

Spread of invading organisms

D.A. Andow¹, P.M. Kareiva², Simon A. Levin³ and Akira Okubo⁴

¹Department of Entomology, University of Minnesota, St. Paul, MN 55108; ²Department of Zoology, University of Washington, Seattle, WA 98195; ³Ecosystems Research Center; Center for Environmental Research; and Section of Ecology and Systematics, Cornell University, Ithaca, NY 14853; ⁴Marine Sciences Research Center, State University of New York, Stony Brook, NY 11794; and Ecosystems Research Center, Cornell University, Ithaca, NY

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Introduction

The invasion of ecosystems by exotic organisms represents a problem of increasing importance; invaders are conspicuous among the flora and fauna of most ecosystems (Mooney and Drake 1986), and in many instances these invaders are major pest species (Wilson and Graham 1986). Since Elton's classic treatise (Elton 1958), there has been great interest in the conditions that make habitats invulnerable (Mooney and Drake 1986), in the life histories and genetics of invaders (Baker and Stebbins 1965), and in the ecological impact of invasions (Mooney and Drake 1986).

Successful invasion involves a number of stages, including initial introduction; establishment in the new habitat; and range expansion. When an invader is a pest species or alternatively, a beneficial species purposely introduced, it would be extremely useful to be able to predict its rate of geographic spread after establishment. In order to make such predictions, one must answer several basic questions:

(i) Does range expansion occur primarily as the sum of many short steps, or does it reflect a few great leaps?

(ii) Do expanding populations achieve an asymptotic (*i.e.*, constant) rate of spread; and if so, how rapidly?

(iii) Can the asymptotic rate of spread of a population, which is observable only over a large geographic area, be related to locally measured demo-

graphic and behavioral parameters?

(iv) How sensitive is spread to variation in habitat?

Our approach to these questions has been to focus on three particularly well-documented examples of successful invasions: the muskrat (*Ondatra zibethica*) invasions of Europe, the cereal leaf beetle (*Oulema melanopus*) invasion of North America, and the small cabbage white butterfly (*Pieris (=Artogeia) rapae*) invasion of North America. Elsewhere (Andow *et al.* 1990) we use these case studies to probe for statistical patterns regarding range expansions, and to quantify the variation in spread among habitats. Here we ask whether microscale observations of individual movement and demography can be used to predict the rate at which an invader's range will expand on a geographical scale. The diffusion model that we apply to this problem is an explicit attempt to address questions (i)–(iii) above: it implies that range expansion is a result of short steps that lead to an asymptotic rate of spread, which can be calculated from microscale observations.

Theoretical predictions

Apart from some early work on epidemics (Brownlee 1911), the first mathematical descriptions of spread originated with population geneticists (Fisher 1937; Kolmogorov *et al.* 1937; Dobzhansky and Wright 1943, 1947). In the ecological literature, the

major early contributions were Skellam (1951) and Kierstead and Slobodkin (1953). These seminal models were based on particular cases of the diffusion and growth equation:

$$\frac{\partial N}{\partial t} = f(N) + D \left[\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \right] \quad (1)$$

in which $N = N(x, y, t)$ denotes local population density (organisms/area) at time t and spatial coordinates x, y . D is the coefficient of diffusion, and $f(N)$ is a function describing net population change from birth and death (Skellam 1973).

Diffusion models have the advantages of being testable and easily quantifiable; moreover, in many cases they provide remarkably good descriptions of animal movement (Kareiva 1983; Okubo 1980). The philosophy underlying their application to biological populations is that the patterns of spread observed at the population level do not depend on the intricate details of how individual organisms move, but rather can be deduced from certain statistical properties of ensembles of organisms; similar assumptions underlie the theory of molecular diffusion and heat flow. The use of such simplistic models can be criticized on the grounds that the underlying assumptions of independent and random movements do not apply to organisms; but the same objections could be raised to the application of diffusion equations to the flow of heat. We think the best way of evaluating diffusion models is to assess how useful they are. If these simple models can explain and describe observed population-level patterns while neglecting the detail of individual behavior, then the fact that organisms violate some of the theory's assumptions is irrelevant at the macroscopic level of description. Indeed, the philosophy behind the use of these models is that they allow us to focus on the key processes underlying patterns, and to ignore noise. To that end, in this paper we determine the adequacy of (1) in explaining and predicting the observed spread of species after they have entered new habitats. In order to do this we consider a colonizing population of size $N = N_0$ with all individuals initially located at $(x, y) = (0, 0)$, and then use (1) to determine how rapidly the

growing population will spread from $(0, 0)$.

