1913 British Ecological Society 2013
CELEBRATING 100 YEARS

100 INFLUENTIAL PAPERS – LONGER COMMENTARY

13 **Hassell, M. P. & May, R. M.** (1973) Stability in insect host-parasite models. *Journal of Animal Ecology,* **42,** 693-726.

The population dynamics of predator-prey and other consumer-resource interactions have a natural propensity to oscillate. Predator numbers increase and drive down the population of their prey which leads to starvation and predator decline. With their predators rare, the prey population recovers and the cycle can begin again. The simplest model of this type of interaction, the Lotka-Voterra predator-prey model, predicts neutral cycles (that is cycles that neither increase nor decrease in amplitude and whose exact form depends on initial starting conditions) while the addition of most types of biological detail leads to diverging cycles resulting in the extinction of the predator or prey. Understanding the biological mechanisms that allow consumer-resource interactions to persist has been a major goal of population ecology.

Studies of parasitoid biology have been central to understanding the ecology of consumer-resource interactions. Parasitoids are insects, almost exclusively varieties of wasps and flies, that lay their eggs in or near the body of their hosts (in most cases another insect). The eggs hatch and a parasitoid larva develops to the adult stage by consuming a single host which it invariably kills. Many (solitary) parasitoids develop alone on the host but other species are gregarious with clutches of larvae feeding together. Parasitoids are very common and a critical component of nearly all terrestrial insect communities. They are also very important in pest control and have been used in many successful biological control campaigns. The wish to understand better how biological control works, as well as how it might be improved, was the initial spur to much of the work on parasitoid ecology.

The relatively simple relationship between consumption and recruitment – one successful parasitism event leads to one or a clutch of new parasitoids a generation later – makes modelling host-parasitoid interactions particularly simple. Also, many host-parasitoid interactions are relatively specific compared with predator-prey interactions justifying a concentration on a single pair of species. However, the fact that parasitoids tend to have a relatively short adult lifespan compared to the lengths of the juvenile stages, plus the fact that in temperate climates they often have only a single generation a year, led to the development of most early parasitoid models in discrete time. Pairs of equations were written down expressing the numbers of hosts and parasitoids in the current generation as a function of the numbers in the last generation (most predator-prey models such as the Lotka-Volterra were continuous time models expressed as differential equations). The difference in model formulation is more than of technical consequence. The time lag inherent in discrete time models is destabilising and the simplest models of host- parasitoid show diverging oscillations. What in the biology of host-parasitoid interactions explains their obvious persistence?

The Australian biologist A.J. Nicholson (1933) [see 2] wrote down a pair of equations which assumed a parasitoid searched randomly for hosts over a fixed time period. At the end of this period the hosts that escaped discovery (the zero term of a Poisson Distribution with parameter the mean number of parasitoid attacks per host) gave rise to adults that reproduced to give rise to the next generation of hosts while those that succumbed produced the next generation of parasitoids. Nicholson's formalism was not very clear (it singularly unimpressed Ronald Fisher who Oxford University Press asked to review a book proposal by Nicholson) and it was only after he started collaborating with the mathematician A.V. Bailey (Nicholson & Bailey 1935) [see 2] that it became clearer and resulted in the Nicolson-Bailey model we know today. The predictions that host-parasitoid interaction can at least in a very simple environment lead to diverging oscillations was strikingly confirmed in a laboratory study by Burnett (1958) involving whitefly and their tiny parasitoids.

But of course host-parasitoid interactions do persist in the wild. In principle there are two simple ways to tame the diverging oscillations of the Nicholson-Bailey model. The first is to make parasitoids less efficient at high densities so that they do not overexploit their hosts, and the second is to give some hosts the ability to avoid parasitoid attack when they are at high densities (a refuge). In the 1960s and early 1970s most attention was paid to the former. Laboratory experiments had suggested that parasitoids at high densities interacted with each other in ways that reduced their searching efficiency, a phenomenon that was called "interference". Much work on this was done at Oxford by George Varley and George Gradwell [see 5] with their student Michael Hassell. A simple host-parasitoid model in which searching efficiency declined with parasitoid population density showed that if interference was strong enough a stable interaction might result.

But by the early 1970s doubts were being raised about interference – yes it could work but it seemed to require unrealistically high parasitoid densities unlikely to be seen in the wild. After completing his DPhil (PhD) at Oxford, Hassell had spent a post- doc year in Carl Huffaker's lab at Berkeley and become more interested in how hosts and parasitoids interacted in more realistic patchy environments. Might searching in a heterogeneous environment explain the persistence of the interaction? Hassell took up a lectureship at Imperial College's Silwood Park campus in 1970 and set up a lab to explore the mechanistic basis of how parasitoids discover their hosts while continuing to model the interactions.

