

An integrative paradigm for the dynamics of monophagous parasitoid–host interactions

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Although much research on exploiter–victim interactions has concerned predators and their prey, over the past 25 years there has been a flurry of theoretical work involving monophagous insect parasitoids and their herbivorous insect hosts. This is, in part, because such tightly coupled systems are apt to be the most likely to exhibit strong top-down control from the third to the second trophic level.

This theory is approaching a crossroad. It is becoming increasingly clear that the community surrounding tightly coupled host–parasitoid interactions cannot be neglected in determining the dynamics of these systems. It is also apparent that spatial scale may be pivotal in the persistence and dynamics of such species couples. In this paper I propose that a general paradigm of the population dynamics of monophagous parasitoid–host associations is emerging, and we are now, more than ever, in a position to investigate it theoretically and experimentally.

Three paradigms of host–parasitoid dynamics

Below I group studies on persistent host–parasitoid population dynamics into three paradigms. These paradigms are distinguished by the role of monophagous parasitoids in the local population dynamics of their hosts (paradigms 1 and 2) and, under the hypothesis that local systems cannot persist for long on their own due to the actions of the parasitoid, by the spatial scale of the system (paradigm 3). The paradigms are not mutually exclusive, and they are intended as conceptual tools for identifying the salient features of host–parasitoid associations which could be most profitably investigated in the future.

Paradigm 1: Tightly coupled control

Most models of monophagous parasitoid–host popula-

tion interactions are developed with the tacit understanding that if the parasitoid were to be omitted from the system, then the host would be regulated by other density dependent forces usually at higher densities than those imposable by the monophage alone. Hence, these models make the important assumption that background regulatory factors, be they resource competition and/or other natural enemies, are weak relative to the host-limiting powers of the parasitoid under question.

Beddington et al. (1978) addressed the issue of the role of monophagous natural enemies in biological control programs by presenting six cases resulting in pest depression to extremely low levels. In these spectacular instances, it could be reasonably hypothesized that it was the release enemy alone which was responsible for host depression and that, therefore, models without background regulatory factors (= host 'self-limitation') could apply. Beddington et al. examined the predictions of a series of mathematical models in which host self-limitation did indeed act, with the object of identifying what ecological factor(s) could be responsible for a parasitoid depressing its host population to very low levels and thus enable it to dominate and regulate its host's dynamics. They identified spatial heterogeneity in the distribution of parasitism as being the most likely candidate for host regulation dominated by a single parasitoid species.

Although heterogeneity in parasitism had been previously evoked as a way in which a single parasitoid or predator could regulate its host (Bailey et al. 1962, Hassell and May 1973, Murdoch and Oaten 1975), it was not until Beddington et al.'s comparison and the concurrent seminal works of Hassell (1978) and May (1978), that intensive search began to identify and explore the mechanisms giving rise to parasitoid-dominated regulatory dynamics. Until the mid-1980s, most of this research concentrated on spatial density dependence in parasitism (i.e., a form of spatial heterogeneity) as a means of producing temporal density dependence and thus population stability. Both direct

(Hassell 1978) and inverse (Hassell 1984) spatial density dependence were shown to stabilize host–monophagous parasitoid interactions, and the prevalence of each in nature was subsequently demonstrated (Walde and Murdoch 1988).

At about this same time it was becoming clear that spatial heterogeneity need not require spatial density dependence, and indeed the former could arise independent of local host density (Chesson and Murdoch 1986). These lines of reasoning culminated in the early 1990s in a series of papers which derived a general population dynamic criterion for density dependent and density independent forms of spatial heterogeneity, set-out methods to measure and distinguish the two, and employed a number of data sets to estimate real levels of heterogeneity in the field (Hassell and Pacala 1990, Pacala et al. 1990, Hassell et al. 1991a, Pacala and Hassell 1991).

Chesson and Murdoch's (1986) and Hassell et al.'s (1991b) studies predict that increasing levels of spatial heterogeneity should generally stabilise host–parasitoid links. Neither work claimed that heterogeneity is a universal stabiliser, and both studies discuss limiting cases. Since these illuminating investigations, others have broadened the list of situations where increasing heterogeneity in risk should have weak or negative effects on stability (reviewed by Taylor 1993a; and see Murdoch and Stewart-Oaten 1989, Hochberg and Lawton 1990, Hochberg et al. 1990, Godfray and Hassell 1991, Godfray and Pacala 1992, Ives 1992, Murdoch et al. 1992, Taylor 1993b, Rohani et al. 1994, Getz and Mills in press). More recent studies have quantified spatial heterogeneity and/or investigated its potential action for real host–parasitoid systems (Driessen and Hemerik 1991, Redfern et al. 1992, Jones et al. 1993, Lampo 1994, Reeve et al. 1994, Hochberg et al. in press).

