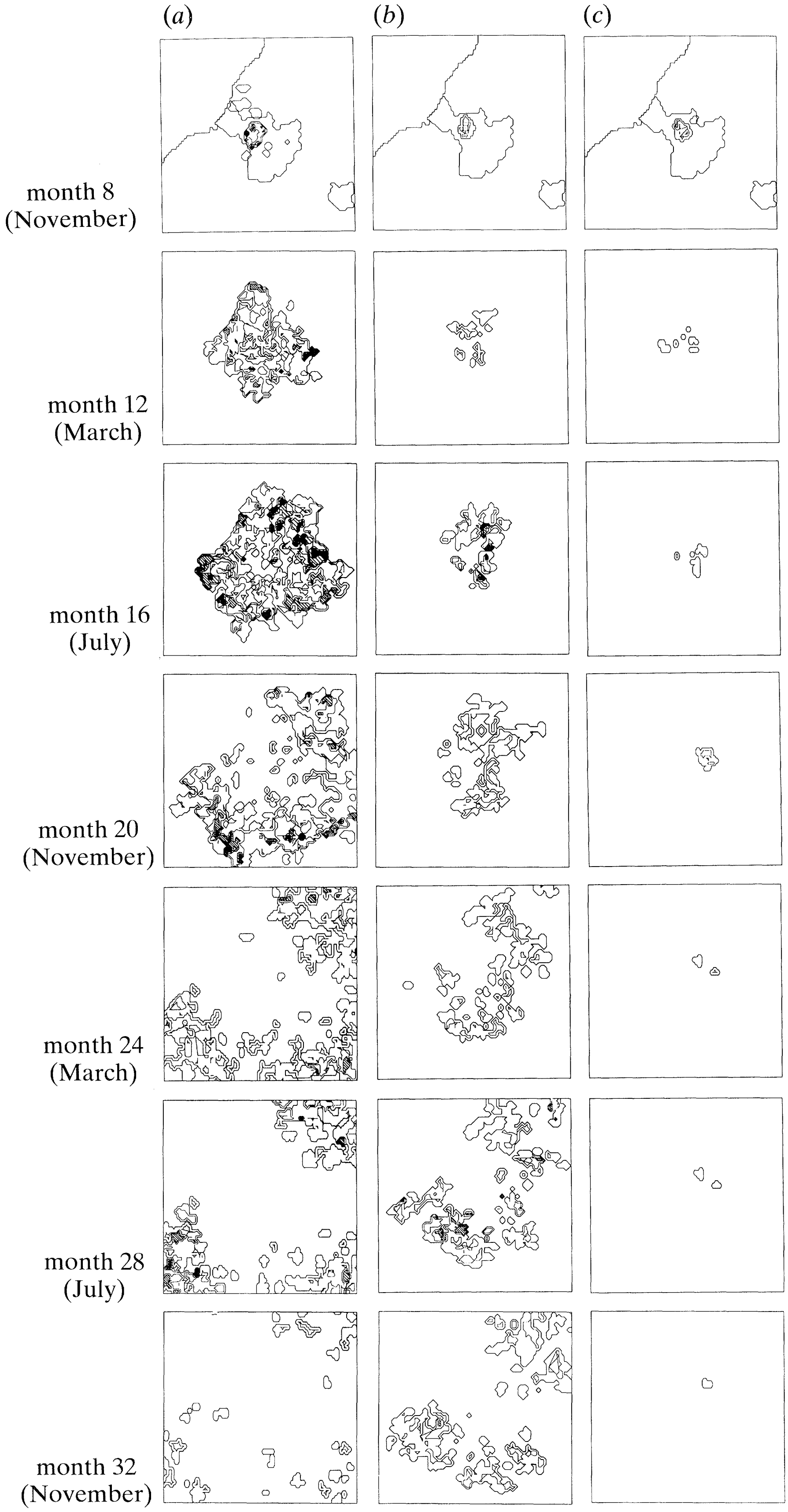

Figure 6. Four-monthly pictures of the simulated spread of rabies in the fox population in and around Bristol. The area depicted is 49.5 km × 49.5 km. (*a*) No control, (*b*) 64 % control, (*c*) 87 % control. Successive contours represent 1–2, 3–4, 4–6 (hatched) and greater than 6 (solid) infected foxes per home range. In these latter instances, many of the infected animals were sub-adults. Rabies was introduced in month 6 (September) and followed until month 48; only the results until month 32 are illustrated. The coastline is shown in month 8, as is the boundary of the cities of Bristol (centre) and Bath (lower right), but thereafter these are omitted for clarity.

