METAPOPULATIONS, DISPERSAL, AND PREDATOR–PREY DYNAMICS: AN OVERVIEW

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INTRODUCTION

The idea that dispersal among local populations may allow the persistence of regional “metapopulations,” despite unstable fluctuations and even extinctions locally, has long been important in ecology (Andrewartha and Birch 1954, 1984, den Boer 1968, 1981, 1987; review in DeAngelis and Waterhouse 1987). An especially popular application of this idea has been to predator–prey interactions (Nicholson 1933, Nicholson and Bailey 1935, den Boer 1968, Murdoch and Oaten 1975, Murdoch 1979, Murdoch et al. 1985, Morrison and Barbosa 1987), as a way of reconciling their persistence in nature with the fact that spatially simple predator–prey systems, both in the laboratory (Gause 1934, Huffaker 1958, Luckinbill 1973) and in models (Nicholson 1933, Nicholson and Bailey 1935), tend to be unstable to the point of extinction.

Dispersal within a population with large-scale spatial subdivision clearly is important in some species and systems. The basic notions of succession and “fugitive” species indicate its role in many instances of interspecific competition (e.g., Levins and Culver 1971, Horn and MacArthur 1972, Levin and Paine 1974, Slatkin 1974, Hanski 1981, 1983). In other cases local extinctions due to bad weather, followed by recolonization, may be common (Birch 1971, Ehrlich et al. 1980, Antonil and Strong 1987, Harrison et al. 1988, D. R. Strong, unpublished manuscript).

For predator–prey interactions, however, evidence of the importance of dispersal is almost wholly indirect. First, it has been argued that not only are simple laboratory or model interactions unstable, but that the features thought capable of producing local stability are either absent (Dempster 1983, Murdoch et al. 1984) or inadequate (Morrison and Barbosa 1987) in many natural interactions. There also is theoretical support for the possibility of dispersal permitting regional persistence despite local instability in two-species predator–prey systems (Taylor 1988b and below). (Similar results also have been obtained for similar systems containing two prey or two predator species [e.g., Caswell 1978, Hastings 1978, Crowley 1979, Hanski 1981, Hogeweg and Hesper 1981], but as these have been primarily concerned with the problem of competitive coexistence rather than predator–prey persistence, I will not consider them further.) There is also some suggestive laboratory evidence, and a few field examples in which dispersal and metapopulation structure may be important. In my view, however, there is not yet any convincing evidence supporting the hypothesized role of population structure and dispersal in any natural predator–prey interaction.

In the following, after summarizing what is known from models, I will concentrate on a review of the empirical, and especially field, data. My aim is not simply to assert that we know very little about dispersal in natural predator–prey systems, but to point out why this is: why large-scale spatial dynamics have been so difficult to study, and how they might better be addressed (see also Reeve 1990).

THE HYPOTHESIS

Dispersal and “among population” spatial structure, the subjects of this review, are usually thought of as distinct from within-population movement and spatial effects. By “population” (or “cell”) is meant the unit within which occur interactions—reproduction, population regulation, predation—and within which most movement is confined. A “metapopulation” (or “system”) is a collection of such local populations, and “dispersal” refers to movement, often once in a lifetime, from one population to another. Movement within a population will almost certainly also be important dynamically (see the massive literature on spatially heterogeneous predation). Its causes and effects, however, are different from those of dispersal: the important within-population movements are part of the predatory interaction itself, and directly affect the stability of the local interactions by determining the distributions of prey and of predation.

This distinction between “among-” and “within-population” processes may be artificial in many sy-
tems. For instance, when dispersal is frequent, and especially when immigration depends on local conditions, predator dispersal and foraging may be indistinguishable. The proposition that population subdivision and dispersal provide an alternative to the stabilizing mechanisms of “classical” predator–prey theory implies, however, that the among- vs. within-population distinction is being made: within-population movement, e.g., foraging behavior, is exactly the stuff of classical theory. In this review I will therefore follow metapopulation theory in treating the among- vs. within-population distinction as real.