The simplest version of (1) to which this analysis can be applied assumes a homogeneous, unstructured population growing exponentially and spreading in a one-dimensional, uniform environment:

$$\frac{\partial N}{\partial t} = D \frac{\partial^2 N}{\partial x^2} + \alpha N \quad (2)$$

where α is the intrinsic rate of population growth. This model predicts that the population will have an infinite speed of propagation, with some individuals instantaneously moving an infinite distance from the point of introduction. This nonsense, which also applies when the model is used to describe the flux of heat, arises because the diffusion approximation is not good at distances far from the release point. However, if we assume that there is some threshold level, $N = N_c$, below which the population cannot be detected, then (2) predicts that that threshold will propagate as a front. Indeed, we can extend the logic to the two-dimensional version of (2), and explicitly predict the average rate of spread for that advancing front. In particular, the velocity (distance/time) for this advancing front, denoted V_c , at time t is given by:

$$V_c = [4\alpha D + (4D/t) \ln \{N_0 / \sqrt{4\pi D t} N_c\}]^{1/2} \quad (3)$$

where D, α, N_c and N_0 are as defined above. This result makes sense only if the bracketed term is positive (which corresponds to the population being large enough or having grown enough that the threshold density for detection is surpassed). For large time, (3) asymptotically approaches:

$$V_c = \sqrt{4\alpha D} \quad (4)$$

Remarkably, this asymptotic rate of spread is independent of the threshold density required for detection.

Equation (2) can be generalized to include nonlinear forms of $f(N)$. Provided $f(N)$ is of a biologically reasonable form, one obtains analogous

results to (4). More precisely, one does not need to rely on the notion of a detection threshold: true advancing fronts form, with asymptotic speeds given by (4), provided α is defined as the per capita growth rate when N is small. This important general result was stated by Fisher (1937) and confirmed mathematically by Kolmogorov *et al.* (1937). The mathematical details concerning exactly which forms of $f(N)$ lead to asymptotic spread at the rate given by (4), and which initial distributions of organisms will converge to an asymptotic front, may be found in Bramson (1983). Less detailed but more accessible discussion may be found in Okubo (1980) or Levin (1986). The extension of these analyses to two-dimensional habitats (Eq. 1) is discussed by Skellam (1951) and Okubo (1980).

The beauty of (2) and its extensions is that they lead to clear-cut predictions based on extrapolations of empirical data across scales of space and time. For a two-dimensional homogeneous habitat, the main qualitative prediction is that the radius of a species range should asymptotically increase linearly with time. More precisely, the slope of this asymptotic linear increase should be $\sqrt{4\alpha D}$. Application of this model in complex habitats is complicated by environmental heterogeneity and the fact that spread is not radial; but it provides a starting point.

Tests of the theoretical predictions

Lubina and Levin (1988) provide a detailed analysis of the application of this approach to the California sea otter, a case in which spread is essentially one-dimensional since the otters stay relatively close to the shoreline. Much earlier, Skellam also applied diffusion models to data on the spread of a mammal species, the muskrat in Europe (Skellam 1951). But both of these studies lacked microscale data on the demography and movements of individual animals; for that reason they could only test the qualitative prediction that the rate of spread should be asymptotically linear, and to try to use macroscale patterns to determine the processes that must be operating on smaller scales. In contrast, the three case studies we selected included sufficient

