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# Of mites and models: an introduction to the symposium proceedings

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It is most remarkable that the study of one group of arthropods, the mites, has generated a disproportionately large contribution to recent progress in the area of theoretical population ecology, and hence, in the development of a theoretical foundation for pest management. It is probably a combination of various factors that has brought this situation about. Mites are very small organisms, allowing the all important large sample sizes, even in laboratory studies, yet, they are large enough to be individually noted and manipulated. The fact that they are terrestrial, flightless surface dwellers simplifies observing, counting and model testing, and alleviates the problem of unwanted dispersal. That several phytophagous mites are major agricultural pests, and that many of their natural enemies are also mites certainly encourages researchers to choose these organisms as their subjects of consideration.

Perhaps the most significant development in furthering our understanding of animal population dynamics is our coming to terms with rejecting the assumption of homogeneity in populations. Starting in the 1960s several authors stressed the importance of spatial heterogeneity, scale, patchiness, space and time lags, and other such concepts that challenged the assumption of homogeneity (e.g. Den Boer, 1968; Maynard Smith, 1974; Roff, 1974; Hilborn, 1975; Hastings, 1977; Crowley, 1978), but little formal theory or experimental work addressed this aspect of ecology until the early 1980s. The mite researchers and theoretical ecologists alike, Huffaker's (1958) population experiments with an orange-feeding spider mite and its phytoseiid predator are generally recognized as a milestone in challenging the homogeneity assumption. These showed that prey and predator were able to coexist for a longer period in a more heterogeneous environment than in a more homogeneous one. This observation has been widely cited as the first demonstration that prey–predator persistence is enhanced by patchiness in the environment (see Taylor, 1991). However, Huffaker's results were more complex than a mere relation between complexity and persistence. One of the most intriguing features of Huffaker's prey–predator dynamics was the occurrence of distinct cycles. This extra dimension has received a lot of attention (e.g. Maynard

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Smith, 1974; Gurney and Nesbitt, 1978), but is still far from being resolved (see Woolhouse and Harmsen, 1987a,b).

Through his population experiments with another acarine prey–predator system, Nachman (1981a) did not only show overall population cycles under greenhouse conditions, but he also stressed the importance of plants as homogeneous patches within a more heterogeneous environment. Of particular importance was his observation that (despite the existence of overall population cycles) local population cycles in poorly connected patches were frequently out of phase with one another (Nachman, 1981b). This work, we believe, opened the door to a major body of research on what has become known as metapopulation dynamics, which has dominated the past decade. The various experimental and theoretical developments that led up to, and consisted of the early stages of this new era of ecological research are eloquently discussed in Nachman's (1988) contribution to the proceedings of the first symposium on population dynamics of plant mites (a meeting that also led to the foundation of the European Association of Acarologists).

In the proceedings of that first symposium, metapopulation models (Diekmann et al., 1988) are presented based on yet another view on what constitutes a patch. This view stems from a paper by Sabelis and Van der Meer (1986) on local dynamics of acarine predator–prey systems. They argue that once a leaf is colonized by one or more spider-mite females their population gradually expands by colonizations of leaves nearby, thereby resembling the expansion of a drop of oil floating on a water surface. Because the predatory mites frequently move from one colonized leaf to the other within the cluster of colonized leaves and tend not to move out of the cluster (until after the prey population is wiped out), Sabelis and Van der Meer (1986) proposed to define a prey patch as being the total infested leaf area within a cluster of colonized leaves. The emphasis is now on the part of the leaf area where the predator–prey interaction takes place, rather than on the leaf area of an individual plant. This idea of a prey patch is schematically outlined in Fig. 1 and forms the basis for the metapopulation models analysed by Diekmann et al. (1988, 1989), Sabelis and Diekmann (1988) and Sabelis et al. (1991). The distinction between plant patch and prey patch is important, which becomes apparent e.g. when defining the risk of predator invasion into either type of patch.

We have now proceeded four years beyond that 'first meeting', and our understanding of metapopulation dynamics has surged ahead, as the current proceedings of the second meeting attest. Whereas major steps forward emerged from the study of insect host–parasitoid systems (e.g. Hassell and May, 1988; Reeve, 1988; Pacala et al., 1990) we find that acarine prey–predatory systems are still playing an inordinately large role in the development of metapopulation theory (Gilpin and Hanski, 1991; Taylor, 1991). Fully

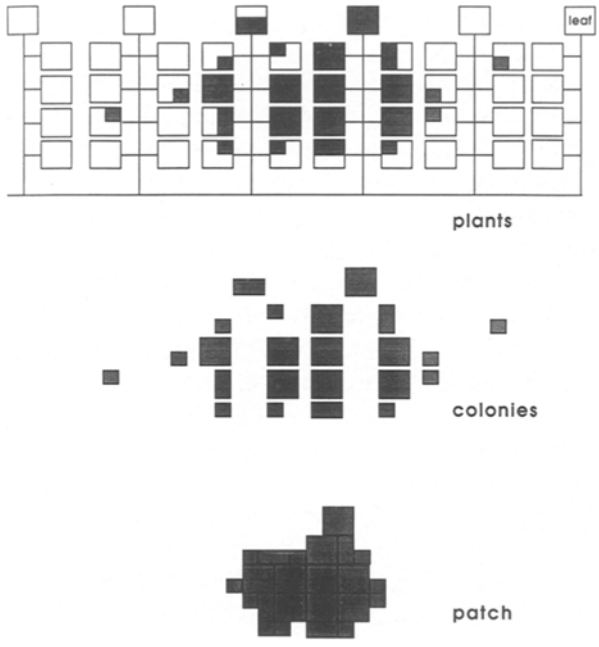


Fig. 1. A schematic diagram of a prey patch, inspired by observations on infestations of two-spotted spider mites in various crops (Sabelis and Van der Meer, 1986).

half of the papers presented in the current proceedings volume make a direct contribution to this exciting area of endeavour.