“Local populations” need not be distinct, bounded entities. The idea of dispersal promoting regional persistence can apply within a single, essentially continuous population which is much larger than the scale over which interactions occur (as in the “neighborhood” competition of Pacala and Silander [1985, Pacala 1986a, b, 1987]). The diffusion models discussed by Hastings (1990) address this situation.

More commonly, however, dispersal and large-scale population structure are thought of in the context of a collection of discrete local populations. The organization of such patches can have either an “island-mainland” or a “metapopulation” structure (Slatkin 1977). In an island-mainland (“source-sink,” Pulliam 1988) situation, however, dispersal is largely a side issue: it is irrelevant to the maintenance of the mainland population on which the persistence of the unstable peripheral populations depends. In contrast, dispersal is of central importance in metapopulations, in which all populations are essentially equivalent and equally affected by dispersal. For this reason I will focus on patchy metapopulation structures in the following.

The assertion that dispersal is important in the persistence of metapopulations in fact contains a spectrum of hypotheses, differing in the nature of the local “instability” they assume. Three categories of hypotheses can be distinguished:

1) Local extinctions and recolonization occur frequently.
2) Isolated local populations frequently would go extinct, but migration (usually) prevents this.
3) Isolated local populations usually would persist but fluctuate, and migration reduces the magnitude of the fluctuation.

As will be seen below, while all of these hypotheses have been studied theoretically, attempts to prove the importance of dispersal in the field have focused on the first, most extreme situation, as have studies of laboratory systems. The more subtle, and in my view more likely, second and third hypotheses thus have received little empirical attention.

Theory

Two distinct types of models of predator–prey metapopulations have been studied. In “cell occupancy” models (Vandermeer 1973, Maynard Smith 1974, Hastings 1977, Zeigler 1977, 1978, Gurney and Nisbet 1978, 1982, Takafuji et al. 1983), the variables considered are how many cells are in each of a set of discrete states of prey and predator occupancy at a given time. These models all assume an inevitable within-cell progression from predator invasion to extinction: they model the first hypothesis above. (In Vandermeer’s [1973] model predators can survive in a cell following prey extinction, presumably on other prey species; all other models implicitly concern monophagous predators, and prey extinction necessarily results in predator extinction.)

The second class of models, in contrast, describes within-cell dynamics explicitly, by standard single-population predator–prey models (Comins and Blatt 1974, Cheung 1975, Zeigler 1977, 1978, Maly 1978, Cowley 1981, Reeve 1988, 1990), or variants of these (Allen 1975, Hilborn 1975), or by detailed system-specific models (Sabelis and Laane 1986, Nachman 1987a, b, Sabelis and Diekmann 1988); dispersal among cells is then added to these within-cell models. Sabelis’ mite models (Sabelis and Laane 1986, Sabelis and Diekmann 1988), address version (1) of the hypothesis: local extinction is an inevitable result of predator invasion. In the remaining models, however, isolated cells can persist indefinitely. These models therefore address the second and third of the hypotheses above; the most thoroughly studied (Crowley 1981, Reeve 1988) do not even permit local extinction, and so deal with only the third of the hypotheses.

The consistent conclusions from these models, as well as the unanswered questions and points of disagreement, have been reviewed in Taylor (1988b; also by Hastings [1990] and by Reeve [1990]), and so will only be summarized here. The basic theoretical conclusion is that persistence can indeed be enhanced by dispersal among populations within a metapopulation, provided some quite loose, and seemingly likely, conditions are met.