Paradigm 2: Mixed control

An alternative view to the tightly coupled control paradigm is one where the monophagous parasitoid contributes to the dynamics of its host, but only in combination with one or more forms of density dependence already present in the system. At least three scenarios are possible under this paradigm. First, the density dependence rendered by the monophage is necessary for host persistence, but its action is always part of a larger suite of extraneous density dependent effects. Second, the monophage has a density dependent (and potentially regulatory) impact on the host, but its presence is not necessary for host persistence. Third, the parasitoid does not contribute to host regulation (and may even detract from it), and it is extraneous density dependence which permits host persistence.

There is a considerable theoretical base showing how host regulation by a monophagous parasitoid can be weakened or compromised by other density dependent factors (see below) and density independent ones (Morrison and Barbosa 1987, Taylor 1992), and how non-regulating parasitoids can persist thanks to other density dependent agents (see below). Hawkins (1992) has presented empirical arguments for why many parasitoids may be dynamically unimportant to their hosts.

In examining the impact of natural enemies in biological control, the studies of Beddington et al. (1978) and Hassell (1978) are, in some ways, also the precursors for the multiple control paradigm of monophagous parasitoid persistence. Their investigations point to two main ways in which multiple limitation factors may intervene in a host's dynamics.

First, density dependence acting on the host lessens the regulatory impact of the parasitoid, and can even permit the persistence of parasitoids which could not otherwise persist in the absence of such density dependence. Examples include host intraspecific competition (Beddington et al. 1978, May et al. 1981, Bernstein 1986, Hochberg and Lawton 1990, Ives 1992), and the actions of natural enemies other than the monophagous parasitoid (May and Hassell 1981, Hassell and May 1986, Hochberg et al. 1990, Briggs 1993, Hochberg and Hawkins 1993, Wilson et al. in press).

Second, density dependence affecting the parasitoid itself, if too strong or too weak, can also compromise its influence as the primary regulatory agent of its host. Either too strong or too weak parasitoid density dependence may necessitate, and in some cases induce, other forms of density dependence to intervene for regulation. Examples include adult mutual interference (Hassell 1978), within-host larval competition (Taylor 1988a), and density dependent sex ratios (Comins and Wellings 1985). Other studies have shown how indirect paths to parasitoid density dependence can also reduce the regulatory influence of parasitoids. These include tendencies towards: low parasitoid powers of population increase (Hochberg and Lawton 1990, Getz and Mills in press), probabilistic host refuges (Hassell and May 1973, Beddington et al. 1978, Hassell 1978, Perry and Taylor 1986, Murdoch 1989, Reeve et al. 1989), and absolute host refuges (Hassell and May 1973, Hassell 1978, Murdoch et al. 1987, Holt and Hassell 1993, Hochberg and Holt 1995, Hochberg et al. in press).

Paradigm 3: Regional control by a single monophagous parasitoid

If paradigm 1 is not a general scenario for local host–parasitoid interactions, then either the link persists via paradigm 2, or the parasitoid contributes to the local extinction of the couplet. It was actually Nicholson (conclusion 40, 1933) who first mooted how

a locally destabilizing parasitoid could persist via the spatial separation of unstable populations. This idea has gained empirical support, for example with the work of Utida (1950), but arguments for why extinction/colonization dynamics could be an important phenomenon for parasitoids were first persuasively presented by W. W. Murdoch and colleagues (Murdoch et al. 1984, 1985). They asserted that five of the six cases of spectacular successes in biological control employed by Beddington et al. (1978) are in fact characterized by locally unstable population dynamics between the natural enemy and the pest. Berryman (1996) has recently extended this claim to the dynamics of a range of forest Lepidoptera and their natural enemies.

The possibility that a locally non-regulatory parasitoid could persist with its host at large spatial scales was initially investigated in a quantitative context by Allen (1975), who showed that as long as large numbers of local (unstable) populations were connected by dispersal, global extinction could be delayed. Subsequently, Münster-Swendsen (1982) showed for a specific system how limited dispersal rates could promote system persistence of a randomly searching parasitoid, and he suggested that such dispersal could more generally combine with local parasitoid density dependence to determine overall parasitoid density dependence. Investigations of large-scale host-parasitoid systems were not conducted in earnest until several years later (reviewed for arthropod predator-prey systems by Taylor 1988b, and see Hassell and May 1988, Reeve 1988, Murdoch et al. 1992, Holt and Hassell 1993), and it is only relatively recent that spatially explicit models of limited dispersal have enjoyed sustained development beyond the aforementioned early investigations (Hassell et al. 1991b, Comins et al. 1992, Solé et al. 1992, Hassell et al. 1994).

