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On the spatial spread of the grey squirrel in Britain

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We present a diffusion-competition model to describe the interaction between the externally introduced grey squirrel and the indigenous red squirrel in Britain. We estimate the model parameters from field data. Solution of the model predicts waves of grey squirrel invasion with speed of invasion typical of that observed in the field. Numerical solution of the model on a two-dimensional domain gives population distributions qualitatively similar to those observed. We suggest that competition alone could account for the observed displacement of the red squirrel by the grey in large regions of Britain. The solutions are qualitatively similar to those for a single species spreading in the absence of competition. The quantitative difference is because competition slows down the speed of advance of the invading species.

INTRODUCTION

Around the turn of this century the North American grey squirrel, *Sciurus carolinensis*, was released from various sites in Britain. The most important centre was that at Woburn Abbey in Bedfordshire (Shorten 1959). Since then the grey squirrel has successfully spread to colonize much of England, Wales and the Scottish lowlands. At the same time the indigenous red squirrel, *Sciurus vulgaris*, has disappeared from these localities (Middleton 1930, 1932, 1935; Shorten 1946, 1953, 1954, 1957; Lloyd 1962, 1983; Arnold 1978; MacKinnon 1978; Reynolds 1985; Williamson & Brown, 1986).

According to Lloyd (1983), the influx of the grey squirrel into areas previously occupied by the red squirrel coincided with a decline and subsequent disappearance of the red squirrel after only a few years of overlap in distribution, though sometimes with an overlap of up to 20 years.

There have been three hypotheses to explain the decline and replacement of the red squirrel (see Reynolds 1981, 1985). (i) Competition with the grey squirrel. (ii) Environmental changes that reduced red squirrel populations independent of the

grey squirrel populations. (iii) Diseases, such as 'squirrel flu' (Edwards 1962), some of which might have been transmitted from the grey squirrel. These hypotheses are not mutually exclusive.

Some well-known squirrel ecologists, particularly Middleton (1932) and Shorten (1954), doubted that the decline of the red could be caused by the advance of the grey. However, to many ecologists the squirrel distribution records in Britain always seemed to indicate a clear negative effect of the greys on the reds (Elton 1958; Williamson 1972) and this is now generally accepted (Gurnell 1987). MacKinnon (1978) presented some reasons why competition would be the most likely among the three hypotheses. Before the introduction of the grey, the red squirrel had evolved without any interspecific competition. Consequently, selection may have favoured modest levels of reproduction with low numerical wastage. The grey squirrel, on the other hand, has evolved within the context of the American fox squirrel, *Sciurus niger*, and thus selection may have favoured more vigorous overbreeding. Both red and grey squirrels can breed twice a year but the smaller red squirrels rarely have more than two or three offspring per litter (MacKinnon 1978), whereas grey squirrels frequently have litters of four or five (Barkalow 1967).

In North America the red and grey squirrels occupy separate niches, i.e. northern conifer forests for red and mixed hardwood forests for grey. Their niches seldom overlap. In Britain, however, the native red squirrel has, in the absence of the grey squirrel, become adapted to live in hardwood forests as well as coniferous forests.

The North American grey squirrel is a large robust squirrel, with approximately a twofold difference in body mass compared with the red squirrel. In separate habitats the two squirrel species show similar social organization, feeding and ranging ecology. Within the same habitat we would expect even greater similarity in their exploitation of resources, and thus it seems inevitable that two species of such close similarity could not coexist in sharing the same resources. Recent research (Holm 1987) also supports the hypothesis that grey squirrels may be at a competitive advantage in deciduous woodland where the native red squirrel has mostly been replaced by the grey.

In summary, it is reasonable to assume that an interaction between the two species, probably largely through indirect competition for resources, but also with some direct interaction, for example, chasing, has acted in favour of the grey squirrel to drive off the red squirrel mostly from deciduous forests in Britain. In this paper we present a simple mathematical model of competition and diffusion of the two species and obtain travelling (invasion) wave solutions of the basic model equations. The model is also used to simulate the random introduction of grey squirrels into red squirrel areas to show how colonization might spread. We compare the results with available data.

Our basic model consists of a coupled set of diffusion-reaction equations, i.e. a continuous, deterministic model. In reality, animal populations contain a discrete number of individuals, and hence demographic stochasticity can arise. However, if the population size is very large, it may be reasonable to model the population in a continuous manner. Another justification for a continuous model is to use biomass rather than population number as the measured quantity. In any case the diffusion-reaction approach provides a very useful metaphor. Along this line of

thought many attempts have been made to model the spatial spread of populations and associated diseases (see, for example, Murray *et al.* (1986)) for the spread of rabies among foxes.