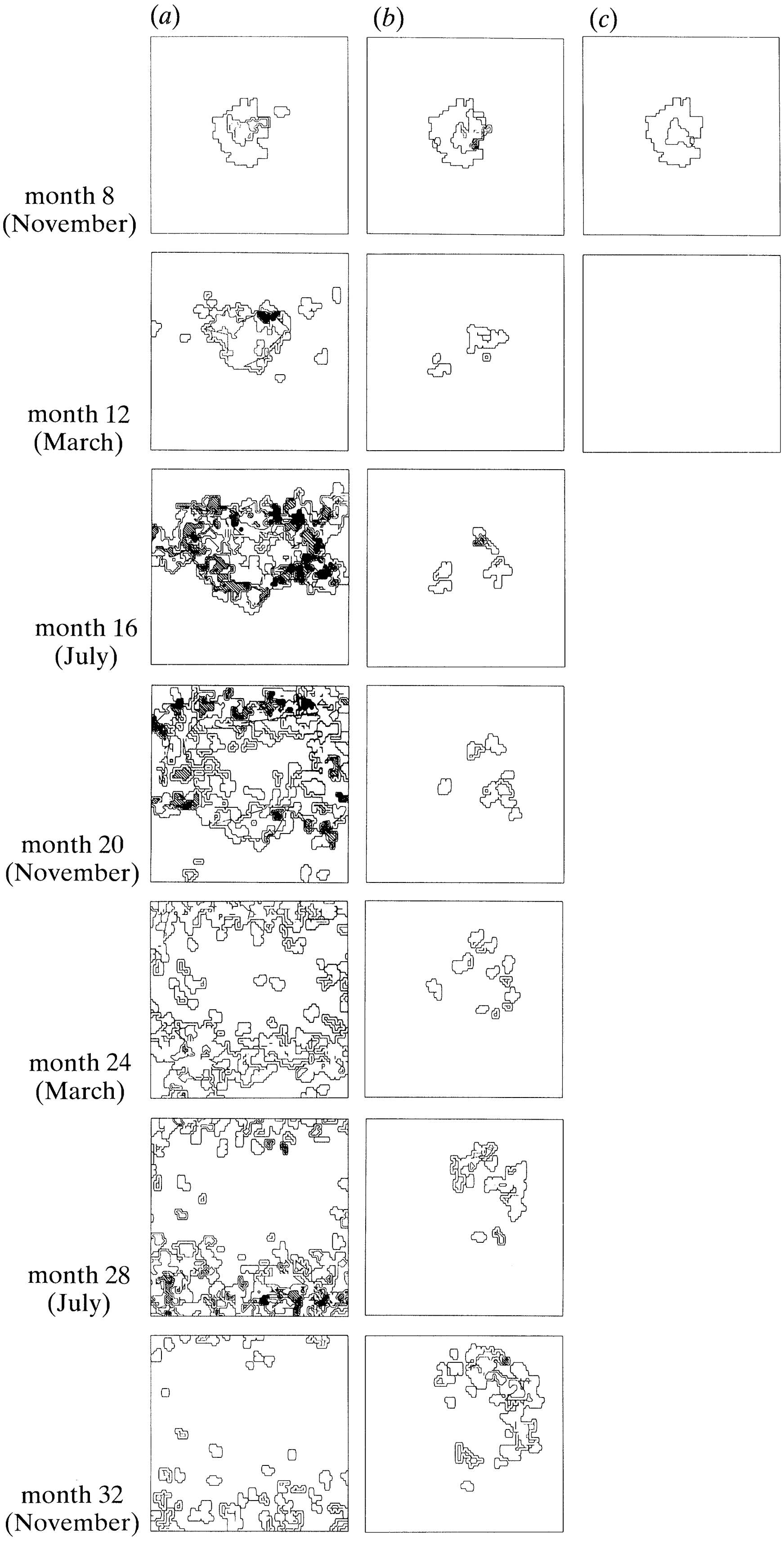

Figure 7. Four-monthly pictures of the simulated spread of rabies in the fox population in and around Leicester. Legend as in figure 6. The boundary of the city of Leicester is shown in month 8, but thereafter omitted for clarity.