An integrative paradigm

Paradigms 1 and 3 state that the parasitoid is capable of regulating its host in the absence of other forms of density dependence on small (paradigm 1) and on large (paradigm 3) spatial scales. Paradigm 2 says that regardless of the parasitoid's regulatory ability when in isolation, in practice it is part of (and may often be dominated by) a larger suite of density dependent effects.

In my view, the fundamental question cutting across all three paradigms is "to what extent (both in terms of intensity within a system, and the distribution of intensities across systems) and via what mechanisms do monophagous parasitoids contribute to or detract from spatial and temporal constancy in the abundance of their hosts?"

A conceptual framework for making some headway towards this problem is a paradigm integrating elements of all three of those discussed above. In this integrative paradigm, multiple forms of density dependence (including the parasitoid) potentially affect host dynamics, and their relative actions may vary considerably in space and in time. The central tenet of the integrative paradigm is that the determination of the dynamically important factors associated with a monophagous parasitoid (e.g., spatial heterogeneity in parasitism) requires concurrent knowledge of its capacity to dominate host density dependence in time and space.

The integrative paradigm differs from Strong's (1986) density-vague paradigm in the important respect that the latter stresses the lack of trend in density dependence over a wide range of host densities. The integrative view makes no assumptions about trends in the actions of population-limiting factors, but rather emphasizes the actions of different factors at different spatial and temporal scales, and the necessity of working in situ (both theoretically and experimentally) if we are to identify the extent to which different ecological factors and different species are important in driving the temporal and spatial dynamics of a focal species link (e.g., a monophagous parasitoid and its herbivorous host).

For example, if we were to study a system under the integrative view we might find: (1) the parasitoid induces local host extinctions in a small fraction of localities where it dominates host dynamics, (2) the host at low densities (possibly having just recolonized following the destabilizing action of the parasitoid) at other localities and not subject to strong density dependence, and (3) host density dependence dominated by other factors (natural enemies, limiting resources) at localities where the parasitoid is dynamically unimportant, due, for example, to hyperparasitoids, competitors, or environmental unsuitability. At some arbitrary time later we might observe that a fraction of previous type (1) systems have been recolonized by the host, but not the parasitoid, and are under control by other density dependent factors. The parasitoid may have since colonized some of the previous type (2) systems, and either dominated and destabilized them, or contributed to host dynamics along with a suite of other factors. Hypothetical scenarios such as these are evidently vast in possibilities.

Needs

We need theoretical explorations and experiments designed to tease out the dynamical role of monophagous parasitoids from their surrounding communities at different spatial scales. Intimidating as this challenge may seem, the nuts and bolts are in place for rapid theoret-

ical developments. In contrast, it is troubling that the three basic paradigms remain virtually unexplored experimentally. I suggest that the first question to ask experimentally is a fundamental one, going to the heart of the three basic paradigms: can an insect parasitoid dominate and regulate the dynamics of its host population at any natural spatial scale?