COMPETITION AND DIFFUSION MODEL

We denote by $S_1(\mathbf{R}, T)$ and $S_2(\mathbf{R}, T)$ the population densities at time T and spatial coordinate \mathbf{R} of grey and red squirrels respectively. Assuming that they compete for the same resources, we use population equations of Lotka–Volterra type with isotropic diffusion, (see, for example, Murray (1989)), namely,

$$\left. \begin{aligned} \partial S_1 / \partial T &= D_1 \nabla^2 S_1 + a_1 S_1 (1 - b_1 S_1 - c_1 S_2), \\ \partial S_2 / \partial T &= D_2 \nabla^2 S_2 + a_2 S_2 (1 - b_2 S_2 - c_2 S_1), \end{aligned} \right\} \quad (1)$$

where a_i are net birth rates, $1/b_i$ are carrying capacities, c_i are competition coefficients, D_i are diffusion coefficients, $i = 1, 2$ for the grey and red respectively and ∇^2 is the Laplacian operator. All parameters are assumed to be non-negative constants. The interaction terms simply represent logistic growth with competition. For the reasons discussed above we further assume that the greys out-compete the reds. Therefore

$$b_2 > c_1, \quad c_2 > b_1. \quad (2)$$

We wish to investigate the above system for the possibility of travelling waves of invasion of grey squirrels that drive out the reds. We put the equations in non-dimensional form and note that, in the absence of diffusion, there are three steady states: $(0, 0)$, $(1, 0)$ and $(0, 1)$ (see appendix). The analysis in the appendix suggests the existence, in one dimension, of travelling waves and, in certain special cases, predicts a wave speed of

$$2(1 - c_1/b_2)^{\frac{1}{2}} (D_1 a_1)^{\frac{1}{2}}. \quad (3)$$

A brief non-technical discussion of spatial dispersal of species is given by Murray (1988).

PARAMETER ESTIMATION

Our model equations (1) contain eight parameters, and the travelling wave speeds depend upon them. Therefore, we need estimations for the parameter values to compare the theoretical wave speed with available data.

(i) *Intrinsic net growth rates: a_1 and a_2*

We use a modified Leslie matrix to estimate the intrinsic net growth rate (Williamson & Brown 1986). In principle the estimates should be those at zero population density, but most reported demographic data refer to populations near their equilibrium density. Three components are considered in estimating the intrinsic net growth rate, namely the sex ratio, birth rate, and death rate. The sex ratio is taken to be 1:1. For birth rates there is a consensus that the first year (juveniles) have only one litter, whereas older animals (adults) generally have two litters in a year (Corbet & Southern 1977). The litter size varies with species, female age, and environmental conditions. For the grey squirrel, Middleton (1930) gives the range of three to five with average 4.2. Shorten & Courtier (1955) estimate the mean sizes to be 2.3 and 3.3 for juveniles and adults, respectively. Southern (1964)

gives the average litter size as three, ranging from one to seven. For the red squirrel, Barrett-Hamilton & Hinton (1921) estimate the mean litter size as three, two litters per year in the south, one in Scotland. Corbet & Southern (1977) give the mean size as three in spring and 3.6 in summer, but summer survival is poorer. MacKinnon (1978) claims that there are rarely more than two or three per litter.

For death rates Barkalow *et al.* (1970) give proportional mortalities such that mortality is 0.753 for age zero to one, decreasing to 0.261 for age four to five increasing afterward and becoming one for age seven to eight. Southern (1964) and Corbet and Southern (1977) give life spans of several years or more in the wild and state that two-thirds are young in autumn populations. Summarizing mortality data for all squirrel species, Gurnell (1987) concludes that there is 15–25% survival in the second year, thereafter 50–70% survival and in good years, survival increases to 50–60% for juveniles and 90–100% for adults.

For our Leslie matrices we consider the autumn population, when the young from both broods would be free living. For both grey and red squirrels, we take survival from first autumn to second autumn as 0.5 and from the second autumn as 0.8, towards the lower end of Gurnell's good food years, to allow for zero population density but variable food supply and other environmental conditions.

In summary, for the grey squirrel, we take first year litter as three, 75% survival to autumn count and half female, whereas for older animals two litters of 4.5 and the same ratios. Thus the transition matrix is

$$\begin{bmatrix} 1.125 & 3.375 \\ 0.5 & 0.8 \end{bmatrix},$$

which yields $a_1 = 0.82$ per year, and a stable age distribution with 2.94 young to one adult or about 75% young. For the red squirrel, we take first year litters as two, 75% survival to autumn count and half female, whereas for older animals two litters of three and the same ratios. Thus the transition matrix is

$$\begin{bmatrix} 0.75 & 2.25 \\ 0.5 & 0.8 \end{bmatrix},$$

which yields $a_2 = 0.61$ per year, and the stable age distribution with 2.07 young to one adult or about 67% young.

(ii) *Carrying capacities: b_1^{-1} and b_2^{-1}*

For the grey squirrels, Southern (1964) and Corbet & Southern (1977) give 1.2–12 ha⁻¹† and 1–13 ha⁻¹, respectively. Shorten & Courtier (1955) found 12 ha⁻¹ in a very favourable habitat and MacKinnon (1978) records 5 ha⁻¹ at Wytham and 6 ha⁻¹ at Alice Holt. Gurnell (1987, pp. 117 and 144) shows ranges of 1–15 ha⁻¹, and 0.6–1.2 ha⁻¹. The higher estimates appear to be the more reliable.

For the red squirrel, Corbet & Southern (1977) give 0.8 ha⁻¹ in east Scotland and 0.5 ha⁻¹ in East Anglia. Middleton (1931) gives 0.74 ha⁻¹, and Gurnell (1987, p. 144) shows 0.5–0.8 ha⁻¹ with a seasonal cycle. All these figures are for favourable habitats.