microscale data to predict quantitatively a rate of spread from short-term, local observations of individual organisms. However, we still faced the problem of measuring the observed rate of spread. The pertinent data come in the form of range maps, which are based on isolated sightings of individual animals and consequently show boundaries that are highly erratic. This means there is no obvious single number that represents the radius of the range. Two-dimensional stochastic versions of (1) can be introduced, but do not resolve the problem of quantifying rates of spread. In addition, the habitats into which species expand may include major topographic irregularities such as mountain ranges and large bodies of water. Under these circumstances, it does not make sense to calculate a rate of spread as though the environment were uniform. Any practical test of simple range expansion models must be sensitive to these complications. One approach is to modify (1) so that it explicitly includes parameters that vary in space, and then to estimate this variation from spatially structured data (Dobzhansky *et al.* 1979); unfortunately, the data are not adequate for this approach (Banks *et al.* 1985). The alternative approach that we adopted is to develop an approximate description using averaged parameters, and to hope that the model predictions continue to apply. For those species invading relatively homogeneous environments, we obtained these averages simply by dividing their range into eight sectors and measuring the radius of spread in each sector separately. For successive points in time we then calculated the average radius as the root mean squared radius (denoted r_s) over the eight sectors. Since the invasions occurred in conspicuously heterogeneous regions, we divided the spread records into sectors whose boundaries reflected the major irregularities (*e.g.*, rivers, mountain ranges, etc.). To extract an average radius for each geographic sector we took the root mean square radius of the maximum and minimum radial distances of the pertinent sector. A detailed discussion of our protocol for measuring spread by using range maps can be found in (Andow *et al.* 1989), where we treat the three species discussed in this paper as well as rice water weevil, for which adequate microscale information is not available to

Table 1. Test of the linear spread hypothesis for range expansion by muskrat, cereal leaf beetle, and small cabbage white butterfly. The linear spread hypothesis predicts that average acceleration of spread is zero. Means with standard errors given.

	df	Average spread rate (km/yr)	Average acceleration of spread (km/yr ²)
Muskrat			
Prague, Czechoslovakia			
S	20	21.3 ± 0.3****	0.27 ± 0.36 ^{NS}
ESE	22	25.4 ± 0.8****	0.51 ± 0.39 ^{NS}
NW	23	18.7 ± 0.5****	-0.05 ± 0.23 ^{NS}
N	19	11.5 ± 0.5****	-0.25 ± 0.25 ^{NS}
W	14	10.3 ± 0.4****	0.04 ± 0.09 ^{NS}
France			
Eure	2	4.6 ± 0.8*	0.23 ± 0.53 ^{NS}
Ardennes	2	0.9 ± 0.3 ^{NS}	0.03 ± 0.16 ^{NS}
Belfort	2	3.0 ± 0.2**	0.10 ± 0.09 ^{NS}
Finland			
Pohj	2	4.0 ± 0.6*	-0.58 ± 0.09 ^{NS}
Piek	2	5.7 ± 0.4**	-0.50 ± 0.04*
Koke	1	6.1 ± 0.1**	
Unsi	1	3.5 ± 1.4 ^{NS}	-
Cereal Leaf Beetle			
Michigan, USA			
NE	5	89.5 ± 2.7****	-0.67 ± 1.82 ^{NS}
ON	4	89.2 ± 3.8****	45.52 ± 24.15 ^{NS}
VI	5	75.8 ± 4.8****	-1.08 ± 3.08 ^{NS}
TN	5	44.8 ± 2.9****	-1.92 ± 1.33 ^{NS}
IL	4	48.6 ± 2.0****	45.03 ± 26.25 ^{NS}
WI	5	26.5 ± 2.3****	-2.51 ± 0.94 ^{NS}
Small Cabbage White			
Quebec City, Canada			
SL	13	73.7 ± 6.2****	7.31 ± 1.48***
Q	4	42.6 ± 3.0***	1.66 ± 1.07 ^{NS}
NE	6	65.2 ± 6.1****	10.89 ± 3.30*
S	16	169.6 ± 13.4****	18.53 ± 3.35****
GP	17	137.8 ± 6.6****	6.85 ± 2.10**
GL	17	145.4 ± 8.7****	10.97 ± 1.84****
New York City, USA			
South	2	153.0 ± 25.5*	63.00 ± 31.03 ^{NS}
South Carolina, USA			
North	3	42.5 ± 2.4***	8.00 ± 1.73*
South	4	27.4 ± 3.9**	-1.30 ± 1.84 ^{NS}
West	3	74.0 ± 15.9*	34.50 ± 12.82 ^{NS}
Florida, USA			
North	2	97.0 ± 23.9 ^{NS}	52.00 ± 14.25 ^{NS}
East	3	14.7 ± 1.7**	-0.99 ± 0.74 ^{NS}
Indiana, USA			
West	2	79.0 ± 21.3 ^{NS}	41.50 ± 17.05 ^{NS}
Chicago, USA			
West	2	91.5 ± 24.8 ^{NS}	50.00 ± 17.39 ^{NS}