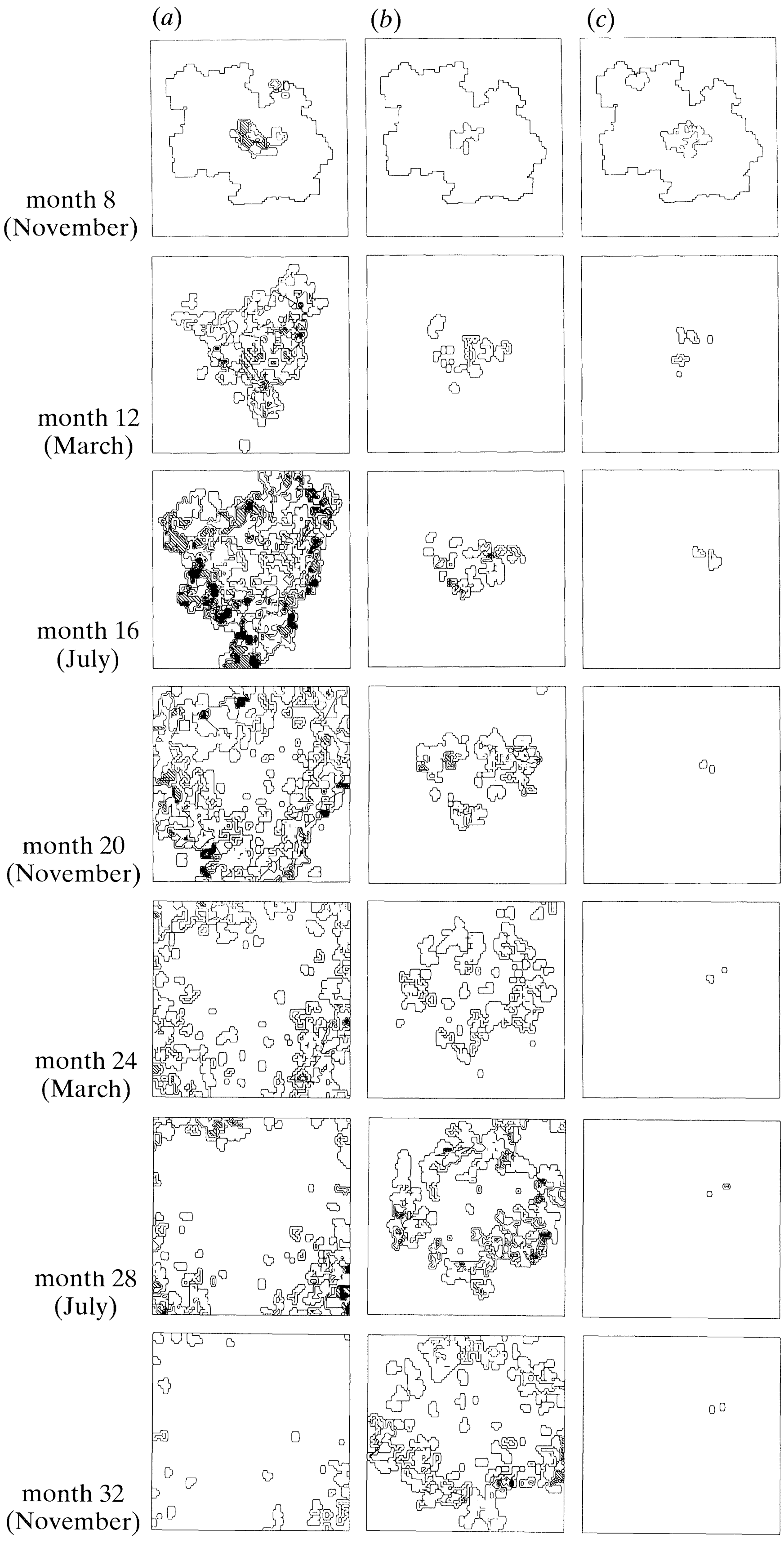

Figure 8. Four-monthly pictures of the simulated spread of rabies in the fox population in and around the West Midlands conurbation. Legend as in figure 6. The boundary of the West Midlands conurbation is shown in month 8, but thereafter omitted for clarity.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Table 6. *A summary of the effect of rabies on three urban fox populations under three control régimes*