From this information we take carrying capacities to be 10 ha⁻¹ for the grey squirrel and 0.75 ha⁻¹ for the red squirrel so that $b_1^{-1} = 10$ ha⁻¹ and $b_2^{-1} = 0.75$ ha⁻¹.

† 1 ha = 10⁴ m²

(iii) *Competition coefficients: c_1 and c_2*

Unfortunately there is no quantitative information in the literature on evaluation of the competition coefficients. In our model, only the ratios $c_1/b_2 = \gamma_1$ and $c_2/b_1 = \gamma_2$ are required for estimation of the minimum speed of travelling waves. As far as the speed of propagation of the grey squirrel is concerned, we only need know γ_1 , whose value is greater than zero and less than one.

As γ_1 appears in the expression of the minimum wave speed as a factor of $(1-\gamma_1)^{\frac{1}{2}}$, the speed is not very sensitive to the value of γ_1 for small γ_1 . We expect that the competition coefficient c_1 , i.e. red against grey, should have a small value. In combination with the smallness of b_2^{-1} , it is reasonable to assume that the value of γ_1 is close to zero. If so the minimum speed of the travelling wave of the grey squirrel, V_{\min} , is approximately given by $2(D_1 a_1)^{\frac{1}{2}}$. To explore the model behaviour in more detail we have taken rather higher values for γ_1 in some of our simulations.

(iv) *Diffusion coefficients: D_1 and D_2*

Direct observation of dispersal is difficult and usually short-term. For grey squirrels, Shorten & Courtier (1955) quote a maximum of 250 m in about 9 days; this would give us a one-dimensional diffusion coefficient at 1.25 km^2 per year (i.e. $365 \times (0.25)^2 \text{ km}^2 / 2 \times 9 \text{ days}$) and a two-dimensional diffusion coefficient as 0.63 km^2 per year. However, this may not correspond to their movement between woodlands. Mosby (1969) quotes an average movement between woodlots of 790 m, and one recorded movement of about 100 km. There have been occasional records of grey squirrels well away from their main population, which suggest that movements of 50–100 km by individual squirrels may be possible. However, these long-distance movements do not seem to have led to persistent populations of the grey squirrels in England.

If we assume that annual dispersal in the grey squirrel takes place primarily between woodlands rather than within a woodland, then the values of diffusion coefficient of the order of 1 km^2 per year estimated above should be too small to be a representative value for the diffusion coefficient. It might not be unreasonable to expect that the diffusion coefficient of grey squirrels is of the order of 10 km^2 per year, rather than 1 km^2 per year. The following argument is very speculative and tentative, but may support the value of diffusion coefficient of the order of 20 km^2 per year.

Consider a patch of woodlands, each having an equal area of A ha and with four neighbours, separated from each neighbour by a distance l . Suppose a woodland is filled with grey squirrels. Take the carrying capacity for grey to be 10 ha^{-1} . The woodland carries $n = 10A$, number of individuals. As the intrinsic growth rate $a_1 = 0.82$ per year, the woodland will contain $22.7A$ animals ($e^{0.82} = 2.27$) in the following year, of which $12.7A$ individuals must disperse. Assuming the animals disperse into the nearest neighbouring woodlands, $12.7/4A = 3.175A$ individuals will arrive at a neighbouring woodland. This woodland will then be filled with grey squirrels in $\tau = 1.4$ years ($10A = 3.175A e^{0.82\tau}$), after which another dispersal will occur; i.e. the grey squirrels disperse to the nearest neighbouring woodlands, on

average, every 1.4 years. Thus the two-dimensional diffusion coefficient for the grey squirrel is estimated (Okubo 1980) as

$$D_1 = l^2/4 \times 1.4 = l^2/5.6 \text{ km}^2 \text{ per year.}$$

Values for D for different values of l are given in table 1. From fig. 7 in Williamson & Brown (1986), the speed of dispersal of the grey can be calculated as 7.7 km per

TABLE 1. TWO-DIMENSIONAL DIFFUSION COEFFICIENTS FOR THE GREY SQUIRREL: EFFECT OF DISTANCE FROM NEIGHBOUR

(For explanation of symbols, see text.)

l (km)	1	2	5	10	15	20
$D_1/(\text{km}^2 \text{ per year})$	0.179	0.714	4.46	17.9	40.2	71.4
$V_{\min}/(\text{km per year}) = 2(a_1 D_1)^{\frac{1}{2}}$	0.77	1.53	3.82	7.66	11.5	15.3
$(a_1 = 0.82 \text{ per year})$						

year. Assuming that the species is travelling with the minimum Fisher wave speed, this gives a value of D_1 of 17.9 km² per year (see table 1). This suggests that a mean separation between neighbouring woodlands of 10 km, which is reasonable, would give a minimum speed of travelling waves that agrees well with the data.

COMPARISON OF THE THEORETICAL RATE OF SPREAD WITH DATA

One of the better sources of information on the spread of the grey squirrel in Britain is provided by Reynolds (1985), who investigated in detail the spreading process in East Anglia during 1960 to 1981. Colonization of East Anglia by the grey squirrel has been comparatively recent. A survey in 1959 (Lloyd 1962) found no reports of the grey squirrel. The red squirrel was present more or less throughout the county of Norfolk both in 1959 and at the later survey in 1971 (Lloyd 1983), but by 1971 the grey squirrel was also recorded for approximately half of the area of Norfolk.

