



Delayed emergence and the success of parasitoids in biological control

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ABSTRACT

Delayed emergence, a life history feature of many insects living in unpredictable environments, can have major consequences for the dynamics of host–parasitoid interactions, which vary according to their physiological interactions. We studied, through simple modeling, the significance of prolonged diapause on the suppression levels achieved by parasitoids and illustrate our case with a system involving a major forest pest, the woodwasp *Sirex noctilio* and two of its parasitoid species that have been introduced into different geographical regions through classical biological control programmes. Our findings suggest that the physiological relationship between parasitoid and host delayed emergence patterns may help understand observed variable success in several bio-control programs. We conclude that for given environments, host delayed emergence and the way in which parasitoids deal with it, should be included in the list of selection criteria of natural enemies of many pests, especially those affecting forests.

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1. Introduction

Successful biological control of insects is stated to depend on the achievement of a reduction of pest populations below some economic threshold and the persistence of such new, low density equilibrium in time (Waage and Hassell, 1982; Kidd and Jervis, 2007). In classical bio-control, natural enemies are collected from areas where the pest is native to, introduced into new geographical regions where an exotic species has become established and is affecting a specific crop. For most biological control programmes of herbivorous insect pests, natural enemies are chosen among parasitoid species (Jervis, 2007).

In seasonal environments, developmental synchrony between parasitoids their herbivorous hosts is an important attribute of classical bio-control programmes. Perfect synchrony can ensure that most hosts are available to foraging parasitoids at any point in time. However, temporal refuges caused by imperfect matching, although may contribute to the stability of the interaction, can also result in a raising of host equilibrium levels (Godfray et al., 1994). Parasitoids collected from different localities, even within the hosts native range, may display different diapause patterns, which may negatively affect synchrony between them and the target pest population (Kidd and Jervis, 2007).

Diapause is a life history feature of many insects, which facilitates temporal synchrony with seasonal variations in their habitat (Tauber et al., 1986; Danks, 1987). For many univoltine species, diapause may simply involve developmental arrest during a single unfavorable season (i.e., simple diapause). However, for many other

species, inhabiting more unpredictable environments, or exploiting unpredictable resources, some of the population may extend diapause for longer periods, resulting in delayed adult emergence (Corley et al., 2004).

While biological control practitioners have long valued the importance of host–parasitoid diapause in natural enemy rearing, liberation and establishment, little is known on the effects of consequent delayed emergence on the success of parasitoids in the field. This is partly because delayed emergence may not be detected through standard rearing processes, which are usually carried out under controlled laboratory conditions. In the field, individuals emerging later will blend in with those that have undergone simple diapauses. Also, research interest has been set mostly on the factors inducing, interrupting or avoiding the dormancy-related physiological changes (e.g., Polgár and Hardie, 2000).

Delayed emergence may have major consequences for the dynamics of host–parasitoid interactions, which vary according to their physiological interactions (Ringel et al., 1998; Corley et al., 2004). This is because parasitoid development, while generally closely related to that of their hosts, can take either of two general forms (Lawrence, 1986). Some parasitoids, known as ‘conformers’, remain in step with host development by having no effect on host physiology instead being affected by host hormones. Others interrupt or interfere with host development, adapting it to their own requirements, are known as ‘regulators’ (Lawrence, 1986). Regulator parasitoids either prevent or interrupt the host they attack from undergoing or extending diapause. Corley et al. (2004) have shown that the relationship between the fractions of the host population subjected to delayed emergence how parasitoids relate to such patterns, are important in determining the stability properties of simple interactions.

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In this paper we extend the findings of Corley et al. (2004) by analyzing the role of the different host–parasitoid physiological relationships (i.e., regulators vs. conformers) on density dependent mortality of host populations. We discuss the importance of such consideration for the practice of biological control, namely selection criteria, by looking into a specific case study. We illustrate our case with a system involving a major forest pest, the woodwasp *Sirex noctilio* F. (Hymenoptera: Siricidae) and two of its parasitoid species (the wasps that have been introduced into different geographical regions through classical biological control programmes. While woodwasps show delayed emergence patterns, the parasitoids respond to host physiological changes either as conformers or regulators. We contrast our theoretical predictions with the recorded impact of these parasitoids on *S. noctilio* populations.

