How variable are rates of colonisation?

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Abstract. The rates of spatial expansion of range following the introduction of animals to new areas are extremely variable between species. Data on a selection of species from a range of taxa show that these rates vary over about five orders of magnitude. The range expansion of a limited number of pest species of aphids have been mapped following colonisation. Studies on rates of colonisation are important as they are central to pest risk analysis. In addition, the observed variation in rates have significant implications for the development of realistic models of metapopulations.

INTRODUCTION

One of the general problems in population ecology is to determine the factors which influence the geographical distribution of a species. Studies on this problem show that the range of a species is in a constant state of variation and this occurs both within the range and externally (Hengeveld, 1989). External flux is typically observed during range expansion or more spectacularly during large scale shifts in distribution in geographical space. Internal flux occurs as populations wax and wane at different localities within the range. The dynamic nature of local populations is related to the factors influencing extinction at each site and the rates of migration between localities (Levins, 1969).

External flux is most readily observed during the establishment and colonisation of new geographic space. Such invasions occur as regular events. For example, Waterhouse & Norris (1987) show that a considerable proportion of arthropod pests and plants with weedy status in the Pacific are exotic in origin. In many cases, these invasions are thought to be modern events.

In this paper, data from changes in geographical range are examined to calculate estimates of the rates of colonisation of a variety of animals. I discuss the significance of these data in the context of 1) pest risk analysis, 2) strategies for population monitoring and 3) the dynamics of metapopulations.

ESTIMATING RATES OF COLONIZATION

After introduction and establishment, the range of a colonising species spreads to become an irregular shape in geographical space. These irregularities can be caused by geographical boundaries, the biotic limits of the organism and stochastic processes. For comparative purposes, estimates of expansion rate need to correct for these constraints. Hengeveld (1989) discusses three related measures that are useful in calculating these

rates: radial increase in range, areal circumference of range and the square root of the area occupied.

Here, I use the slope of the relationship between the square root of the area colonised as a function of time to examine variation in the rates of colonization of animals from a broad range of taxa. In order to make comparisons between these organisms, I have assumed that the square root of area colonised increases linearly with time. This assumption is fairly robust but needs qualification when detailed studies of colonization processes are being considered (Hengeveld, 1989). In some other cases, I use estimates of radial spread following introductions.

RESULTS

Elton (1958) and Hengeveld (1989) illustrate the geographic expansion of various organisms in different parts of the world. From these sources, I have examined with rates of colonization of the Japanese beetle (*Popillia japonica*), the red deer (*Cervus elaphus*), Himalayan thar (*Hemitragus jemlahicus*) and the muskrat (*Ondatra zibethicus*). From other literature sources, I have estimated rates of colonization for two species of earthworm (*Aporrectodea rosea* and *A. caliginosa*), the buffalo fly (*Haematobia exigua*), screwworm fly (*Cochliomyia hominivorax*) and the aphids, *Diuraphis noxia* and *Therioaphis trifolii*.

The data presented in Table 1 are derived from studies on colonisation events monitored for periods of time from one year to 100 years and over a very large range of spatial scales. For the limited set of studies examined, the logarithmic values of the colonization rates varied between –2.60 to 2.35.

TABLE 1. Estimates of the rates of colonization (km per annum) of a range of species; based on analysis of distribution maps or published estimates of area colonised.

Species	Country	Log rate	Method	Reference
Aporrectodea rosea	Ireland	– 2.60	Radial	Curry & Boyle
Aporrectodea caliginosa	Netherlands	– 2.00	Radial	Hoogerkamp et al.
Hemitragus jemlahicus	NZ	– 0.37	Radial	Hengeveld
Cervus elaphus	NZ	0.28	Sq Rt	Hengeveld
Haematobia exigua	Australia	0.95	Sq Rt	Tillyard
Popillia japonica	USA	0.99	Sq Rt	Elton
Ondatra zibethicus	Czech Rep.	1.30	Sq Rt	Hengeveld
Cochliomyia hominivorax	Libya	1.90	Sq Rt	Lindquist et al.
Diuraphis noxia	USA	2.29	Sq Rt	Anon.
Therioaphis trifolii	Australia	2.35	Sq Rt	Wilson et al.

DISCUSSION

These results show that, in animals, rates of colonization vary over about five orders of magnitude. This represents a front moving at about 5 m per annum and approaching 250 km per annum for the slowest and the fastest rates, respectively. These data represent a small selection of studies on colonization rates of animals from a range of taxa and, in many cases, they are derived from monitoring studies undertaken following the accidental introduction of pests into a new geographical area.