The paper by Van de Klashorst and coworkers is a particularly exciting contribution, because it reports the results of a long-term, large-scale experiment where the numerical dynamics of prey and predator are recorded on three scales: tree, mini-orchard, orchard (collection of mini-orchards). With its companion paper by Lingeman and Van de Klashorst, which introduces to acarologists a powerful statistical tool for the analysis of time series data sets, this paper provides a first glimps into the structural dynamics of real-world metapopulations. The experimental results strongly support the theoretical concepts of partial prey–predator uncoupling leading to a-synchronous dynamics among mini-orchards which in turn leads to overall metapopulation persistence. However, the paper also points out some weaknesses and challenges in metapopulation experiments in general. Despite a very labour-intensive approach, it is clear that the sample sizes were insufficient to reveal the smaller-scale dynamic processes. As a result, some important questions about prey–predator coupling were left unanswered. The same problem was encountered by Walde and co-workers, who faced the difficult task of operationally defining 'local extinction' as the dynamic opposite of 'persistence'. Their contribution is particularly important, in that it stresses the role of pro-

cesses other than patchiness, especially predator utilization of two or more sources of food, in population maintenance.

As an extension of earlier work (Sabelis et al., 1991), Jansen and Sabelis consider an expanded, tractable, tri-trophic model of patch state transitions within the Lotka–Volterra paradigm. They explore the importance of prey dispersal, where the prey organism is, of course, also the 'predator' to the plant. As so often, tractability is achieved here at the expense of realism, which begs for further work. However, the results of their simulations and stability analyses are opening new facets, such as the phenomenon of bistability, where only depending on timing and dosis of the predators introduced the system either moves to stable limit cycles in the herbivore–plant interaction (thus, with predators extinct) or to a stable equilibrium for plant, prey and predator populations. Jansen and Sabelis argue that this form of bistability can offer an alternative explanation for pesticide-induced outbreaks of spider mites and failures of predator introduction with respect to long-term establishment.

In another paper, Janssen and Sabelis provide a clear-cut view on the major features of what constitutes a prey patch (as in Fig. 1) and the predator–prey dynamics within such a patch. They discuss an extremely simple model of local predator–prey dynamics and a literature review of data on life tables and predation in the Phytoseiidae. This model shows the capacity of phytoseiid mites to wipe out local populations of spider mites and provides general conditions under which local prey elimination is possible.

One further aspect of metapopulation ecology which deserves special attention is stressed in the paper by Takafuji and Tsuda. This paper reminds us that heterogeneity in an organism's environment also has consequences for the evolution of traits, such as diapause, consequences which in turn feed back into the population dynamics of the organism in question and its predators. In a similar vein Dunley and Croft explore the consequences of populations structure and dispersal capacity for the evolution of pesticide resistance.

Alternative food sources are of major importance for the persistence of populations of predatory mites. Bakker and Klein test the hypothesis that plants maintain local populations of predators as bodyguards in their battle against herbivores by providing food (phloem exudates) to natural enemies of the herbivores. In this sense the interaction between the host plant and predatory mites may have a transtrophic character. The evidence from the cassava green mite/predatory mite system on cassava in South America underscores the complexity of such interactions and its influence on predator persistence. A similar conclusion can be extracted from McMurtry's paper on generalist phytoseiid predators, although here persistence is promoted by alternative prey (as with Walde and coworkers), not on availability of plant-produced food substances.

Interactions among two or more predators are addressed by Croft and co-

workers, and by Clements and Harmsen. The first team describes field experiments where two species of phytoseiid mites interact in a very complex manner, while the second team describes the interaction of one phytoseiid and one stigmaeid, based on laboratory experiments and model simulations of local population dynamics. The major conclusion of both papers is that the efficacy of pest control is enhanced by exploiting the natural enemy complex, as compared to the impact of the most effective predator species when acting alone.

For a solid theoretical foundation for designing IPM strategies there is still a long way to go. Such a theoretical foundation must be able to cope with multi-species interactions, alternate food sources, heterogeneity in patterns of crop management, and so on. In the meantime, practical IPM of mites in various crop systems must and will continue. The search for new predators, including non-phytoseiid ones, in various tropical environments deserves high priority (Gerson). New applied system models for both strategic and tactical management of various crops will have to be constructed, and existing ones will have to be refined (Wilson and coworkers). Criteria must be defined, and rules established for the introduction and management of biological control agents, natural as well as possible future bio-engineered ones (Hoy).

To us, the proceedings present an up-to-date, and well-integrated view of where we stand in relation to advances in theoretical biology and population ecology. Moreover, the proceedings clarify how theoretical insights will in the future guide us in the design of IPM strategies for mite management, but it also reminds us of certain limitations, problems and pitfalls that we are likely to encounter. Thinking ahead to the third meeting, tentatively planned for Copenhagen in 1995, we expect significant progress in modelling the dynamics of spatial patterning and evolution in metapopulations (Hassell et al., 1991; May, 1991; Boerlijst et al., 1992), in developing experimental approaches to test these models and, last but not least, in the biology of plant-inhabiting mites. In view of the fact that similar developments take place in the study of parasite–host, parasitoid–host, herbivore–plant and other predator–prey systems, we strongly urge that representatives from related subdisciplines be invited to participate in, and contribute to the next symposium on population dynamics of plant-inhabiting mites.

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