2. Methods

This paper is an extension of Corley et al. (2004), where the dynamic properties of prolonged diapause in host–parasitoid systems were studied using the May (1978) equation system. Here, we have incorporated density dependence in the host population as in Beddington et al. (1978). The dynamic properties of the host–parasitoid density dependent models are well known (see Hassell, 2000a for a detailed explanation). The equations for conformer (Eq. (1)) and regulator (Eq. (2)) parasitoids and host delayed emergence are detailed below.

$$N_t = \frac{\lambda \alpha N_{(t-1)}}{e^{\frac{\lambda N_{(t-1)}}{k} (1 + \frac{aP_{(t-1)}}{k})^k} + e^{\frac{\lambda(1-\alpha)N_{(t-2)}}{k} (1 + \frac{aP_{(t-2)}}{k})^k}} + \frac{\lambda(1-\alpha)N_{(t-2)}}{e^{\frac{\lambda N_{(t-2)}}{k} (1 + \frac{aP_{(t-2)}}{k})^k}}$$

$$P_t = \frac{\lambda \alpha N_{(t-1)} (1 - (1 + \frac{aP_{(t-1)}}{k})^{-k})}{e^{(-\lambda N_{(t-1)})}} + \frac{\lambda(1-\alpha)N_{(t-2)} (1 - (1 + \frac{aP_{(t-2)}}{k})^{-k})}{e^{(-\lambda N_{(t-2)})}} \quad (1)$$

$$N_t = \frac{\lambda \alpha N_{(t-1)}}{e^{\frac{\lambda N_{(t-1)}}{k} (1 + \frac{a}{k} (P_{t-1} + P_{t-2}))^k} + e^{\frac{\lambda(1-\alpha)N_{(t-2)}}{k} (1 + \frac{a}{k} (P_{t-2} + P_{t-3}))^k}} + \frac{\lambda(1-\alpha)N_{(t-2)}}{e^{\frac{\lambda N_{(t-2)}}{k} (1 + \frac{a}{k} (P_{t-2} + P_{t-3}))^k}}$$

$$P_t = \frac{\lambda \alpha N_{(t-1)} (1 - (1 + \frac{a(P_{t-1} + P_{t-2})}{k})^{-k})}{e^{(-\lambda N_{(t-1)})}} \quad (2)$$

For all equations N_t is the number of hosts, P_t the parasitoids at time t , λ is the host rate of increase, α represents the fraction in simple diapause and $1 - \alpha$ is the proportion undergoing delayed emergence, a is the area of discovery, k is the degree of clumping (represented here as the k parameter of the negative binomial distribution), and K is the carrying capacity of hosts in absence of parasitism.

As natural enemy pest density suppression may be seen as the reduction of pest equilibrium densities in relation to the equilibrium that would be achieved in the absence of natural enemies, for models with density dependence in the host population, suppression ($1 - q$) is defined as a relationship between the new equilibrium density, N^* the carrying capacity, K (Hochberg and Holt, 1999; Hassell, 2000b; Kean and Barlow, 2000) as follows,

$$q = \frac{N^*}{K}$$

Models were analyzed numerically by simulation. The simulations were performed for 40 values of α between 0 and 1 (with a separation of 0.025 between consecutive values) 35 values of λ between 0 and 3.5 (with a separation of 0.1 between consecutive values), resulting in a grid of 1400 combinations of parameters. In

order to prevent aliasing, an additional 792 combinations of random values of both parameters in the same interval were generated. On each of these combinations, 10 simulations with initial random values of hosts and parasitoids were carried out. The resulting values were plotted in a phase diagrams of λ vs. α , as in Kean and Barlow (2000).

3. Results and discussion

Our results illustrate that the levels of host suppression that may be achieved by parasitoids, is highly sensitive to the host rate of increase (λ), both for conformer or regulator-type species. For either type of host–parasitoid interactions studied here, at higher λ values, lower containment levels were attained. Ricker maps for conformer and regulator-type parasitoid species are shown in Fig. 1a and b.