The modelling side of the work was greatly enhanced when Robert (Bob) May, on the invitation of the Silwood Park Director, Richard (Dick) Southwood [see 55 & 72] began in 1972 to spend his summers at Imperial. May, an Australian, trained as a physicist in Sydney but had been attracted to ecology by Robert MacArthur (another ex-physicist) and was by then about to join the faculty at Princeton. His main research interests were community ecology and studies of single-species populations that revealed biological chaos, but during his extended summer breaks in the UK he collaborated widely with British ecologists, bringing new degrees of mathematical rigour to many different areas of theoretical ecology.

Stability in Host-Parasitoid Models began by reviewing the problem, the instability of the Nicholson-Bailey (and how it was made worse by adding realistic host handling times by parasitoids or limited egg supplies) and the inadequacies of interference. It then develops a new model in which hosts and parasitoids are distributed across patches in the environment within which search occurs randomly (as in the Nicholson- Bailey model). If the number of hosts and parasitoids are exactly proportional then the model collapses to the Nicholson-Bailey case. But if parasitoids tend to aggregate to patches of high host density then the system stabilises. The precise extent of the aggregation required for the system to persist depends on the details of the underlying host distribution as well as the intrinsic growth rate of the host.

Hassell & May (1973) set forth a rather general treatment of parasitoids searching for hosts in a patchy environment though the cost of this generality was a model that could not be easily analysed. Most of the results they presented came from a simple model in which hosts were distributed across patches of two types; a single high density patch and many low density patches. But at the same time they were working on much more mechanistic models of parasitoid (and predator) searching which explicitly include behaviours such as long-range attraction and area-restricted search. In a further paper the following year (Hassell & May 1974) they explored in detail how this behaviour might be incorporated into a host-parasitoid model and what effect different types of searching may have on population density and stability.

Hassell & May (1973; 1974) together established the importance of spatial heterogeneity in the persistence of host-parasitoid interactions (and by extension other consumer-resource systems). They are the 13th and 14th most cited papers in *Journal of Animal Ecology* and their citations have grown together in lockstep (differing in October 2012 by only 3). The group around Hassell continued to refine their understanding of host-parasitoid systems in heterogeneous environments over the next three decades. Shortly afterwards May (1978) produced a very elegant phenomenological model that assumed that the probability a host avoids parasitoid attack was the zero term of a negative binomial distribution. The negative binomial is described by two parameters, the mean number of attacks per host and a “clumping parameter” which can be thought of as describing the heterogeneity in the distribution of parasitoid attack. Stability requires heterogeneity to be above a threshold so that some hosts escape attack (or equivalently that parasitoid efficiency is reduced at high density because they are competing together for the same subset of hosts). Note that the hosts that escape attack need not be in low-density patches (as in the original Hassell & May model) but might be in any patch that just happened to form a refuge (as anticipated earlier by Nicholson & Bailey). Steve Pacala, another sabbatical visitor to Silwood in the late 1980s, developed with Hassell and May a means of partitioning the density-dependent and density-independent components of parasitoid searching as well as estimating relevant parameters from data (Pacala, Hassell & May 1990). Other progress in this area is summarised in a monograph (Hassell 2000). The theoretical studies also influenced much experimental work. For example, the UC Santa Barbara group led by

William (Bill) Murdoch dissected the mechanisms by which the important orange tree pest, the red scale, was regulated by its parasitoids. Key is spatial heterogeneity and the refuge from parasitoids enjoyed by scales on certain parts of the plant (Murdoch *et al.* 1996).

Science is a social as well as a professional activity, as well illustrated by the footnote to the title of Hassell & May (1974): "*The order of authorship was determined from a twenty-five-game croquet series held at Imperial College Field Station during summer 1973." [The footnote was reinserted by the authors at proof stage after being removed by the *Journal of Animal Ecology* editor]. Croquet was played every lunch time during May's summer visits on a pitch at Silwood Park customised by a large population of rabbits. Visitors were invited to play though inevitably lost due to the huge home-team advantage knowledge of the pitch's precise topography afforded. Visitors also frequently declared themselves disadvantaged by the alleged tactic of being asked complex ecological questions mid-stroke. This was a different game from the traditional English vicarage-lawn contest!

Charles Godfray

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