Reynolds (1985) gathered a bulk of records to construct a series of maps showing the annual distribution of the grey and red squirrels for the period of 1960 to 1981 by the use of grids of 5 × 5 km squares. Based on the maps of Reynolds, Williamson & Brown (1986) evaluate the rate of spread of the grey squirrel during 1965 to 1981, and present the cumulative frequency of the spreading rate, which shows the rate predominantly between 5 and 10 km per year; the mean rate of spread of the grey squirrel is calculated to be 7.7 km per year.

The uncertainty of our estimation of the diffusion coefficient makes it difficult to obtain the theoretical mean speed of travelling frontal waves of the grey squirrel. If we take $D_1 = 17.9 \text{ km}^2 \text{ per year}$, however, we obtain

$$V_{\min} = 2(a_1 D_1)^{\frac{1}{2}} = 2(0.82 \times 17.9)^{\frac{1}{2}} \text{ km per year} = 7.66 \text{ km per year,}$$

which agrees with the observed 7.7 km per year.

NUMERICAL RESULTS

In this section we present some numerical simulations in one and two dimensions. Figure 1*a* illustrates the special case (discussed in the appendix) where the parameters are such that the system reduces to a Fisher system with non-dimensional wave speed given by (3). In figure 1*b* we choose parameters estimated from observations (as discussed above). In the case of two spatial dimensions, a general analytic treatment is very difficult. Numerical simulations, however, show that an initial small scattered distribution of greys in a predominantly red population will eventually drive out the reds (figure 2).

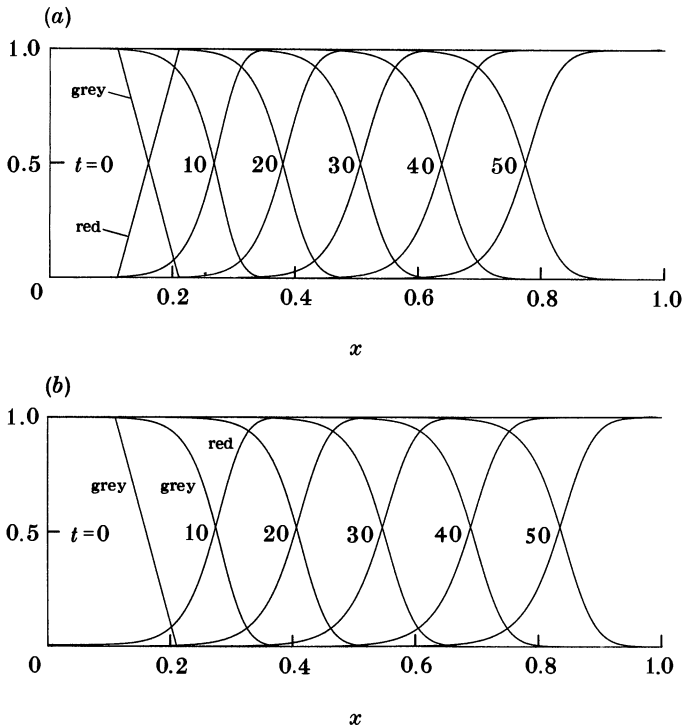


FIGURE 1. Numerical solution of the model equations in the form given in the appendix. (a) $\gamma_1 = 0.5, \gamma_2 = 1.5, \alpha = 1, \kappa = 1, (D_1 = D_2 = 10^{-4})$, profiles at $t = 0, 10, 20, 30, 40, 50$. Initial conditions are $\theta_1 = 1 \ x \leq 0.15, \theta_1 = (0.21 - x)/(0.21 - 0.15), 0.15 < x \leq 0.21, \theta_1 = 0 \ x > 0.21, \theta_2 = 1 - \theta_1$. This is the special Fisher case discussed in detail in the appendix. A wave of grey squirrel population moves into the region initially containing only reds and drives the latter out. Eventually the waves travel with a constant profile and wave speed (0.0141) that agrees with the minimum Fisher wave speed (A10*a, b*). (b) Travelling waves for the case $\gamma_1 = 0.1, \gamma_2 = 1.5, a_1 = 0.82, a_2 = 0.61, (\alpha = 0.82/0.61), \kappa = 1, (D_1 = D_2 = 10^{-4})$. Initial conditions for θ_1 are the same as (a), but $\theta_2 = 1$ for all x . Travelling waves of greys move forward to the right, receding waves of reds move to the right. The wave speed = 0.0148 agrees with (A10*a, b*). Profiles at times $t = 0, 10, 20, 30, 40, 50$.