The fundamental requirement is asynchrony of cell fluctuations. Asynchrony (and indeed deterministic stability) can arise from fixed spatial heterogeneity (Comins and Blatt 1974, Cheung 1975; cf. Maynard Smith 1974), or from independent, stochastic local factors (spatio-temporal variability) in the absence of mean or deterministic differences among cells. In cell-occupancy models the probabilistic dispersal process itself generates spatio-temporal variability. In models with explicit within-cell dynamics, spatio-temporal variability can take the form either of demographic stochasticity within small populations (Nachman 1987a)
or in dispersal among cells (Hilborn 1975), or of environmental variation in population parameters (if on roughly the spatial scale of populations) (Crowley 1981, Reeve 1988, 1990).

Persistence also places requirements on dispersal rates. If local extinction is inevitable following predator invasion, both prey and predator populations must be able, on average, to replace themselves before going extinct. This generally requires (Maynard Smith 1974, Zeigler 1977) that dispersal rates be above some minimal level (but see Hastings 1977), and predator invasion not be too rapid relative to prey colonization. If local extinction is not inevitable there apparently are no minimum dispersal rates for persistence (Crowley 1981, Nachman 1987b, Reeve 1988). Dispersal must also not be so great as to synchronize the system. In cell-occupancy models the probabilistic nature of colonization is a powerful source of asynchrony (Taylor 1988b), so most such models find no upper limit on prey dispersal rates (Maynard Smith 1974, Hastings 1977, Zeigler 1977; cf. Takafuji et al. 1983). Demographic or environmental spatio-temporal stochasticity, however, is only weakly desynchronizing, so in models depending on it dispersal rates must be below some modest level, which depends on the magnitude of the stochastics (Crowley 1981, Nachman 1987b, Reeve 1988).

Maintenance of asynchrony also depends on the metapopulation's size: persistence is enhanced in systems with more cells (Maynard Smith 1974, Hilborn 1975, Zeigler 1977, Crowley 1981, Nachman 1987b, Reeve 1988), especially when dispersal is only to nearby cells, because the likelihood of all cells becoming synchronized is decreased (Crowley 1981).

A final requisite for metapopulation persistence is that there be some local density-dependent factor(s). Although most metapopulation models have unstable local dynamics, they do all contain some source(s) of density-dependent population regulation, including that intrinsic to coupled predator-prey models (Taylor 1988b). If this were not the case, extinctions or population explosions (leading, in nature, to resource limitation or some other density regulation) would almost certainly occur (Reeve 1988, 1990, Taylor 1988b). Furthermore, stronger within-population density dependence (and thus less instability, or even better, actual stability) enhances persistence and constancy (Reeve 1988, 1990).

Laboratory Studies

Outcomes resembling the preceding theoretical conclusion have been observed in several laboratory studies of population spatial structure, dispersal, and persistence in predator-prey systems; indeed, much of the theoretical work was in response to these laboratory results, and especially to Huffaker's (1958) famous mite study.

The best of the laboratory studies is that of Pimentel et al. (1963). This study involved a parasitic wasp and one or the other of two fly hosts, in replicated experimental systems composed of small boxes connected by tubes. The interactions consistently persisted longer in larger systems (more boxes), or systems with reduced parasite dispersal, than in smaller systems or ones with freer dispersal.

Huffaker (1958) also found that his two mite species persisted longest in the most complex environment. This persistence, however, was only for three oscillations, and only one prey female survived each of the previous population crashes. Since the study was entirely unreplicated, it seems quite likely that it was only by luck that this "persistence" occurred in the most complex system. Persistence for two or more oscillations was found by Huffaker et al. (1963) in both replicates of a complex system, but some doubt is raised about this result as well, since all three replicates of a similar system with larger cells went extinct after only one oscillation. Given the lack of replication of some trials, and the fact that within-cell dynamics as well as system structures varied between trials, these studies can do no more than suggest that some aspect of spatial complexity may have enhanced persistence; stronger, more mechanistic conclusions are inappropriate.

Enhancement of persistence is even more questionable in the mite study of Takafuji (1977). In this case no systems persisted beyond one oscillation; the more subdivided system lasted a longer time simply because it took predators longer to disperse from the single release site and exterminate the prey. A later experiment with uniform initial distributions did find longer persistence, with some recolonization of patches, in the system with reduced dispersal (Takafuji et al. 1983), but this again was unreplicated; a replicated experiment found no consistent effect of cell number on persistence.