Location	Bristol			Leicester			West Midlands		
level of control[a]	0%	64%	87%	0%	64%	87%	0%	64%	87%
duration in months	35	42+[b]	41	37	42+[b]	5	35	42+[b]	34
number of infected foxes	5131	2514	124	5286	2074	4	7658	3690	109
number of rabid emigrants	23	17	0	27	22	0	31	14	0
delay in peripheral occupancy	11	16	N/A[c]	5	28	N/A[c]	7	13	N/A[c]

[a] Level of control is the percentage of the fox population removed in successive 40% campaigns.
[b] Rabies was still present in month 48 at the end of the simulation.
[c] N/A denotes that no infected foxes became resident in peripheral home ranges.

level of control a slower rate of spread occurred, so that infected foxes were present in all months of the simulation. However, this level of control reduced the total number of infected foxes during the simulation to 45% of the uncontrolled level, and also reduced the numbers of infected foxes dispersing beyond the simulation area. With 87% control, the duration of the disease incident was still up to 41 months (in the case of Bristol), although the disease was successfully eradicated, and only 1% of the uncontrolled number of foxes were infected. As 87% of the fox population were removed, the incidence of the disease was also much reduced.

To examine the effects of different levels of control on the chances of containing a rabies event, the number of rabid foxes moving out of the control zone, the time taken for rabies to reach the edge of the simulation area, and the number of cases when rabies did not reach the periphery of the control zone in the same four urban areas, a control radius of 19 km was used; the number of simulations performed for each level of control depended upon the variability of the results. Table 7 summarizes the results. For all four urban areas, the number of infected foxes leaving the simulation area decreased, and the mean delay to peripheral occupancy increased, as the level of control increased. With a 92% level of control, only a fox that dispersed within the first few months of the rabies incident, and proceeded to move a long distance, managed to reach the peripheral home ranges. Low levels of fox control (up to 64%) were only successful in containing the disease in simulations for the West Midlands and Leicester, and even in these cases the best success rate achieved was 10%. The two urban areas with the highest fox densities, Bournemouth–Poole and Bristol, showed no success with low or moderate levels of rabies control, but had the highest rates of success (100% and 98%) at the highest level of control (92%). These two areas also showed the longest delays before infected animals were resident in home ranges on the periphery of the simulation area.

To illustrate the total number of foxes, the number of infected foxes, the persistence of rabies, and the number of infected foxes resident in home ranges on the periphery of a control zone with different levels of control, a three year simulation of a 25 km × 25 km square centred on Bristol was used (figure 9). The year began on 1 April, and rabies was introduced in September. For the uncontrolled population, 50 simulations were run, with 20 for each of the controlled populations. The timing of each 40% cull is shown on the figure, as are the months during which infected foxes dispersed out of the area. With the uncontrolled outbreak there was a dramatic decline in the fox population within a year, and the sudden rise in the number of infected foxes living at the edge of the simulation area shows the speed which the wave front attained as it passed out of the area. The fox population decline thereafter was caused by small pockets of infected animals left in the tail of the wave front. Successive culls had significant effects in reducing absolute numbers of infected animals, but three culls produced an endemic situation within the simulation area. This situation was stable, and showed the effect of a high level of culling which failed to eradicate the disease.

(*c*) *The effects of timing of the outbreak and a delay in control operations on the probability of eliminating rabies*

To examine the effect of the time of year of the rabies outbreak on the chances of successful control, the same four cities were used. Rabies was either introduced at the beginning of month 3 (June), when the cubs are still around the natal earth and extra-territorial movements by the adults are rare, or month 6 (September), immediately before the main dispersal period, when there is the greatest potential for geographic spread. In addition, for each case, rabies control began either in the following month or after a delay of three months. The results were similar for each city; a three month delay in the onset of control generally reduced the chances of successfully controlling the disease by 10–20%. For the lowest density fox population (Leicester), this almost reached a 40% reduction. For all four cities the maximum difference in the chances of successful control occurred with intermediate levels of fox control (about 78%), and at higher levels of population reduction this difference was reduced to below 10% in almost all instances (again Leicester had the greatest difference, 22%).