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References

- Allen, J. C. 1975. Mathematical models of species interactions in time and space. – *Am. Nat.* 109: 319–342.
- Bailey, V. A., Nicholson, A. J. and Williams, E. J. 1962. Interactions between hosts and parasites when some individuals are more difficult to find than others. – *J. Theor. Biol.* 3: 1–18.
- Beddington, J. R., Free, C. A. and Lawton, J. H. 1978. Modelling biological control: on the characteristics of successful natural enemies. – *Nature* 255: 58–60.
- Bernstein, C. 1986. Density dependence and the stability of host-parasitoid systems. – *Oikos* 47: 176–180.
- Berryman, A. A. 1996. What causes population cycles of forest Lepidoptera? – *Trends Ecol. Evol.* 11: 28–32.
- Briggs, C. J. 1993. Competition among parasitoid species on a stage-structured host and its effect on host suppression. – *Am. Nat.* 141: 372–397.
- Chesson, P. L. and Murdoch, W. W. 1986. Aggregation of risk: relationships among host-parasitoid models. – *Am. Nat.* 127: 696–715.
- Comins, H. N. and Wellings, P. W. 1985. Density-related parasitoid sex-ratio: influence on host-parasitoid dynamics. – *J. Anim. Ecol.* 54: 583–594.
- , Hassell, M. P. and May, R. M. 1992. The spatial dynamics of host-parasitoid systems. – *J. Anim. Ecol.* 61: 735–748.
- Driessen, G. and Hemerik, L. 1991. Aggregative responses of parasitoids and parasitism in populations of *Drosophila* breeding on fungi. – *Oikos* 61: 96–107.
- Getz, W. M. and Mills, N. in press. Host-parasitoid coexistence and egg-limited encounter rates. – *Am. Nat.*
- Godfray, H. C. J. and Hassell, M. P. 1991. Encapsulation and host-parasitoid population biology. – In: Toft, C. A., Aeschlimann, A. and Bolis, L. (eds), *Parasite-host associations*. Oxford Univ. Press, Oxford, pp. 131–147.
- and Pacala, S. W. 1992. Aggregation and the population dynamics of parasitoids and predators. – *Am. Nat.* 140: 30–40.
- Hassell, M. P. 1978. The dynamics of arthropod predator-prey systems. – Princeton Univ. Press, Princeton, NJ.
- 1984. Parasitism in patchy environments: inverse density dependence can be stabilizing. – *IMA J. Math. Appl. Med. Biol.* 1: 123–133.
- and May, R. M. 1973. Stability in insect host-parasite models. – *J. Anim. Ecol.* 42: 693–726.
- and May, R. M. 1986. Generalist and specialist natural enemies in insect predator-prey interactions. – *J. Anim. Ecol.* 55: 923–940.
- and May, R. M. 1988. Spatial heterogeneity and the dynamics of parasitoid-host systems. – *Ann. Zool. Fenn.* 25: 55–61.
- and Pacala, S. W. 1990. Heterogeneity and the dynamics of host-parasitoid interactions. – *Philos. Trans. R. Soc. Lond. B* 330: 203–220.
- , May, R. M., Pacala, S. W. and Chesson, P. L. 1991a. The persistence of host-parasitoid association in patchy environments. I. A general criterion. – *Am. Nat.* 138: 568–583.
- , Comins, H. N. and May, R. M. 1991b. Spatial structure and chaos in insect population dynamics. – *Nature* 353: 255–258.
- , Comins, H. N. and May, R. M. 1994. Species coexistence via self-organizing spatial dynamics. – *Nature* 370: 290–292.
- Hawkins, B. A. 1992. Parasitoid-host food webs and donor control. – *Oikos* 65: 159–162.
- Hochberg, M. E. and Lawton, J. H. 1990. Spatial heterogeneities in parasitism and population dynamics. – *Oikos* 59: 9–14.
- and Hawkins, B. A. 1993. Predicting parasitoid species richness. – *Am. Nat.* 142: 671–693.
- and Holt, R. D. 1995. Refuge evolution and the population dynamics of coupled host-parasitoid associations. – *Evol. Ecol.* 9: 633–661.
- , Hassell, M. P. and May, R. M. 1990. The dynamics of host-parasitoid-pathogen interactions. – *Am. Nat.* 135: 74–94.
- , Elmes, G. W., Thomas, J. A. and Clarke, R. T. In press. Mechanisms of local persistence in coupled host-parasitoid associations: the case model of *Maculinea rebeli* and *Ichneumon eumerus*. – *Philos. Trans. R. Soc. Lond. B*.
- Holt, R. D. and Hassell, M. P. 1993. Environmental heterogeneity and the stability of host-parasitoid interactions. – *J. Anim. Ecol.* 62: 89–100.
- Ives, A. R. 1992. Density-dependent and density-independent parasitoid aggregation in model host-parasitoid systems. – *Am. Nat.* 140: 912–937.
- Jones, T. H., Hassell, M. P. and Pacala, S. W. 1993. Spatial heterogeneity and the population dynamics of a host-parasitoid system. – *J. Anim. Ecol.* 62: 251–262.
- Lampo, M. 1994. The importance of refuges in the interaction between *Contarinia sorghicola* and its parasitic wasp *Aprostocetus diplosidis*. – *J. Anim. Ecol.* 63: 176–186.
- May, R. M. 1978. Host-parasitoid systems in patchy environments: a phenomenological model. – *J. Anim. Ecol.* 47: 833–843.
- and Hassell, M. P. 1981. The dynamics of multiparasitoid-host interactions. – *Am. Nat.* 117: 234–261.
- , Hassell, M. P., Anderson, R. M. and Tonkyn, D. W. 1981. Density dependence in host-parasitoid models. – *J. Anim. Ecol.* 50: 855–865.
- Morrison, G. and Barbosa, P. 1987. Spatial heterogeneity, population “regulation” and local extinction in simulated host-parasitoid interactions. – *Oecologia* 73: 609–614.
- Münster-Swendsen, M. 1982. Interactions within a one-host-two-parasitoids system, studied by simulations of spatial patterning. – *J. Anim. Ecol.* 51: 97–110.
- Murdoch, W. W. 1989. Ecological theory and biological control. – In: Jain, S. and Botsford, L. (eds), *Applied population biology*. Junk, Dordrecht.
- and Oaten, A. 1975. Predation and population stability. – *Adv. Ecol. Res.* 9: 2–131.
- and Stewart-Oaten, A. 1989. Aggregation by parasitoids and predators: effects on equilibrium and stability. – *Am. Nat.* 134: 288–310.
- , Reeve, J. D., Huffaker, C. B. and Kennett, C. E. 1984. Biological control of olive scale and its relevance to ecological theory. – *Am. Nat.* 123: 371–392.
- , Chesson, J. and Chesson, P. L. 1985. Biological control in theory and practice. – *Am. Nat.* 125: 344–366.
- , Nisbet, R. M., Blythe, S. P., Gurney, W. S. C. and Reeve, J. D. 1987. An invulnerable age class and stability in delay-differential parasitoid-host models. – *Am. Nat.* 129: 263–282.
- , Briggs, C. J., Nisbet, R. M., Gurney, W. S. C. and Stewart-Oaten, A. 1992. Aggregation and stability in meta-population models. – *Am. Nat.* 140: 41–58.