NS Not statistically significantly different from zero

* p < 0.05

** p < 0.01

*** p < 0.001

**** p < 0.0001



Fig. 1. Spread of muskrat from Prague in five sectors. The S/ESE and ESE/N boundaries roughly separate the eastern European plain; the N/NW boundary distinguishes spread down the Oder River from spread down the Elbe River; the NW/W and W/S boundaries isolate the poorly known W sector.

justify inclusion in this paper. As mentioned earlier, we can use measurements of range radii to test models such as (2) by first determining whether spread attains a constant rate, and secondly by asking whether that rate is predicted by (4). In (Andow *et al.* 1989) we report analyses of the linear spread prediction, which is the weaker test of the theory. A summary of these results appears in Table 1. Here we focus on whether use of microscale data, which allow us to estimate coefficients of diffusion (*i.e.*, D) and population growth (*i.e.*, α), yield appropriate predictions of spread at the macroscale. This test of theory has never before been performed.

Our independent estimates of α and D were obtained from published accounts. We estimated intrinsic rates of population growth either from life table data or by calculating the slope of $\log(N)$ versus time for populations growing without limiting resources. We estimated diffusion coefficients from mark-recapture data by using the formulas:

$$D = \frac{M_s(t)}{4t} = \frac{2M_D(t)^2}{\pi t},$$

where $M_s(t)$ is the mean squared displacement and $M_D(t)$ is the mean displacement of recaptured organisms 't' time units after their release (Skellam

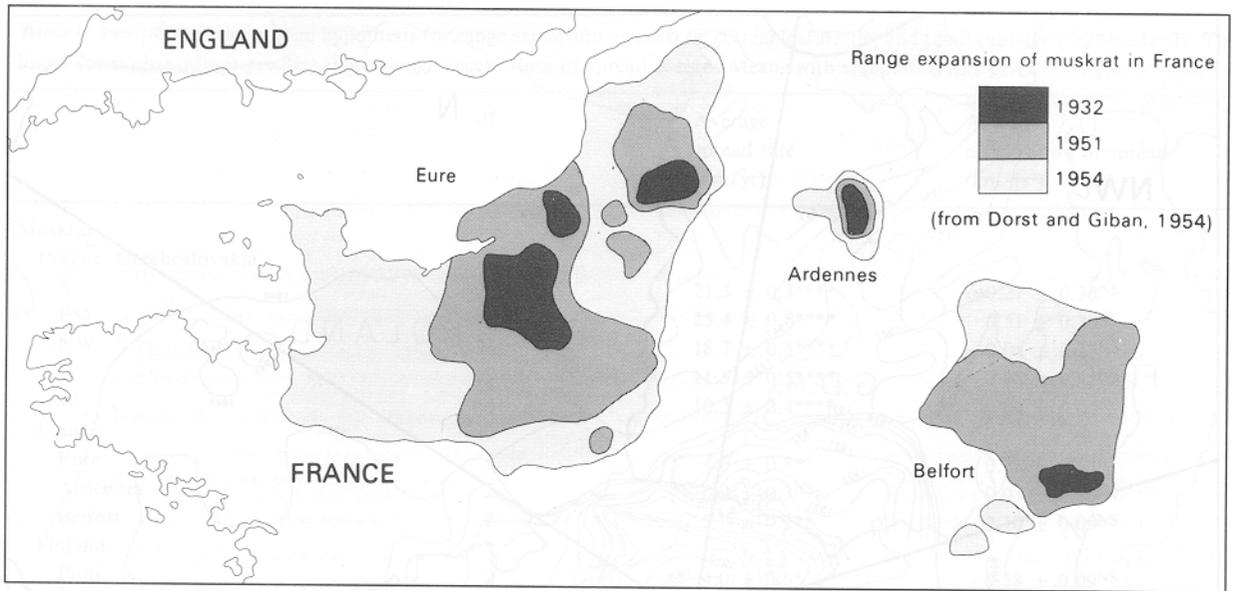


Fig. 2. Spread of muskrat in France at three localities.