There are few detailed case studies on range expansion in aphids following invasion, even though these events are very common. For example, Carver et al. (1993) list the aphid fauna of 23 countries in the Pacific. The vast majority of the 44 recorded species found in this region are introductions; presumably an accidental by product of the rapid growth of commerce and trade in the past 200 years. In those cases where the spread of aphid populations has been monitored, the spatial resolution of the monitoring program has often been of limited value. For example, the distribution of *Acyrthosiphon kondoi*, following the accidental introduction of this species to Australia and the USA, was monitored on a relatively coarse scale (Walters & Dominiak, 1978; Berberet et al., 1983). The pests, *Diuraphis noxia* and *Therioaphis trifolii* have been monitored in detail (Smith, 1959; Anon., 1987–1992; Wilson et al., 1981; Wellings & Dixon, 1987) and the data associated with these species suggest that some aphids may have amongst the fastest rates in the animal kingdom (Table 1). Both these species have anholocyclic life-cycles and, because they have the potential to reproduce throughout the year, are likely to have higher rates of colonisation than holocyclic species. Loxdale et al. (1993) suggest that short distance local migration may be a feature of aphid biology. In the host alternating species, *Phorodon humuli*, they suggested that migratory distances of 20 km may be common. This suggests that rates of colonisation in holocyclic species could be up to an order of magnitude lower than anholocyclic species. Similar inferences can be drawn from data on the spread of the heteroecious species *Hyadaphis tataricae* in the USA (Voegtlin, 1982; Voegtlin & Stoetzel, 1988). At present, we lack appropriate data to undertake within species comparisons of colonization processes for pests that have been recorded as exotics at a range of locations. However, the existing data are useful for making some generalisations about the consequences of variation in rates of colonization.

Pest risk analysis studies need: 1) information on the probability pathway that will result in an exotic species reaching a new location, 2) an understanding of the factors resulting in the establishment of a population, 3) data on the predicted rate of spread of the species following establishment, 4) estimates of the potential geographical distribution of the species at the new location and 5) an economic assessment of the predicted losses to the commodities susceptible to attack by the exotic species within the predicted range. Steps 4) and 5) are relatively well understood; the latter through extrapolation of crop loss studies in the home range of the pest, the former through models like CLIMEX (Sutherst & Maywald, 1985) that project potential geographical distribution and locality favourability on the basis of existing distributional data. The combination of information derived from these steps can be used to give a general estimate of the likely economic impact of a pest species, once it has spread to its maximum limits. In the case of aphid pests, a predictive scenario has been completed for *D. noxia* entering Australia (eg. Evans et al., 1989; Hughes & Maywald, 1990).

The first three steps are poorly described. The data presented in this paper show that the predicted rates of spread are very variable for different sorts of organisms. The development of an accurate method for predicting colonization ability is important in the decision making framework required to support pest risk analysis. This is needed because variation in the rate of colonization will determine the time taken to occupy the maximum range in the new locality. This influences the predicted economic impact of the pest and the adoption of pest management strategies.

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Information on the likely rate of colonisation may be valuable in deciding on monitoring procedures needed to track the spread of pests. For organisms with low or medium rates, a regional monitoring system with a quarantine boundary determined by the colonisation potential of the pest may be useful. On the other hand, for organisms with very high rates, monitoring may have little value as the pest front moves so rapidly. Knowledge of the rate of movement of the colonisation front may also be useful in designing the spatial distribution of release sites for biological control agents. If biological control agents colonise new areas at rates relatively lower than their hosts (as seems likely), then it may be appropriate to design release networks that will facilitate rapid occupation of the range likely to be occupied by the host. Releases made on grid with distance of 1/2 the predicted annual rate of spread of the biological control agent would give regional establishment over the shortest time interval. This assumes that sufficient agents can be mass-reared and that resources are available to make releases on the scale needed.

Rates of colonisation may also provide insights into the dynamics of metapopulations. As Hengeveld (1989) points out, the range of species is in a constant state of flux. The data presented in this paper focus on external flux by examining aspects of range shift in new locations. However, these rates of colonisation may be everyday phenomena and reflected in the rates of exchange between local populations of a regional population. To date, models of metapopulation dynamics have made limiting assumptions about inter-locality movement. For example, Reeve (1990) modelled for these effects by assuming that migrants leaving patches collect into a single pool and then redistribute evenly to all localities. In contrast, Comins et al. (1992) modelled metapopulations with restricted dispersal. In their system, migrants were only able to shift to adjacent localities. These two approaches consider opposite ends of a dispersal continuum and show that the dynamics and stability properties of metapopulations may be very sensitive to the assumptions made about internal flux.

In the case of long term studies on the population dynamics of aphids at a number of localities, it is clear that the level of spatial variation in dynamics can be considerable (Wellings et al., 1985). If the rate of colonization is a species characteristic, we might expect the internal flux of different species to vary over a broad range of values with a similar variation as the data presented in Table 1. Our understanding of general dynamics of species within its range requires further studies on the rates of exchange between localities in order to determine the possible effects on the spatial responses of populations.

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