A change in the time of the rabies outbreak had less effect on the chances of successful control. The mean difference in all of the simulations was less than 10%, again with Leicester, the lowest density population,

Table 7. *Results of a number of simulations, with varying levels of control, for each city*

(In all cases a 19 km radius of control was used)

number of simulations	level of control (%)	% of cases with no infected emigrants	mean number of infected emigrants[a]	% of cases with no infected peripheral home ranges	mean delay (months) in occupancy of peripheral home ranges by infected foxes[b]	rabies control success rate (%)
Bournemouth–Poole						
20	0	0	21 ± 4	0	11 ± 3	0
20	40	0	15 ± 4	0	15 ± 2	0
20	64	0	10 ± 4	0	23 ± 7	0
20	78	30	3 ± 2	35	30 ± 7	25
20	87	95	1	90	23 ± 26	85
40	92	98	1	100	—	98
Bristol						
20	0	0	23 ± 6	0	11 ± 3	0
20	40	0	19 ± 3	0	14 ± 4	0
20	64	0	11 ± 5	0	21 ± 4	0
20	78	35	2 ± 2	30	33 ± 9	25
40	87	92	1	97	36	92
40	92	100	—	100	—	100
Leicester						
20	0	0	33 ± 7	0	8 ± 4	0
20	40	5	26 ± 5	5	16 ± 4	5
20	64	10	16 ± 5	10	24 ± 7	10
40	78	70	2 ± 2	75	30 ± 10	60
40	87	90	1 ± 0	95	25	88
40	92	92	1 ± 0	97	4	90
West Midlands						
20	0	0	32 ± 6	0	9 ± 4	0
30	40	7	24 ± 6	7	13 ± 4	7
30	64	3	24 ± 6	3	19 ± 6	3
50	78	34	5 ± 3	26	29 ± 9	24
30	87	90	1 ± 0	87	29 ± 16	80
30	92	90	1 ± 0	97	6	87

[a] This was calculated only for simulations where infected foxes emigrated from the simulation area. Where more than one individual left the simulation area, the standard deviation is also given.
[b] This was calculated only for simulations where infected foxes occupied a peripheral home range. Where more than one simulation had foxes in this category, the standard deviation is also given.

showing the greatest difference (35 %). Although the difference in the chance of successful rabies control was less marked with a change in the time of year of the outbreak, the variation was greater with a higher level of fox control (87 %). This seasonal difference may therefore have a more substantial effect than is first apparent, as the results in table 7 show that a level of fox control of at least 87 % is required to have a significant chance of controlling the spread of the disease.

(*d*) *The effect of size of the control area on rabies spread*

The effect of changing the area of fox control was examined for each city by adjusting the total area of the simulation. The current government policy would involve fox reduction in a 19 km radius around the origin of the outbreak (C. L. Cheeseman, personal communication). For these simulations, four radii of control were considered; 15 km, 17 km, 19 km and 23 km, giving control zones of 707 km^2, 908 km^2, 1134 km^2 and 1662 km^2 respectively. The spread of rabies was examined for each size of control zone for all four cities, initially with no fox reduction, and then with up to five successive control campaigns of 40 % population reduction in each campaign. Figure 10 (*a–d*) shows the variation in the chances of successfully eradicating the disease in each city with increasing area and increasing levels of fox control.

For all sizes of control zone, the control area with the lowest fox density (Leicester; see table 5) had the greatest chance of successfully controlling the outbreak, and the control area with the highest density (West Midlands) had the least chance of success. Within each city, as the area of fox control increased, the chance of successfully eradicating the disease increased. However, the effect was density dependent, so that the increase was least in the low-density control area (Leicester), with the West Midlands showing the greatest change in success when the control zone was increased from a radius of 15 km to 23 km. In nearly all cases, the effect of prolonging the series of control campaigns, by an additional 40 % population re-