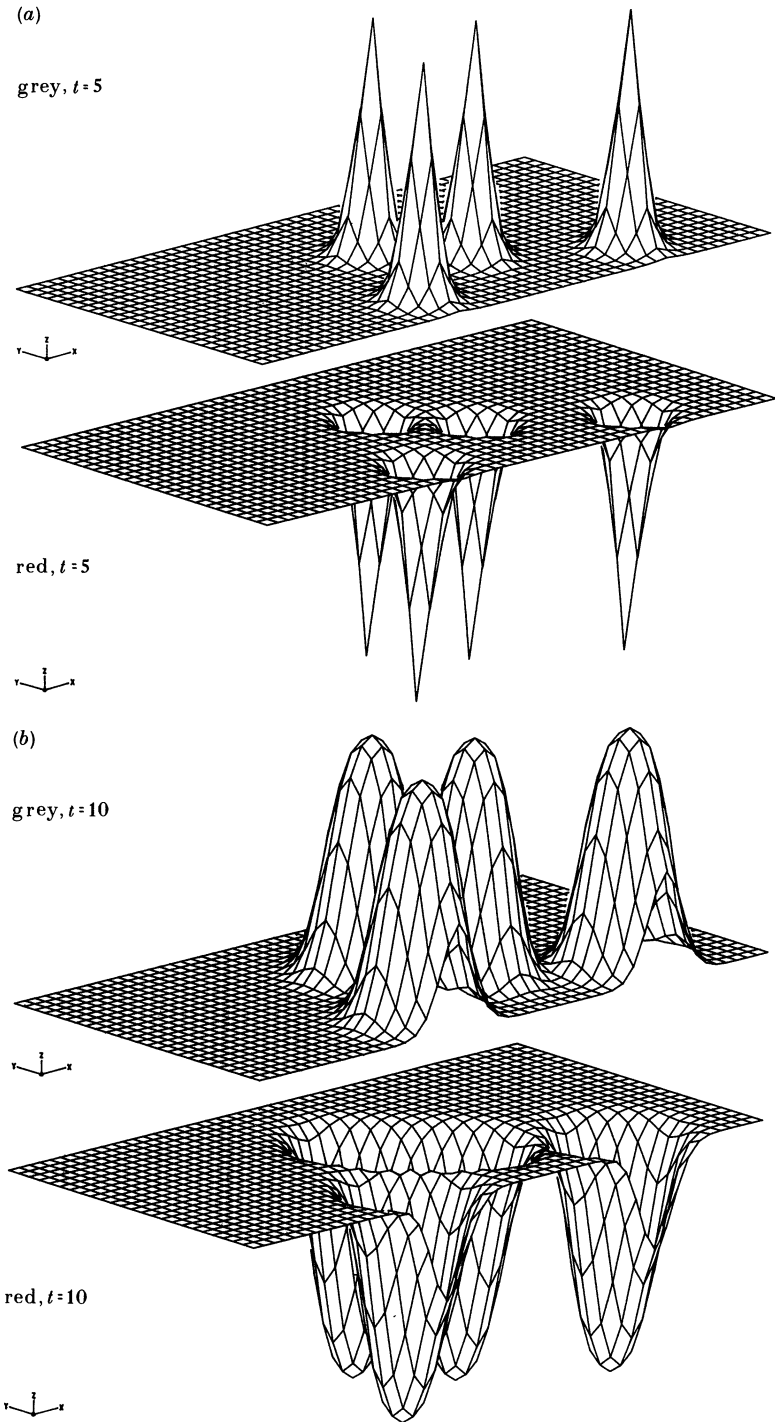


FIGURE 2. Two-dimensional numerical solution of the dimensionless version of (1) on a 4.9×2.4 rectangle with zero flux boundary conditions. The initial distribution consists of reds at unit normalized density, seeded with small pockets of greys of density 0.1 at points (1.9, 0.4), (3.9, 0.4), (2.9, 0.9) and (2.4, 1.4). (a) Surface plot of solution at $t = 5$: the base density of greys is 0.0, and of reds 1.0. Solutions at subsequent times: (b) $t = 10$; (c) $t = 20$; (d) $t = 30$. Clearly as the system evolves the greys begin to increase in density and spread outwards while the reds recede. Eventually the greys drive out the reds. Parameter values: $\gamma_1 = 0.2$, $\gamma_2 = 1.5$, $\alpha = 0.82/0.61$, $\kappa = 1$ ($D_1 = D_2 = 10^{-3}$).

