THE DECLINE OF THE REGULATION PARADIGM IN CLASSICAL BIOLOGIAL CONTROL AND THE POSSIBLE ROLE OF RARE SPECIES

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INTRODUCTION

Many and arguably most theoretical studies into the factors responsible for regulation in host–natural enemy associations have implications for classical biological control programs (Hochberg and Holt, 1999). This is because model analysis usually yields information about the ability of the natural enemy to depress host populations to low, more or less constant levels. Only a handful of the over 100 theoretical studies conducted since the publication of M. P. Hassell's monograph in 1978, however, have called into question the regulation paradigm (Morrison and Barbosa, 1987; Murdoch, 1990; Hochberg, 1996; Hochberg and Holt, 1999).

The first objective of this paper is to briefly discuss why the regulation paradigm, although applicable to biological control, is only one of three basic ways in which a biological control program might be an economic success. Actual biological control releases provide the most pertinent information regarding the factors responsible for success in classical biological control. However, it is often a difficult if not an impossible task to determine exactly why a release is a success or a failure, let alone more finely dissect out how species' biologies and release logistics might influence the actual level of success. Biological control of agricultural pests often involves releases over large areas to combat relatively mobile pest populations. Such activities require considerable effort to document the spread and establishment of the natural enemy, and to unravel potentially complex dynamic scenarios caused by the effects of pest movement on population dynamics (Comins *et al*., 1992; Hochberg and Ives, 1999).

The second objective of this paper is to present a novel way to assess success in biological control: employing victims (hosts or prey) that are rare and possibly even the objects of conservation efforts.

AN INTEGRATED PARADIGM FOR THE IMPACT OF MONOPHAGOUS PARASITOIDS

The vast majority of theory on parasitoid-host dynamics focuses on monophagous enemies and the unequal exploitation across time and space of hosts by the parasitoid (Hochberg and Holt, 1999; Bernstein, 2000). Depending on the actions of a handful of driving factors, dynamics may be either stabilized or destabilized by parasitoids, or the parasitoids will have no appreciable impact on dynamics due to the effects of other forms of density dependence affecting the pest, the parasitoid, or both. These are the three basic (and abstract) outcomes of classical biological control in which the introduced enemy is able to establish.

Based on a survey of over 100 modeling studies on parasitoid-host associations, Hochberg and Holt (1999) concluded that two major notions emerge, which can explain the impact of monophagous parasitoids on their host populations. These concern the density and the uniformity of host exploitation by the parasitoid.

Exploitation density is the power of population increase of the parasitoid; that is, the mean number of female parasitoids produced per adult female when hosts are not limiting. In contrast,

exploitation uniformity is the evenness in the distribution of mortality risk over the host population. Exploitation uniformity is influenced by the relative distributions of hosts and searching adult female parasitoids.

It comes as little surprise that the overall impact of a monophagous parasitoid on the pest increases with both the density and uniformity of exploitation; however, these two values have interesting, often neglected, effects on the outcome of a natural enemy introduction. The classic "desirable" outcome of pest regulation to low densities is straddled by two *a priori* "undesirable" outcomes, these being either little impact on pest density or overexploitation of pest populations, leading to unstable dynamics. Previous studies have called into question the extent to which regulation is either a desirable or reasonable outcome in classical biological control (Murdoch *et al.*, 1985; Murdoch, 1990; Hochberg, 1996). Indeed, when combinations of the two main ingredients of parasitoid impact are analyzed, it becomes clear that the most impressive successes in biological control (*sensu* Beddington *et al.*, 1978) often involve systems in which the pest population is destabilized by the parasitoid. Moreover, cursory exploration of proxy estimates of uniformity ($1/CV^2$) and density (acP) of exploitation in Table 3 of Hassell and Pacala (1990) indicates that the two may be positively correlated across species. This would suggest that there is an *ecological* basis for an association between uniformity and density of exploitation, whence enemy species most likely to have a regulatory effect (low uniformity) are also those with the least impact on their victim populations (low exploitation density). Having made this observation, I stress due caution, since mathematical models were employed by Hassell and Pacala in the estimates of CV^2 and acP. There are more than one observation for many of the systems they employed and the measure of acP relative to the victim's own intrinsic rate of increase (needed to determine final impact, see Hochberg and Holt 1999) is not available.