1973). The key question is: When these estimates for α and D are substituted into (4), do they predict the observed rate of range expansion (after allowing some time for the asymptotic behavior to be reached)? Note that there is no circularity or curve fitting in this test of the theory.

The match between theory and observed rates of spread

Five muskrats were released near Prague in 1905 (Fig. 1). The species' subsequent range expansion provided the basis for Skellam's assertion that indeed this spread did attain a linear rate of increase, as predicted by theory. We have gone beyond this to ask whether theory predicts the precise rate of muskrat spread. In addition to the Prague release of muskrats (Ulbrich 1930; Hoffman 1958; Frank and Härle 1964, 1967), we have also examined the spread subsequent to releases in France (Dorst and Giban 1954, Fig. 2) and Finland (Artimo 1960, Fig. 3). The observed asymptotic rate of spread in muskrats ranged between 0.9 and 25.4 km/yr (Table 1 and (Andow *et al.* 1990)). We relied on two different mark-recapture studies to estimate diffusion coefficients in muskrats; a study in the Nether-

lands yielded $D = 51.2 \text{ km}^2/\text{yr}$ (von Trooswijk 1976), while one in Finland yielded $230.1 \text{ km}^2/\text{yr}$. Our estimate of per capita rate of population growth was extracted from published survivorship and reproductive schedules (Perry 1982), which we put into a Leslie matrix format. Applying standard methods to this matrix (Pielou 1977), we estimated muskrat α to range between 0.2/yr and 1.1/yr. Using equation (4) we then calculated maximum and minimum spread rates. This agreement between theory and observation was good: predicted spread ranged between 6 and 32 km/yr, whereas observed spread ranged between 1 and 25 km/yr.

The second invasion we analyzed was that of the cereal leaf beetle, whose first North American record was from southwestern Michigan in 1958 (Haynes and Gage 1981). Since United States entomologists feared that this beetle would become a serious pest of wheat, its spread was monitored carefully by the Cooperative States Research Service. Compiling these data (Anonymous 1963, 1965a, b, 1967, 1968, 1969, 1970, 1971, 1973, 1974, 1976; Wilson 1974; Wilson and Treece 1968; Wilson *et al.* 1969, 1970, 1972), we constructed maps of range expansion, which we divided into six sectors as indicated in Fig. 4. By analyzing the changing distribution of beetles over very brief time peri-

ods (on the order of days), Sawyer and Haynes (1985) estimated a diffusion coefficient of 52,000 cm^2/min . We translated this coefficient into an annual rate by assuming 10 hours of beetle activity per day and 120 days of activity per year, which implies a coefficient of 0.4 km^2/yr . Intrinsic rates of increase for cereal leaf beetles were obtained from rates of population growth observed after the beetles had just colonized wheat fields; these rates ranged between 1.6 and 1.9/yr. When equation (4) is used to extrapolate these microscale beetle data into macroscale predictions, the theory is wrong by two orders of magnitude (see Table 2). The cereal leaf beetle is spreading much faster than the microscale data suggest should be possible. It is unlikely that this discrepancy is due to erroneously low microscale estimates: rates of population growth in wheat fields and rates of movement where there is no wheat should be overestimates of the averages for this species. We interpret the failure of (4) to predict cereal leaf beetle spread as an indication that the macroscale spread is governed by processes not observable on the microscale used by Sawyer and Haynes (1985). Such processes could be long-range movement on air currents and hitchhiking on human transport.

