

BIOLOGICAL CONTROL LESSONS: MODELING SUCCESSES AND FAILURES IN NEW ZEALAND

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INTRODUCTION

Clearly the effectiveness of biological control projects cannot improve unless the ecologies of the agent and target are better understood; specifically, we need to be able to predict impacts. To this end, we have been using models as tools to help understand and explain the effects of biological control agents, using both general theory and specific models. In the first case, we test and develop theory that holds hope of providing genuinely useful answers, and in the second we use specific models to provide information on the behavior of particular systems and the reasons for it. Here, we briefly outline our approach in both areas, and describe some results that offer insights into the causes of success or failure in biological control.

THEORY

In terms of general theory, we visit two relatively untrodden areas of this otherwise well-traveled ground: whether metapopulation structure can account for high, stable levels of biological control and how habitat abundance might affect pest suppression by a biological control agent. First, we consider whether metapopulation structure could provide an answer to the “biological control paradox” (e.g., Berryman, 1992), whereby simple random search models cannot give both stability and the high levels of suppression sometimes observed (>90%). By metapopulation structure, we mean standard random-search host-parasitoid models with host density-dependence applied to a grid of subpopulations, linked by local dispersal of hosts and parasitoids. It is well known that connecting populations by dispersal in this way confers considerable stability on any system, so it was an obvious question to ask: can it account for the stability of biological control and obviate the need to invoke models with parasitoid aggregative behavior, for example. We found that it gives only a partial answer: the maximum level of host suppression consistent with stability increases from the 67% possible in simple, non-spatial random-search models, to 84% in a metapopulation model. Much higher levels of suppression were possible, approaching 100%, if the model was started with uniformly low parasitism levels across all cells of the grid. But if a realistic biological control scenario was simulated, with hosts at carrying capacity in all cells but the parasitoid at low levels only in one cell corresponding to a release site, then the limit of stable suppression possible was 84% (Kean and Barlow, 2000a).

The second area of theory we investigate is the effect of habitat abundance in the landscape on pest density and biological control. Particularly for highly dispersive pests, theory suggests that habitat density should affect local density of the pest due to losses incurred through dispersal and, therefore, may affect the impact of any biological control agent. Taking the weevil *Sitona discoideus* Gyllenhal in lucerne (alfalfa) as an example, only 0.3% of the landscape on the Canterbury Plains in New Zealand's South Island consists of lucerne, and the whole *Sitona* population has an obligatory dispersal phase following summer aestivation. Models suggest that if the area of lucerne increased, current levels of suppression by the braconid parasitoid *Microctonus aethiopoidea* (Loan) would be maintained in percentage terms, but that the absolute pest density would increase (Kean and Barlow, 2000b). In this sense, biological control would cease to become effective, simply because of an increase in habitat abundance for the pest. Such an effect is likely to be general, to an extent depending on the dispersiveness of the pest.

SPECIFIC MODELS

We have been using specific models to predict the phenology of introduced parasitoids and to explain both the levels of parasitism achieved and the degrees of pest suppression associated with these. The case studies involve the pests *S. discoideus*, the Argentine stem weevil (*Listronotus bonariensis* [Kuschel]), and the common wasp (*Vespula vulgaris* [L.]). These cases span a range of parasitism levels and degrees of population suppression. A model for control of *S. discoideus* by *M. aethiopoidea* accounted for initial success, which involves suppression of around 75%, and predicted that this would be sustained. Note that this suppression level takes the weevil below the damage threshold and is considerably less than the 90% or more required in some other systems. Field testing 10 years later suggested that this prediction was realized, though at lower levels of parasitism than predicted by the model. So this example of successful biological control had host suppression of around 75% associated with a parasitism level of about 40%. Preliminary modeling of Argentine stem weevil in New Zealand ryegrass pastures suggested that this pest was also successfully controlled by another introduced species, *Microctonus hyperodae* Loan. Here a suppression level similar to that achieved against *S. discoideus* (75%) was associated with a higher parasitism level of around 75%. In the case of the common wasp parasitoid *Sphexophaga vesparum vesparum* (Curtis), biological control failed. Parasitism levels were less than 10%, and there was no measurable impact on wasp nest density.

All of these three case studies have been modelled in some detail (e.g., Barlow and Goldson, 1993; Barlow *et al.*, 1994, 1996; Kean and Barlow, 2000a,b, 2001), although the work on Argentine stem weevil is still in progress, and the models suggest reasons for success or failure. In summary, control of *S. discoideus* succeeded because a small proportion of *M. aethiopoidea* atypically, and unexpectedly, continued developing during summer among emerging hosts in the lucerne crop rather than arresting their development as the hosts leave the crop to aestivate elsewhere. This continued development allows more generations of the parasitoid, reducing the effective generation time ratio (GTR, Kindlmann and Dixon, 1999) of parasitoid:host, and gives an added measure of synchrony. Parasitoids can build up in the crop and “ambush” weevils returning from the aestivating sites in autumn before they can oviposit. Moreover, the presence of abundant weevils emerging in the crop during early summer facilitates this build-up (Barlow and Goldson, 1993; Kean and Barlow, 2000b, 2001).

Successful control of Argentine stem weevil appears to be due to the high searching efficiency of the parasitoid, synchrony between host and parasitoid, a low GTR (with at least one more generation of parasitoids per year than of hosts), a large summer-autumn peak of weevils allowing parasitoid buildup at this time, and limited density-dependence in the host in the presence of abundant ryegrass resource. On the other hand, the failure of *S. vesparum vesparum* to control wasps was associated with a low searching efficiency, a high mortality of parasitoid cocoons, and high GTR. The high GTR arises from the delayed emergence period for overwintering cocoons, which can be anything from two to four years, giving a GTR of around 2.5 in terms of the length of a sexual generation or life of a colony for the wasp (1 year) (Barlow *et al.*, 1996).

Much simpler models can also provide some of these insights if they are sufficiently realistic to capture at least the essence of the biology. To do so, for our case studies we found that they needed to differ from the usual parasite-host models in the literature. In particular, we found it useful to use disease/host or microparasite models, since these are formulated as differential equations rather than difference equations so they allow for the possibility of overlapping generations and different generation lengths for host and parasitoid. In summary, such models suggest that percent parasitism depends on the product $[R_0 Tr]$, where R_0 = parasitoid's net reproductive rate (new parasitoid adults produced per parasitoid adult), T = parasitoid's development time, and r = host intrinsic rate of increase. Percent host suppression, on the other hand, depends on $[R_0/(Tr)]$. The generation time ratio for parasitoid:host is proportional to $[Tr]$, so the smaller the GTR the greater the percent suppression. Of the three

biological control case studies, *S. discoideus*/*M. hyperodae* has a low R_0 and low GTR, *L. bonariensis*/*M. hyperodae* has a high R_0 and low GTR, while *V. vulgaris*/*S. vesparum vesparum* has a low R_0 and high GTR. The most consistent difference is in GTR: the successful examples have a low GTR whereas the unsuccessful one has a high GTR. Study of the more detailed models suggests that host-parasitoid phenological synchrony is a consistent additional factor predisposing, or necessary for, success.

CONCLUSIONS

Our own experience in modeling real systems suggests that these are rarely simple and often quirky. Consequently, although simple models can give useful qualitative insights if the models are suitably realistic, these have to be tempered by details of behavior and ecology that seem to be system-specific. However, this requirement may simply reflect the fact that there are still relatively few well-studied systems. Perhaps more examples will enable a loftier view and the greater sense of order and predictability that future biological control is likely to need.

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