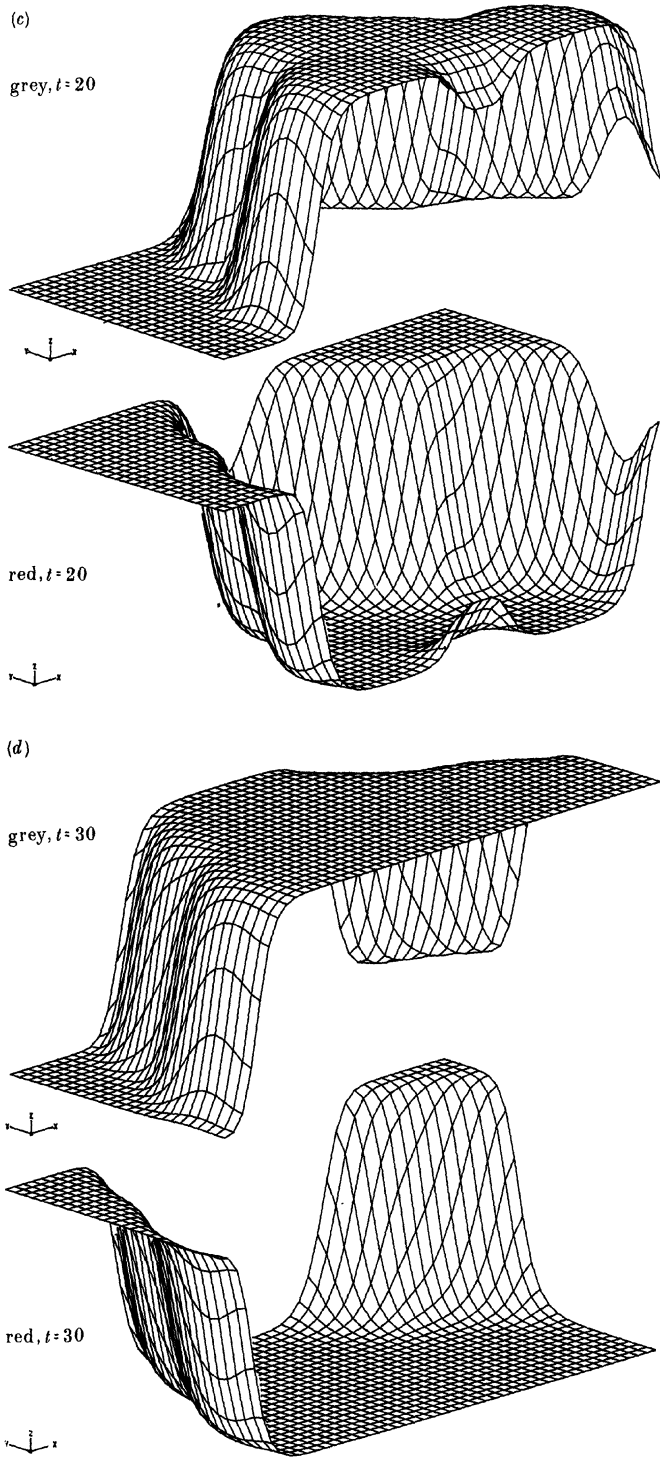


FIGURE 2. For description see opposite.

DISCUSSION AND CONCLUSIONS

This paper concludes that the spread of a species overcoming another in competition is not very different qualitatively from the spread of one without important ecological interactions. In the classical model of Skellam (1951), a species with exponential growth and random diffusion will spread out with a wave of advance that eventually has a constant radial speed. Here we show analysis and simulation, that the same result appears to be true in one and two dimensions when the expanding species meets a uniformly distributed competitor. The difference is that, under competition, the wave of advance is slower. Many maps have been published of the advance of the grey squirrel over England and Wales, and the retreat of the red squirrel (Middleton 1930, 1932, 1935; Shorten 1946, 1953, 1954, 1957; Lloyd 1962, 1983). The grey was introduced at several sites. Spread occurred at each site, and the spreading waves coalesced. In our view, figure 2 is a reasonable representation of the major patterns seen in the maps.

It also seems from the maps that there is a variation in the rate of spread of the grey. The spread appears faster in the Midlands and south of England than it has in northern England, Scotland and Ireland, but the maps are unfortunately of too coarse a scale, and too widely separated in time, for a detailed analysis. So we have relied on the yearly 5 km \times 5-km surveys of Reynolds (1985) in making our calculations. Undoubtedly the actual rate of spread, and the course of competition, will be affected by climate and habitat, by the density of trees, the proportion of coniferous and broadleaved trees, and so on. Without better information on these variables and on the parameters of our model, we cannot attempt a detailed match. What we can say is that the broad features of the ecological replacement are captured by our model. Simple diffusion, logistic population growth and some general form of competition are sufficient to account for the progressive replacement of the red squirrel by the grey in England and Wales.

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APPENDIX 1. ANALYSIS OF MODEL EQUATIONS

Here we consider the one dimensional version of the model system (1) and write it in non-dimensional form by setting

$$\theta_1 = b_1 S_1, \theta_2 = b_2 S_2, t = a_1 T, x = X(a_1/D_1)^{1/2} \text{ where } \theta_i = \theta_i(x, t), i = 1, 2$$

and X is the spatial dimension. These are the non-dimensional population densities at dimensionless time t and spatial coordinate x . Defining $\kappa = D_2/D_1$, the ratio of diffusion of red squirrels to grey squirrels, $\alpha = a_2/a_1$, the ratio of red squirrel growth rate to grey squirrel growth rate,

$$\gamma_1 = c_1/b_2 \quad \text{and} \quad \gamma_2 = c_2/b_1.$$

the non-dimensional system becomes

$$\left. \begin{aligned} \partial\theta_1/\partial t &= \partial^2\theta_1/\partial x^2 + \theta_1(1-\theta_1-\gamma_1\theta_2), \\ \partial\theta_2/\partial t &= \kappa\partial^2\theta_2 + \alpha\theta_2(1-\theta_2-\gamma_2\theta_1), \end{aligned} \right\} \quad (\text{A } 1)$$

where, from relations (2) in the main text, we have

$$\gamma_1 < 1, \quad \gamma_2 > 1. \quad (\text{A } 2)$$

The system (A 1) with condition (A 2) has three ecologically relevant (that is non-negative) steady states in the absence of diffusion, which are: (0, 0), unstable node; (1, 0), stable node; (0, 1), saddle point. A phase plane analysis of the spatially homogeneous situation suggests the possibility of a solution trajectory from (0, 0) to (1, 0). Thus, when diffusion is included, there is the possibility of a travelling wave solution joining these two critical points (Murray 1989). This corresponds to the ecological situation where the greys (θ_1) outcompete the reds (θ_2) to extinction.