The final invasion we examined involves the small cabbage white butterfly, *Pieris rapae*. This butterfly has invaded North America several times (Scudder 1887; Shapiro 1974); here we examine its spread from Quebec, New York City, Charleston, Florida, Chicago, and Indiana. All data were taken from Scudder's detailed account of *Pieris rapae* spread (Scudder 1887), and only spread from Quebec was broken into sectors (Fig. 5). We estimated diffusion coefficients for these butterflies from data collected by Jones *et al.* (Jones *et al.* 1980) on the daily movements of marked females. Mean displacements for butterflies ranged between .5 and 1.2 km/day , which corresponds to diffusion coefficients between 0.16 and 0.92 km^2/day . To convert these daily rates into annual rates, we multiplied by life expectancy for adults (the caterpillar stage is sedentary), which ranges from 10–20 days, and by the number of generations per year, which ranges from 3–7 depending on locale (Harcourt 1966; Parker 1970). The resulting yearly diffusion coeffi-

cients are between 4.8 and 129 km^2/yr . We obtained estimates of intrinsic rate of increase by combining egg-to-adult survivorship (5–15%, Parker 1970), number of female eggs per female (100–600, Harcourt 1966; Baker 1968; Suzuki 1978), and number of generations per year. Performing these calculations, we found that α for *Pieris rapae* in North America could range between 9 and 31.5/yr. Once again, substituting our microscale information into (4), we calculated an expected range of spread rates for these butterflies and contrasted the prediction with the observed range in spread rates (Table 2). The ranges agree surprisingly well (13–127 versus 15–170 km/yr) even to the extent that where we would predict higher spread rates because of more generations (*i.e.*, more southern locales), we indeed observed the higher spread rates.

Discussion

In this paper we have examined the usefulness of diffusion models as aids to understanding observed patterns of spread, and as devices for prediction. Our central thesis has been that the principal objective of any modeling effort is to abstract those details that are relevant to patterns on particular scales of investigation, separating signal from noise by suppressing unnecessary detail. Thus, the adequacy of a particular model can be evaluated only relevant to the purposes at hand, and to particular scales of investigation.

When this philosophy is applied to models of spread, it is clear that the most useful models are not necessarily those that retain great detail at the level of the individual behavior. Thus, even for highly intelligent animals that make extensive use of environmental cues in navigating, the population level patterns may be as well described by models that assume individuals move randomly as by models that include complex navigational behavior (especially if movements are not correlated among individuals). When simple models adequately capture population spread even though complex behaviors are known to be involved, we follow the principle of parsimony; that is, the most appropri-