My conclusion from these diverse elements is that pest regulation is neither necessary for successful biological control nor desirable if regulation means sacrificing the ability of the parasitoid to depress the population of the pest. This is discussed in more detail elsewhere (Ives and Hochberg, 2000).

EXPLOITATION UNIFORMITY AS A MEDIATOR OF LIMITATION IN CONSERVATION BIOLOGY

The vast majority of theoretical models on parasitoid-host associations are conceptually simple, thereby necessitating many assumptions, but requiring few parameters to analyze (Hochberg and Holt, 1999). Very few attempts have been made at the other extreme: detailed, mechanistic descriptions of host and parasitoid populations (e.g., Godfray and Waage, 1991; Hochberg *et al.*, 1996). The reason is that understanding the population processes driving a particular system requires knowledge about (1) the life cycles of the two species; (2) parameter estimates of the population processes; and (3) independent data to validate model predictions, whereas none of these are necessary for constructing and analyzing a simple, analytical model of parasitoid-host dynamics (e.g., Hassell, 1978).

Traditionally, we view the uses of simple/abstract and complex/realistic models as being at opposite ends of a continuum. Simple/abstract models are used to identify small numbers of generalized processes that, in isolation or combination with one another, have marked effects on population dynamics. Examples are the uniformity and density of exploitation discussed above. Modifying such models to real systems means subdividing the populations (e.g., into age classes), incorporating other interacting populations (e.g., crops, other natural enemies attacking the pest), fractioning measurable parameters from the simplified compound parameters employed in analytical models, and adding abiotic driving variables such as weather. This is a daunting task even for the simplest of pest systems, but can yield considerable insight as found in the unorthodox example below.

IS THERE A PLACE FOR CONSERVATION BIOLOGY IN BIOLOGICAL CONTROL?

If we are going to test the regulation paradigm for biological control, a good place to look is host species that at least appear to be regulated to low and constant densities. The obvious first place to look is biological control programs themselves, but an alternative is to identify rare species and their parasitoid complexes and then investigate the factors responsible for limitation in the (rare) victim population. Examples of such limiting factors include specialist and generalist natural enemies, competitors, and limiting resources. We wish to know to what extent each factor is responsible for limitation and regulation in the victim population. This objective is not new–it is the basis for the key-factor approach (Royoma, 1996), frequently employed in the 1950s and 1960s.

Together with colleagues I investigated how the uniformity and density of exploitation could function in a system involving a rare butterfly (*Maculinea rebeli* Hirose) and its monophagous parasitoid (*Ichneumon eumerus* Wesmael) (Hochberg *et al*., 1996, 1998). This butterfly is the object of conservation efforts throughout its distribution in Western Europe, and lives in small, closed populations rarely numbering more than a thousand adults. *Ichneumon eumerus* is even rarer than its host, being found on a small subset of sites inhabited by the host. It is important when working with rare species, particularly those that are the objects of conservation efforts, to make clear that permits (if required) must be obtained and destructive sampling must be held to an absolute minimum.

We parameterized a mechanistic model of this system with the information available on the biology of the butterfly, its host plant, and its host ants, and on the distribution of parasitism and searching behavior of the parasitoid (Hochberg *et al*. 1996, 1998; Thomas and Elmes 1993). Based on this model, we estimated the uniformity and density of exploitation of *I. eumerus*. Our conclusion is that this natural enemy cannot have an appreciable regulatory impact on the butterfly population. This is because the distribution of attacks on the butterfly larvae are not sufficiently aggregated, meaning that if the low observed density of exploitation were increased, then the parasitoid would induce both the local extinction of the butterfly and of itself. Alternatively, even if the risk of parasitoid attack were sufficiently less uniform than observed (potentially permitting the parasitoid to regulate the butterfly), the observed density of exploitation is too low for the parasitoid to have a major (regulatory) impact on the butterfly population. Therefore, in conclusion, the parasitoid has a small impact on the host population (reducing its density by about 15%) and is ecologically unable to drive host regulation.

CONCLUSIONS

The challenge to the regulation paradigm in classical biological control dates back almost 20 years (Murdoch *et al*., 1985). It is disappointing given the weight of evidence that has accumulated during the intervening period that alternative paradigms have not been embraced by biological control researchers. In my opinion, whether we use biological control attempts or conservation programs on rare species, the challenge is to show unambiguously that a specialized natural enemy can both be the dominant limiting factor and regulate the population of its victim. I for one believe that this will be the exception rather than the rule.

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