We seek travelling wave solutions to (A 1) of the form

$$\theta_i = \theta_i(z), \quad i = 1, 2, \quad z = x - Vt, \quad V > 0, \quad (\text{A } 3)$$

so that θ_1 and θ_2 represent wave solutions of constant shape travelling with velocity V in the positive x -direction. Under this transformation, equations (A 1) become

$$\left. \begin{aligned} -Vd\theta_1/dz &= d^2\theta_1/dz^2 + \theta_1(1-\theta_1-\gamma_1\theta_2), \\ -Vd\theta_2/dz &= \kappa d^2\theta_2/dz^2 + \alpha\theta_2(1-\theta_2-\gamma_2\theta_1). \end{aligned} \right\} \quad (\text{A } 4)$$

Appropriate boundary conditions are:

$$\theta_1 = 1, \quad \theta_2 = 0, \quad z = -\infty; \quad \theta_1 = 0, \quad \theta_2 = 1, \quad z = +\infty. \quad (\text{A } 5)$$

That is, asymptotically, the grey (θ_1) drives out the red (θ_2) as the frontal wave propagates with speed V . Hosono (1988) has investigated the existence of travelling waves for the system (A 4) and (A 5) under certain conditions on the values of the parameters. In general, the system of ordinary differential equations (A 4) cannot be solved analytically. However, in the special case where $\kappa = \alpha = 1$ and $\gamma_1 + \gamma_2 = 2$, we can add equations (A 4) to get

$$-Vd\theta/dz = d^2\theta/dz^2 + \theta(1-\theta), \quad \theta = \theta_1 + \theta_2, \quad (\text{A } 6)$$

which is the well known Fisher equation (see, for example, Murray 1989), which can exhibit travelling wave behaviour. However, the boundary conditions for θ , from (A 5), are

$$\theta = 1 \quad \text{at} \quad z = \pm\infty \quad (\text{A } 7)$$

which suggest that, for all z $\theta = 1 \Rightarrow \theta_1 + \theta_2 = 1$.

Substituting (A 8) into the first of (A 4) we have

$$-Vd\theta_1/dz = d^2\theta_1/dz^2 + (1-\gamma_1)\theta_1(1-\theta_1), \quad (\text{A } 9a)$$

which is again the Fisher equation for θ_1 with boundary conditions (A 5). Thus the wavefront speed for the grey will be greater than or equal to the minimum Fisher wave speed for (A 9a), that is

$$V \geq V_{\min} = 2(1-\gamma_1)^{\frac{1}{2}}, \quad \gamma_1 < 1. \quad (\text{A } 10a)$$

Similarly, from (A 8) and the second of (A 4), the equation for θ_2 is

$$-Vd\theta_2/dz = d^2\theta_2/dz^2 - (\gamma_2 - 1)\theta_2(1 - \theta_2), \quad (\text{A } 9b)$$

with boundary conditions (A 5). Thus

$$V \geq V_{\min} = 2(\gamma_2 - 1)^{\frac{1}{2}}, \quad \gamma_2 > 1, \quad (\text{A } 10b)$$

for the red. As $\gamma_1 + \gamma_2 = 2$, these two minimum wave speeds are equal. In terms of dimensional properties, the minimum wave speed is given as

$$V_{\min} = 2(1 - c_1/b_2)^{\frac{1}{2}}(D_1 a_1)^{\frac{1}{2}}. \quad (\text{A } 11)$$

A simple heuristic argument (Murray 1977) shows, in general, that the travelling wave solution of the grey squirrel will evolve into that of speed $V = V_{\min}$ given by (A 11). We can choose a point $x = R(t)$ sufficiently large so that the total number of grey squirrels to the right of R may be an arbitrary small value. In other words, the point R is in the leading edge of the advancing front of the grey squirrel where $0 < b_1 S_1 \ll S_2 \approx b_2^{-1}$ and hence S_1^2 is negligible compared with S_1 . In this situation the first of (1) is approximated by

$$\partial S_1 / \partial t = D_1 \partial^2 S_1 / \partial x^2 + a_1(1 - \gamma_1) S_1, \quad \gamma_1 < 1.$$

Solving this equation for Heaviside type initial conditions and evaluating $R(t)$ from the condition that

$$\int_{R(t)}^{\infty} S_1 dx = M_1, \quad \text{a fixed small value,}$$

we obtain an asymptotic value of the spread of propagation of the front as

$$dR/dt = 2(1 - \gamma_1)^{\frac{1}{2}}(D_1 a_1)^{\frac{1}{2}},$$

which is indeed the minimum speed of propagation given by (A 11).