Taken together, these laboratory studies do suggest enhanced persistence due to dispersal within metapopulations. Given the serious methodological problems in several of them, and the extremely artificial scale and structure of all of them, however, I believe they provide much weaker evidence for the metapopulation hypothesis than is commonly asserted.

Natural Populations

Murdoch et al. (1985), after reviewing several cases of successful biological control, challenge a number of equilibrium-based assumptions concerning arthropod predator-prey interactions. One of their assertions is directly pertinent to metapopulation dynamics: they find that in only one case is there good evidence of an
interaction which is persistent on a local scale, and that in several others local extinctions of some sort definitely occur. They therefore conclude that extinction of local populations may well occur in most of these systems, and thus that migration may be essential to their regional persistence. They do not, however, claim that this is the case, and in fact they provide little positive evidence for it: in some of their examples there is no more evidence of local extinctions than of local persistence, and several other cases do not appear to involve true metapopulation structures.

Two of the cases examined by Murdoch et al. (1985) involve mosquito larvae, with either backswimmer bugs (Notonecta) or mosquito fish (Gambusia) as predators. In both systems the predators do sometimes eliminate all larvae from a site (pond or tank). However, refuges, i.e., tanks unsuitable for predators, apparently are important in maintaining mosquito populations, implying an island–mainland rather than metapopulation structure. Furthermore, while a pond or tank may constitute a “population” for the predators, a mosquito population presumably is much larger. Finally, neither predator is dependent on mosquitoes for prey, and so they do not themselves go extinct as a result of having temporarily eliminated mosquitoes from a site. In short, dispersal is important in mosquito populations as a direct consequence of their complex life cycle, but mosquito–predator interactions do not resemble the usual metapopulation–dispersal scenario at all closely.

In two other cases, the olive scale and the cottony–cushion scale, most extinctions are on a spatial scale of individual trees (Murdoch et al. 1985), or even smaller (Huffaker et al. 1986). This spatial scale is almost certainly smaller than the foraging range of the natural enemies, and so these extinctions are probably more properly interpreted as within-population phenomena. One larger, probably truly population-level extinction of olive scale (extinction from an entire grove) is described by Murdoch et al. (1984), but the absence of recolonization over the following 12 yr argues against the role of dispersal in maintaining populations at this spatial scale.

Finally, for two forest pests, winter moth in Nova Scotia and larch sawfly in Manitoba, local extinction is suggested by the fact that pests were not found at some sites, following suppression by enemies (Murdoch et al. 1985). For winter moth, however, little effort had in fact been made to find the moth; as Murdoch et al. (1985) conclude, local extinction is far from proven. Furthermore, persistent populations of moths and parasitoids in town and orchards may serve as population “mainlands” maintaining ephemeral “islands” in the forests.

The evidence for extinction and subsequent recolonization is considerably stronger for larch sawfly: the failures to find the pest, and sometimes also its parasites, were despite intensive sampling efforts and often were followed by reappearance in later years (Murdoch et al. 1985). Although extinction is difficult to prove, these data clearly are strongly suggestive of it. Unfortunately, nothing apparently is known about where and how the insects were persisting, i.e., where the colonists came from to re-establish populations. How well this system corresponds with the metapopulation hypotheses and models discussed above therefore also is not known.

Turning from predator–prey to plant–herbivore interactions, two well-known systems have been proposed as examples of metapopulation processes. One of these is the biological control of Opuntia cactus by Cactoblastis cactorum in Australia. The dynamics of this interaction, following the initial destruction of the cactus infestation by the moth, were described by Nicholson (quoted in Monro 1967) and Dodd (1959) in archetypal metapopulation terms: small, widely dispersed clumps of cactus lasted long enough to reproduce and disperse before being found and destroyed by the moth. Monro (1967, 1975, Osmond and Monro 1981; also Birch 1971, Myers 1987), however, describes a very different situation in which both cactus and moth persist at fairly stable densities throughout most of their range. The plant apparently does not suffer local extinctions, and the moth does so only in marginal populations. Interestingly, the apparent stability of this interaction has been attributed to within-rather than among-population heterogeneity and movement (Monro 1967, Caughley 1976, Myers et al. 1981).