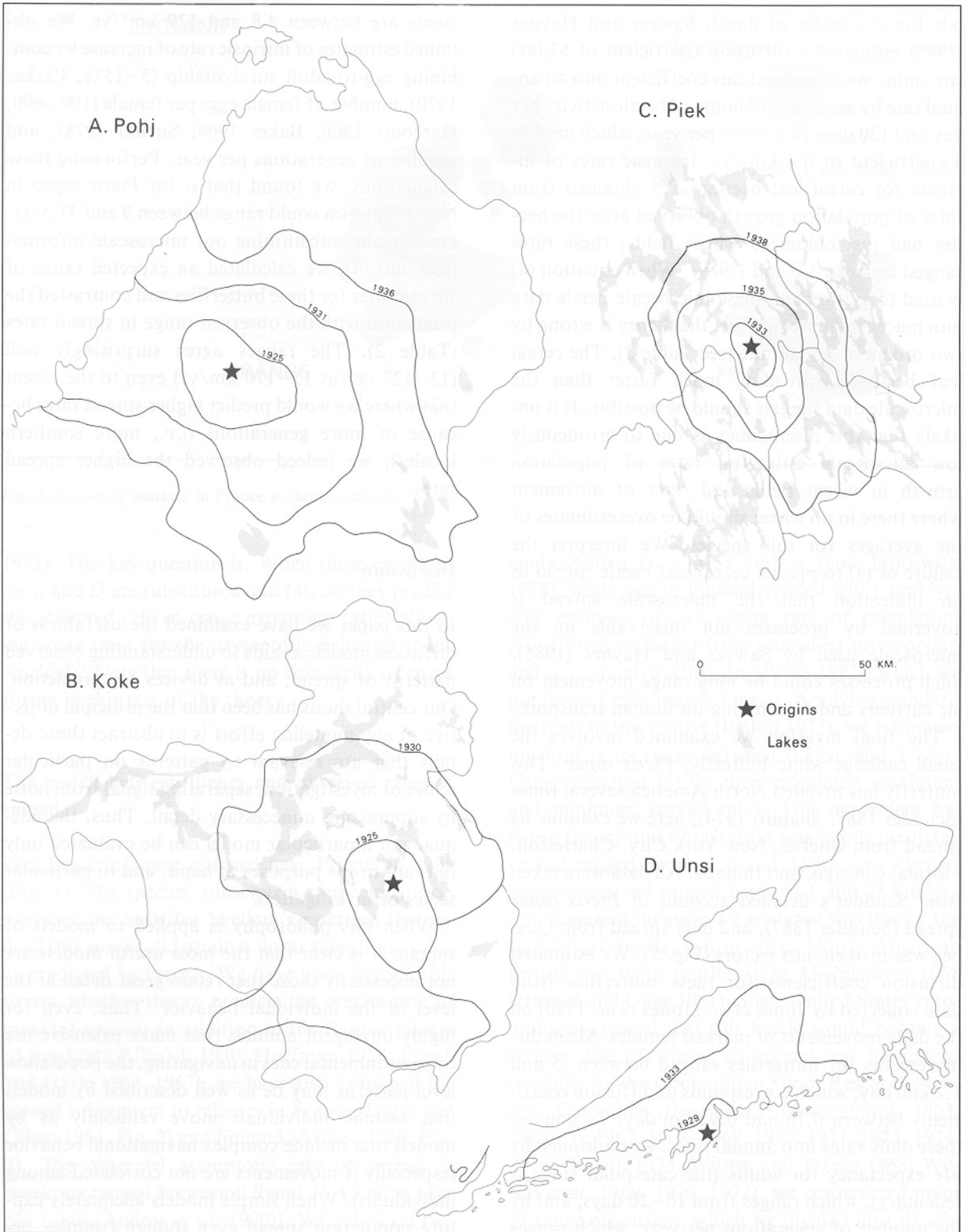


Fig. 3. Spread of muskrat in Finland at four localities. A. Northern Pohjanmaa (Pohj) release in 1923. B. Southern Kokemäenjoki (Koke) release in 1923. C. Pieksämäki (Piek) release in 1932. D. Coastal Unsimaa (Unsi) release in 1924. Muskrats were released at 2×2 km².

Table 2. Comparing observed rates of spread to the rates predicted by a population growth and diffusion model.

Invading species	Finite rate of increase (yr ⁻¹)	Diffusion coefficients (km ² /yr)	Predicted rates of spread (km/yr)	Observed rates of spread (km/yr)
<i>Oulema melanopus</i>	1.6–1.9	0.4	1.6–1.7	26.5–89.5
<i>Pieris rapae</i>	9–31.5	4.8–129	13–127	14.7–170
<i>Ondatra zibethica</i>	0.2–1.1	51.2–230.1	6.4–31.8	0.9–25.4

order to focus on essential features. The diffusion model is an approximation. It must be understood that its predictions can be valid only across a range of scales, and that it is not possible *a priori* to know what those scales will be, unless fairly complete knowledge is available concerning all modes of transport of individuals. Across the range of scales where the model applies, it can represent a powerful tool for interpreting observed patterns of spread.

What are the future extensions of this approach? For heterogeneous landscapes, detailed simulation models have proven useful adjuncts to the basic theory, as in Murray's discussion of the potential spread of rabies in England (Murray 1986, 1987). Two-phase models such as those implicit in Mollison's scheme (Mollison 1977) or others that take into account higher-order moments in the movements of individuals, seem to hold promise when knowledge is available on two scales of movement. For example, for diseases such as influenza, it seems reasonable to use models such as those of Rvachev (see Rvachev and Longini 1985) to explain inter-city transport, and couple them with diffusion models to describe the spread from points of introduction. Similar models should also apply to the spread of agricultural and other pest species, such as the Africanized bee *Apis mellifera*.

Finally, for the fragmented habitats that characterize many environments, percolation theory models provide a new and complementary set of techniques, just beginning to be applied to ecological problems (see for example, Turner *et al.* 1988). Durrett (personal communication) has conjectured analogous results for these systems, mirroring the results proved for first passage percolation (Cox and Durrett 1981) and for a variety of interacting particle systems (Durrett 1988, Chapters 1, 3, and 11). Thus, there now exist a variety of mathematical

methods, in varying states of development and requiring varying degrees of detail, for describing the spread of introduced species. The success achievable with even the simplest models such as those described in this paper, is cause for optimism concerning the usefulness of these approaches.

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