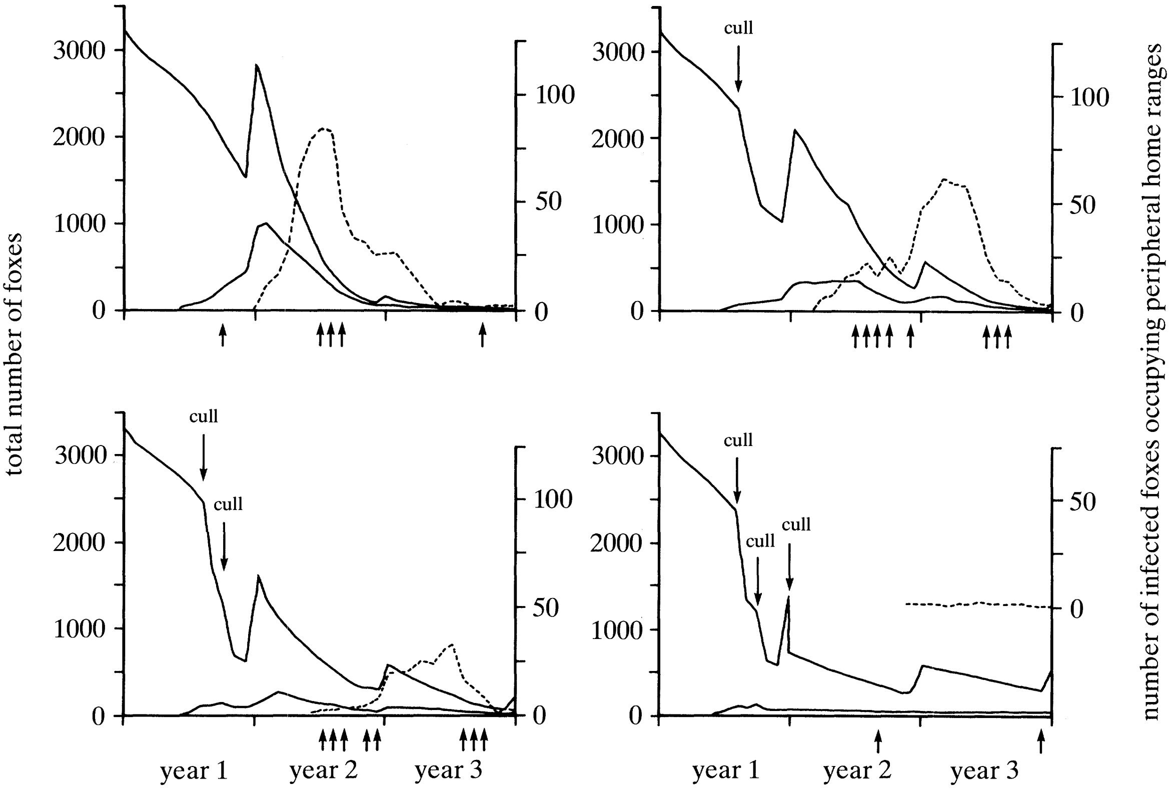

Figure 9. The effects of an outbreak of rabies in Bristol on the fox population with different levels of control. The simulation area was 25 km × 25 km, and rabies was introduced in September. All simulations were run for three years. The left axis shows the total fox population at the end of each month (upper solid line) and the total number of infected foxes (lower solid line). The right axis shows the total number of infected foxes occupying peripheral home ranges (broken line). The lower arrows show the timing of each infected fox emigrating from the area of the simulation, the upper arrows the timing of each cull.