We also show that delayed emergence and the physiological interaction between pests and natural enemies can have important consequences on biological control success. The levels of host

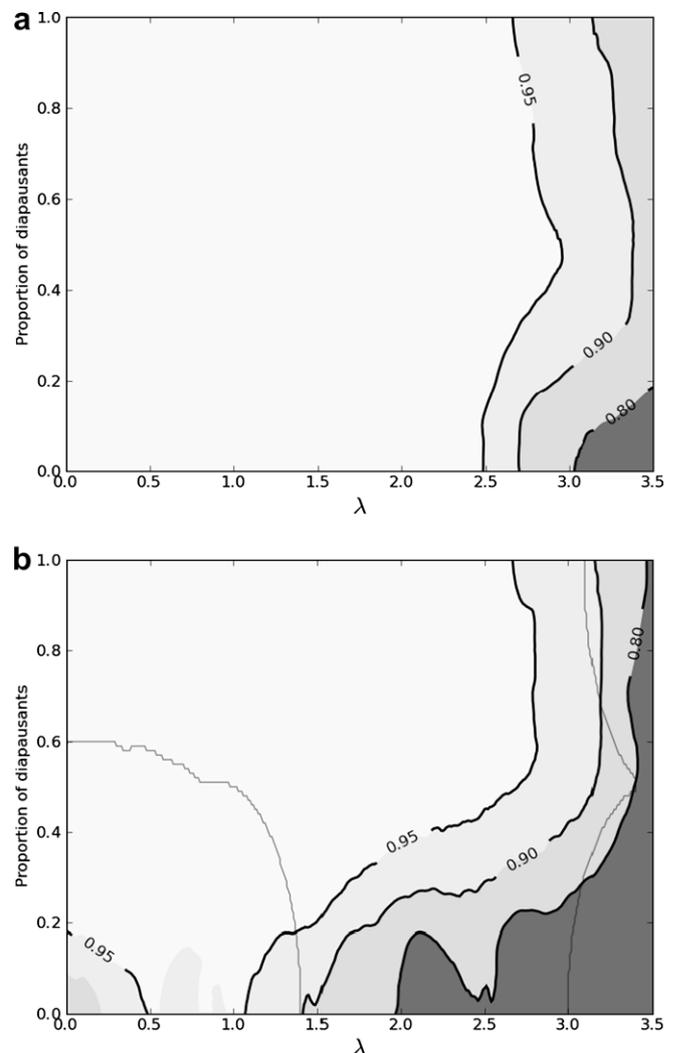


Fig. 1. Phase diagrams of the suppression level for (a) conformer (b) regulator parasitoids simulated here as a function of host rate of increase (λ in the X axis), the proportion of hosts delaying emergence (proportion of diapausants – Y axis). The suppression level is expressed as grayscale contour lines. Lighter is higher, the absolute values of regulation are showed in the contour lines. The light grey line plot (b) indicates the stability boundary for the regulator-type parasitoids. For conformer type parasitoids the model is stable for all combination of parameters studied.

suppression achieved by conformer and regulator parasitoids are different, under different delayed emergence fractions. While conformers do best whenever host delayed emergence affects a small proportion of the population, regulator parasitoids are less affected by host development as they rapidly consume their hosts. Recall here that the fraction of the host population undergoing extended diapause, relates closely to the environmental conditions in which the populations dwell (Tauber et al., 1983).

The comparison between both types of host–parasitoid physiological interaction is shown in Fig. 2. As expected, the regulator-type parasitoids are capable of increased host population suppression at higher host delayed emergence fractions. Note however, that for high λ values, that is when the host population is growing fast, the interaction becomes unstable for the regulator types, in which case the conformer type can also achieve significant host suppression levels.

The differences we note through simple models in host suppression levels, between regulator and conformer type parasitoids, may partly explain variable success in bio-control programs of pests that undergo delayed emergence. We illustrate our point by looking into the interaction of *S. noctilio* and its parasitoids in Australia (Taylor, 1981). Extended developmental cycles, ranging from 1 to 3 years are well known for this species; the fraction delaying emergence probably related to the effects climate has on the trees within which woodwasp larvae develop (Morgan and Stewart, 1966; Morgan, 1968). Because *S. noctilio* is a major threat to pine forestation, a remarkable biological control agenda has been established in the invaded regions (Taylor, 1981).