REFERENCES

- Arnold, H. R. (ed.) 1978 *Provisional atlas of the mammals of the British Isles*. Produced for the Mammal Society by the Biological Records Centre, Institute of Terrestrial Ecology, Monks Wood, Huntingdon.
- Barkalow, F. S. 1967 A record Gray squirrel litter. *J. Mammal.* **48**, 141.
- Barkalow, F. R., Hamilton, R. B. & Soots, R. F. 1970 The vital statistics of an unexploited gray squirrel population. *J. Wildl. Mgmt* **34**, 489-500.
- Barrett-Hamilton, G. E. H. & Hinton, M. A. C. 1921 A history of British mammals, parts 20 and 21. London: Gurney and Jackson.
- Corbet, G. B. & Southern, N. N. (eds) 1977 *The handbook of British mammals*, 2nd edn. Oxford: Blackwell.
- Edwards, F. B. 1962 Red squirrel disease. *Vet. Rec.* **74**, 739-741.
- Elton, C. S. 1958 *The ecology of invasions by animals and plants*. London: Methuen.
- Gurnell, J. 1987 *The natural history of squirrels*. London: Christopher Helm.
- Holm, J. 1987 *The case of the vanishing squirrel*. Lecture presented at the Linnean Society/London Natural History Society meeting on 26 November 1987, Burlington House, Piccadilly, London, U.K.
- Holm, J. 1987 *Squirrels*. London: Whittet Books.
- Hosono, Y. 1988 Singular perturbation analysis of travelling waves for diffusive Lotka-Volterra competitive models. *IMACS transactions on scientific computing*, vols 1.1 and 1.2, *Numerical and applied mathematics* (ed. W. F. Ames and C. Brezinski.).

- Lloyd, H. G. 1962 Squirrels in England and Wales 1959. *J. Anim. Ecol.* **31**, 157–165.
- Lloyd, H. G. 1983 Past and present distribution of red and grey squirrels. *Mamm. Rev.* **13**, 69–80.
- MacKinnon, K. 1978 Competition between red and grey squirrels. *Mamm. Rev.* **8**, 185–190.
- Middleton, A. D. 1930 The ecology of the American grey squirrel (*Sciurus carolinensis*) in the British Isles. *Proc. zool. Soc. Lond.*, part 3, 809–843.
- Middleton, A. D. 1931 *The grey squirrel*. London: Sidgwick & Jackson.
- Middleton, A. D. 1932 The grey squirrel in the British Isles, 1930–1932. *J. Anim. Ecol.* **1**, 160–167.
- Middleton, A. D. 1935 The distribution of the grey squirrel (*Sciurus carolinensis*) in Great Britain in 1935. *J. Anim. Ecol.* **4**, 274–276.
- Mosby, H. S. 1969 The influence of hunting on the population dynamics of a woodlot gray squirrel population. *J. Wildl. Mgmt* **33**, 59–73.
- Murray, J. D., Stanley, E. A. & Brown, D. L. 1986 On the spatial spread of rabies among foxes. *Proc. R. Soc. Lond. B* **229**, 111–150.
- Murray, J. D. 1989 *Mathematical biology*. Heidelberg: Springer-Verlag.
- Murray, J. D. 1988 Spatial dispersal of species. *Trends Ecol. Evoln* **3**, 307–309.
- Okubo, A. 1980 *Diffusion and ecological problems*. Heidelberg: Springer-Verlag.
- Reynolds, J. C. 1981 The interaction of red and grey squirrels. Ph.D. thesis, University of East Anglia, Norwich, U.K.
- Reynolds, J. C. 1985 Details of the geographic replacement of the red squirrel (*Sciurus vulgaris*) by the grey squirrel (*Sciurus carolinensis*) in eastern England. *J. Anim. Ecol.* **54**, 149–162.
- Shorten, M. 1946 A survey of the distribution of the American grey squirrel (*Sciurus carolinensis*) and the British red squirrel (*S. vulgaris leucourus*) in England and Wales in 1944–45. *J. Anim. Ecol.* **15**, 82–92.
- Shorten, M. 1953 Notes on the distribution of the grey squirrel (*Sciurus carolinensis*) and the red squirrel (*Sciurus vulgaris leucourus*) in England and Wales from 1945 to 1952. *J. Anim. Ecol.* **22**, 134–140.
- Shorten, M. 1954 Squirrels. *New Nat.*, monograph 12, London: Collins.
- Shorten, M. 1957 Squirrels in England, Wales and Scotland, 1955. *J. Anim. Ecol.* **26**, 287–294.
- Shorten, M. 1959 Squirrels in Britain. In *Symposium on the gray squirrel* (ed. V. Flyger), pp. 375–378. *Mid Dept Res. Ed.* Maryland, U.S.A.: publication no. 162.
- Shorten, M. & Courtier, F. A. 1955 A population study of the grey squirrel (*Sciurus carolinensis*) in May 1954. *Annls appl. Biol.* **43**, 494–510
- Skellam, J. G. 1951 Random dispersal in theoretical populations. *Biometrika*, **38**, 196–218.
- Southern, H. N. (ed.) 1964 *The handbook of British mammals*, 1st edn. Oxford: Blackwell.
- Williamson, M. 1972 The analysis of biological populations. London: Edward Arnold.
- Williamson, M. & Brown, K. C. 1986 The analysis and modelling of British invasions. *Phil. Trans. R. Soc. Lond. B* **314**, 505–522.