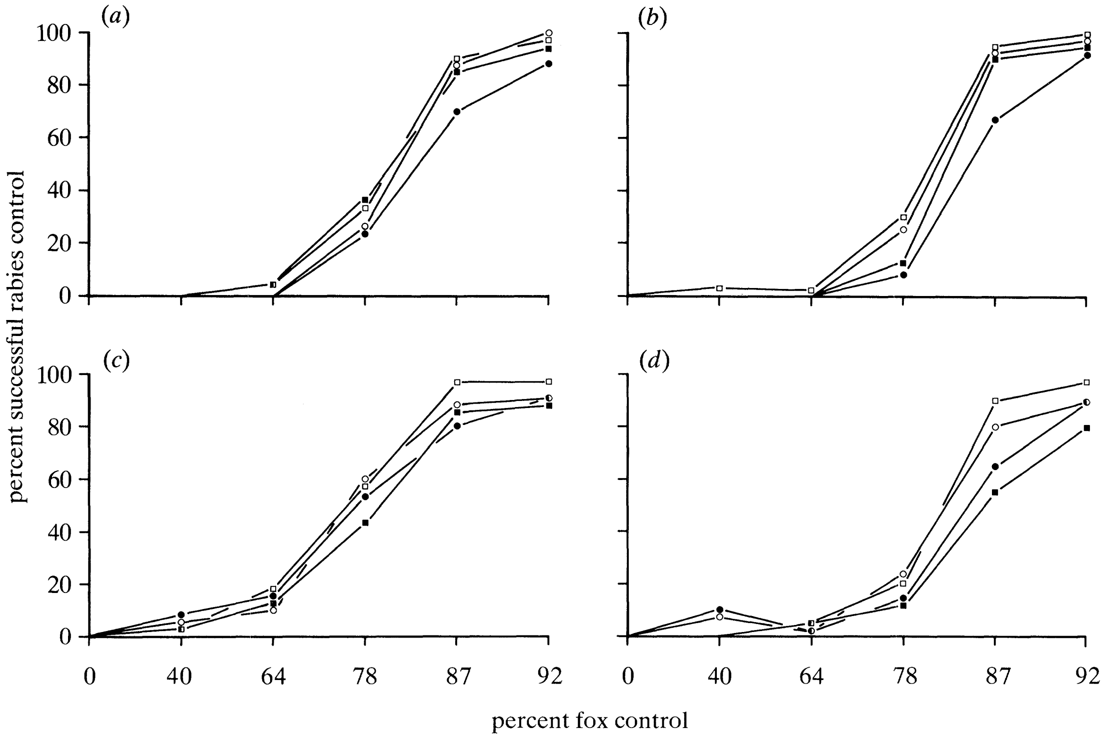

Figure 10. The chance of successful rabies control in (*a*) Bournemouth and Poole, (*b*) Bristol, (*c*) Leicester and (*d*) the West Midlands conurbation, with control zones of different sizes. Closed circle: radius of control zone 15 km. Closed square: radius of control zone 17 km. Open circle: radius of control zone 19 km. Open square: radius of control zone 23 km.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

duction, was greater than the effect of increasing the radius of the control zone from 15 km to 23 km, i.e. increasing the area of the control zone 2.35 times.

5. DISCUSSION

The aim of this study was to simulate an initial outbreak of rabies in an urban environment to examine both the spread of the disease from a focal point infection in a high-density fox population and the effect of different control strategies. To this end, a new stochastic simulation model was needed to reflect the high density and high degree of spatial heterogeneity seen in British urban fox populations. Throughout, the parameters used have been based on an extensive data base collected from long-term studies on urban foxes. Models such as this are, of necessity and definition, a simplistic representation of reality. It is important to balance the number of parameters required for understanding the behaviour of the model with simplicity of construction. Information that will improve the performance of the model, without increasing its complexity, include more accurate data on rural fox population densities, and a better understanding of fox contact rates and how these interact with population density.

As a result of the nature of the problem for which the model was produced, it is almost impossible to validate the output by comparison with field data. The high fox density found in many urban environments results in very high disease prevalence and dramatic population crashes. Monthly prevalence rates relate to the time of rabies introduction, rather than seasonal changes in fox behaviour, and in the areas simulated, long-term disease prevalence is not sufficient to produce oscillations in the incidence of the disease. However, if 87 % population reduction is taken as the minimum threshold for disease eradication, the absolute fox density after control is 0.28–0.40 adult foxes km^{-2}. This agrees closely with Anderson *et al.*'s (1981) figure of 0.3–0.5 foxes km^{-2}.

The simulation model showed that heterogeneity of the fox population density can markedly affect the variance in the velocity of the wave front in the short term. Such localized changes in fox population density may account for the large variation observed (0–80 km per year) in the speed of propagation of rabies on the continent. This heterogeneity also partly accounts for the reduced chances of successfully containing the rabies outbreak with the present model when compared with the results of previous work using a homogeneous model (Smith & Harris 1989). An increase in heterogeneity of the fox population density will increase the variation in front wave velocity as a result of the greater variation in dispersal distance and home range size. This will result in less-accurate predictions with the simulation model when such local factors are unknown and so not incorporated in the model. Hence, in areas of uncertain fox density, or areas of known heterogeneity, the area of a fox control operation should be enlarged to accommodate this uncertainty. The importance of local variations in fox density on the pattern of rabies spread also highlights the need for more detailed information on fox population densities in rural environments in Britain.

Maximizing the chance of successfully eradicating a rabies outbreak depends upon both the proportion of foxes removed and the initial fox density in the area. With low to moderate levels of fox control, the greatest chance of successful eradication occurred in simulations for the two cities with the lowest fox density. However, if the level of fox control was increased in these two areas to 92 %, the chance of successful control was lower than in simulations for areas with a higher urban fox density. This was because, in the lower density populations, the rate of rabies spread was often quicker, but involved fewer individuals. Moderate levels of fox control in such situations had only a small chance of removing the few infected foxes. The higher level of control, which was only achieved with repeated control campaigns over six to eight months, was less successful compared with the higher density areas, because of the greater speed of propagation in low-density areas. Urban areas with high fox population densities had a greater number of infected foxes and a slower front wave velocity. Thus, low levels of fox control were much less likely to eradicate the disease, but high levels of fox control would do so before infected animals reached the edge of the simulation area, whether disease spread was by dispersal or neighbour to neighbour transmission. In the high-density areas, the proportion of healthy foxes which were infected and survived the passing of the rabies front was very small, and after the front wave had passed the surviving fox population was only about 1 % of the original level. Such high levels of disease prevalence would be very unusual in most wild populations, and on the continent, for instance, rabies has been estimated to kill only about half of the fox population (Bögel *et al.* 1981). The very large proportion of an urban fox population likely to be infected highlights the particular problems posed by rabies control in British urban areas.