Several parasitoid species were introduced into different regions of Australia, to suppress growing *S. noctilio* populations. Among these, *Megarhyssa nortoni* and *Rhyssa persuasoria*, two idiobiont, regulator-type parasitoids showed to be better control agents in some regions (i.e., Tasmania), whereas, *I. leucospoides* – a physiological conformer parasitoid – achieved higher parasitism rates in pine plantations located in Victoria. A key difference between the above mentioned regions is their climate. Victoria experiences warm and dry summers which, among other things, favor *S. noctilio* development (approximately only 9% of the population

experience delayed emergence). In turn, Tasmania, located further south, has a colder and wetter regime which leads to a much higher population fraction extending their development time inside pine trees (more than of 50%; Taylor, 1978). The different fractions of the pest population extending their life cycle in either geographical region could explain the observed variations in suppression levels achieved by both parasitoid types. Note that according to our model, regulator-type parasitoids (i.e., *M. nortoni* and *R. persuasoria*) are expected to achieve higher suppression levels than conformers (i.e., *I. leucospoides*), when the fraction in prolonged diapause of the host population is high.

Delayed adult emergence is an adaptive feature of several forest insects living in unpredictable environments (Hanski, 1988). For instance, delayed emergence is common in seed and cone feeding species, where mast seeding patterns can affect resource availability and predictability (Turgeon et al., 1994). Although delayed emergence is a life history characteristic, it is known that the timing (duration) and frequency of diapause within a population is determined by environmental factors such as temperature and photoperiod (Tauber et al., 1986).

Delayed emergence may have unmistakable effects on the population ecology of single species (for example, see Menu and Debouzie, 1993). Spread-out adult surfacing, can dampen peak population intensities of pests and extend their duration through a slower, time-displaced population build-up process. It is possible also that postponed emergence patterns, again by changing outbreak frequency, duration or intensity, may influence the spread rates of established populations (Mahdjoub and Menu, 2008). Delayed emergence can also affect species interactions as has been shown for host–parasitoid interactions (Ringel et al., 1998; Corley et al., 2004).

Here we show that for insect pests that undergo prolonged diapause, such as may be the case of many forest insects, parasitoid suppression is affected by the degree and extension of the population undergoing delayed emergence. We illustrate our case by contrasting our theoretical findings with empirical observations. We conclude that the physiological relationship between parasitoids and their target hosts' emergence patterns, for given environments, should be included in the list of selection criteria of natural enemies of many insect pests.

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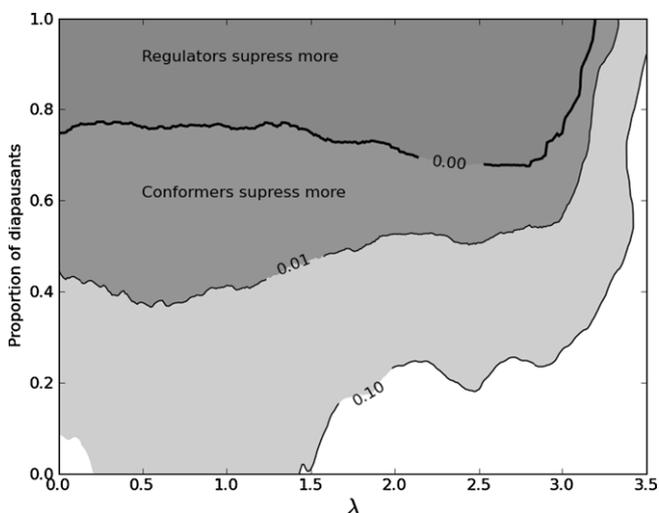


Fig. 2. Phase diagrams of the suppression level for the conformer minus the level of the regulator one as a function of host rate of increase (λ in the X axis), the proportion delaying emergence (proportion of diapausants – Y axis). Positive values indicate that the suppression level is higher for the conformer type, the negative on the other hand indicates higher levels for the regulator. The differences are expressed as grayscale contour lines. Lighter is higher, the absolute values of regulation are showed in the contour lines. The isoline of value 0 (shown in bold) distinguishes the areas in which either type of parasitoid performs best.

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