Van der Meijden’s (1979) report of “local extinctions” in the ragwort–cinnabar moth interaction often also is cited as an example of regional persistence through dispersal. The “populations,” however, are in fact simply within-population patches: they are small, closely situated, and generally annual clumps of plants. An individual moth oviposits on many such clumps, and “extinction” occurs as part of the life cycle of the plant or due to weather (van der Meijden 1971), regardless of herbivory. Three other intensive studies of this interaction in other areas (Dempster 1971a, b, Myers 1976, 1980, Myers and Campbell 1976, Dempster and Lakhani 1979, McEvoy 1985, McEvoy et al. 1989), indicate that the plant probably is always present in a given locale, though perhaps at such low densities that it is “nearly extinct” (Myers 1987). (It appears from McEvoy et al. [1989] that the moth may have been locally extinct. If true, however, this was due to competition from a flea beetle, rather than to an unstable predator–prey interaction.) It is again worth noting that, as with Opuntia–Cactoblastis, within-population spatial heterogeneity and movement has been
emphasized as the explanation for the persistence of cinnabar moth populations (Dempster 1971a, b, Myers 1976, 1980, Myers and Campbell 1976).

CONCLUSIONS

Models, laboratory studies, and analogy from competitive interactions, all suggest that metapopulation structures and dispersal should be important in predator–prey systems. Why then is there so little evidence for this from nature? The short answer is simply that few studies have looked specifically for such evidence: none of the field studies reviewed above was designed as a study of metapopulation processes. This contrasts sharply with the attention that has been given to within-population spatial processes, and even single-species or competitive metapopulations, but of course does not bear on the real importance of any of these processes.

A more constructive explanation for the lack of good field evidence is the emphasis on local extinction (by Murdoch et al. [1985], as well as by me in the preceding review of plant–herbivore examples). Implicitly, only the most extreme version of the metapopulation hypothesis has been addressed. This approach has a major virtue: local extinction and recolonization, if observed, is sufficient proof for both the absence of local stability and the importance of metapopulation structure and dispersal. It also is all that can be done with purely observational data on local densities. It has an equally important disadvantage, however: extinction, being a negative proposition, may be very difficult to prove in any but the simplest situations.

Furthermore, proving local extinction is more than is necessary, in terms of the general metapopulation hypothesis (i.e., versions [2] and [3], as well as [1]). Observational data on densities, however, will be of little use in addressing the effects of dispersal when extinctions do not occur: as shown by Reeve (1990), the local dynamics of locally stable and of dispersal-maintained locally unstable systems may be virtually indistinguishable.

At a minimum, data on dispersal is also needed; ideally, these would describe movement within an entire system, but even data on movement in and out of a single local population would be useful. From such data, the role of dispersal and system structure could be analyzed by manipulation of specific models like those of, e.g., Sabelis and Laane (1986) and Nachman (1987a, b) for greenhouse mite systems.

Ultimately, however, experimentation, replicated manipulation of dispersal among natural (or semi-natural, e.g., greenhouse) populations, seems necessary (Reeve 1990; he also discusses specific experimental protocols). This may be impossible in many cases, and will be difficult in most others. The history of population ecology, however, clearly demonstrates the difficulty of making convincing inferences about complex ecological processes from purely observational data. It is therefore difficult to see any way to establish firmly whether and when dispersal and large-scale population structure really are important in the persistence of predator–prey interactions, other than by careful experimentation. In the absence of such experimentation, we can only speculate.

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LITERATURE CITED