The rate of spread of the rabies front was slightly greater for the Leicester simulations, where fox density was lowest. This was shown by the shorter time taken to occupy peripheral home ranges and the greater number of infected animals leaving the simulation area compared with the other cities. Both Bournemouth–Poole and Bristol had a large area of water at the edge of the simulation area, and this reduced the number of dispersing animals leaving the simulation area. As the level of fox control increased, the total number of infected animals that dispersed from the simulation area decreased, the delay to occupancy of peripheral home ranges by infected animals increased, and the rate of spread of the rabies front decreased and began to fragment. If rabid animals were contained within the control zone, then it was likely that the disease would be successfully eliminated. However, in a field situation the exact area covered by infected animals may be unknown, as may the rate of spread. Should the control operation be undertaken in a high-density fox population, the low number of infected emigrating foxes and the long delay until infected animals reached peripheral home ranges could produce an erroneous assumption that rabies control had been successful. This is because, at high levels of fox control, the disease may be contained within the control area for about 30 to 40 months before it is transmitted to foxes outside the control area.

In a real rabies event, it is clearly important to monitor the spread of the disease and the effectiveness of the culling operation, and that fox control and vigilance should be maintained for a reasonable period after the last confirmed case of rabies. With a very small number of infected foxes surviving a control campaign, the chance of detecting individual infected animals is low, especially if the level of vigilance drops (Bacon 1981). Detection of the early stages of a rabies epizooty is equally problematical; Bacon (1981) showed that, with a probability of 10% of reporting an individual rabid fox, it would be two to four months before the disease is reported. The present simulations showed that a delay greater than one month in commencement of control will reduce the chance of success significantly (at least by 10–20%, and possibly up to 40% or more). These results demonstrate the importance of commencing fox control as soon as transmission to the fox population is suspected.

For all the cities analysed, the simulation model predicted that a very large proportion of the fox population had to be removed to eradicate rabies. To achieve a population reduction of approximately 87% would require three campaigns of 50% reduction, four campaigns of 40% reduction, five campaigns of 30% reduction or eight campaigns of 20% reduction. Field trials in Bristol have shown that only about 30% of the fox population is reached with a single baiting campaign (Trewhella *et al.* 1991). If successive campaigns are to be done, it is unrealistic to assume that they would be independent of each other. A more likely response is a diminishing proportion culled in each successive campaign. Hence attaining very high levels of fox population control in an urban area is problematical. It would certainly involve several months of control, and in low-density cities the disease could spread beyond the control zone during that period. One strategy may be to increase the size of the control zone. However, an increase of 4 km in the radius of the control zone, from 19 km to 23 km, produced a mean increase in the chances of successfully controlling the disease of less than 6%. To ensure success with only a moderate level of fox control would, therefore, require a control zone of unmanageable size. It has been estimated that 323 people are needed to undertake a fox control operation in an area of radius 19 km (Harris *et al.* 1991), and any increase in the radius of the control zone has a dramatic effect on the size of the control area, and hence the number of people needed for the control operation.

These simulations have shown that high-density heterogeneous urban fox populations, as found in many English cities, pose particular problems for controlling a rabies outbreak, and that reliance on the past experience of fox rabies control in Europe and North America is not adequate for planning a rabies control operation in urban areas of Britain. Instead, computer simulations have been used to identify particular problems, evaluate the consequences of different control strategies, and to identify where more data are needed. As certain parameters used in the simulations can only be estimated at present, reliance on the exactness of the figures must be avoided. However, the estimated parameters are realistic approximations, given the current knowledge of fox population biology and rabies spread. Not only does the use of this simulation model provide a valuable tool in planning a rabies control operation, it also helps unite the bodies of theoretical and practical knowledge on rabies spread.

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