- Nicholson, A. J. 1933. The balance of animal populations. – *J. Anim. Ecol.* 2: 131–178.
- Pacala, S. W. and Hassell, M. P. 1991. The persistence of host-parasitoid associations in patchy environments. II. Evaluation of field data. – *Am. Nat.* 138: 584–605.
- , Hassell, M. P. and May, R. M. 1990. Host-parasitoid interactions in patchy environments. – *Nature* 344: 150–153.
- Perry, J. N. and Taylor, L. R. 1986. Stability of real interacting populations in space and time: implications, alternatives and the negative binomial k_c . – *J. Anim. Ecol.* 55: 1053–1068.
- Redfern, M., Jones, T. H. and Hassell, M. P. 1992. Heterogeneity and density dependence in a field study of a tephritid-parasitoid interaction. – *Ecol. Entomol.* 17: 255–262.
- Reeve, J. D. 1988. Environmental variability, migration, and persistence in host-parasitoid systems. – *Am. Nat.* 132: 810–836.
- , Kerans, B. L. and Chesson, P. L. 1989. Combining different forms of parasitoid aggregation: effects on stability and patterns of parasitism. – *Oikos* 56: 233–239.
- , Cronin, J. T. and Strong, D. R. 1994. Parasitoid aggregation and the stabilization of a salt marsh host-parasitoid system. – *Ecology* 75: 288–295.
- Rohani, P., Godfray, H. C.J. and Hassell, M. P. 1994. Aggregation and the dynamics of host-parasitoid systems: a discrete-generation model with within-generation redistribution. – *Am. Nat.* 144: 491–509.
- Solé, R. V., Valls, J. and Bascompte, J. 1992. Spiral waves, chaos and multiple attractors in lattice models of interacting populations. – *Phys. Lett. A* 166: 123–128.
- Strong, D. R. 1986. Density-vague population change. – *Trends Ecol. Evol.* 1: 39–42.
- Taylor, A. D. 1988a. Parasitoid competition and the dynamics of host-parasitoid models. – *Am. Nat.* 132: 417–437.
- 1988b. Large-scale spatial structure and population dynamics in arthropod predator-prey systems. – *Ann. Zool. Fenn.* 25: 63–74.
- 1992. Deterministic stability analysis can predict the dynamics of some stochastic population models. – *J. Anim. Ecol.* 61: 241–248.
- 1993a. Heterogeneity in host-parasitoid interactions: 'Aggregation of risk' and the ' $CV^2 > 1$ rule'. – *Trends Ecol. Evol.* 8: 400–405.
- 1993b. Aggregation, competition and host-parasitoid dynamics: stability conditions don't tell it all. – *Am. Nat.* 141: 501–506.
- Utida, S. 1950. On the equilibrium state of the interacting population of an insect and its parasite. – *Ecology* 31: 165–175.
- Walde, S. J. and Murdoch, W. W. 1988. Spatial density dependence in parasitoids. – *Annu. Rev. Entomol.* 33: 441–466.
- Wilson, H. B., Hassell, M. P. and Godfray, H. C. J. in press. Host-parasitoid food-webs: dynamics, persistence and invasion. – *Am. Nat.*