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The persistence of simple host-parasitoid systems with prolonged diapause

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Abstract. *Many univoltine insect populations can spread adult emergence in time through a phenomena known as prolonged diapause. With the exception of a few works, the dynamic consequences of prolonged diapause in coupled host parasitoid populations remains an open question. We modified the classical Nicholson-Bailey model to consider synchronic prolonged diapause in a model lacking other stabilising features. Our results add evidence to past work in that they show that this phenomena may be of little importance to the stability of hostparasitoid systems. However, the model predicts long-term persistence through abrupt oscillations. This feature may in itself help explain the population behaviour of many insect populations exhibiting outbreak dynamics and sets the emphasis on the importance of looking into transient dynamics.*

Introduction

Prolonged or extended diapause, the state in which a part of a population remains in diapause for a longer period than the rest, is a common life history feature of many insect populations (Darks 1987). Through such mechanism, adult emergence is spread through time, a characteristic which can prove adaptive in unpredictable environments (Menu and Debouzie 1992, Menu 1993, Menu et al. 2000). However, in contrast with what has been observed for some plant species with dormant seeds which await appropriate conditions for germination, prolonged diapause for the majority of insects is typically time limited and thus complete cohort emergence is completed in less than 3 years (Hanski 1988).

Most work on prolonged diapause has focused on single populations because an important issue refers to why such trait has been selected for in a number of insect species (see for example, Debouzie and Menu 1992, Menu et al. 2000). In other words to what degree is prolonged diapause a strategy to deal with unpredictable environments (Philipi and Seger 1989). However, some recent work has shown that prolonged diapause can also have important dynamic consequences when interacting populations are considered. For instance, in systems involving parasitoids -insects which lay their eggs in or on other insects-, host diapause may promote stability because of the differential development rates between host and parasitoid (Hassell et al. 1993), or because hosts in prolonged diapause are in a refuge (Ringel et al. 1998). Indeed, temporal asynchronies between predator and prey as well as partial refuges are widely thought important events to the dynamics of predator-prey interactions (Hassell and Anderson 1989).

Parasitoids are not only remarkably abundant in nature (probably nearly 25% of all insects are parasitoids) (Godfray 1994), and are outstanding agents of biological control of insect pests, but have a very diverse biology. In consequence, parasitoids may relate to host physiology and development in a variety of ways. For instance, koinobiont species typically allow hosts to move and develop after attack, whereas idiobionts will kill or permanently paralyse hosts during parasitoid oviposition (Godfray 1994). Thus, concerning diapausing patterns, parasitoids may respond, in addition to the stimuli offered by environmental cues common to most free-living insects, to their hosts hormones as an additional cue (Lawrence 1986). Indeed, it is not uncommon to observe that parasitoid phenology is tightly coupled with the host's diapausing patterns (see for examples Beckage 1985, Hanski 1988).

Through some recent work we have shown that the stability conditions of the host-parasitoid model derived by May (1978) which considers aggregation of parasitoid attacks as a distinctive feature, can be enhanced, albeit slightly, by including host prolonged diapause (Corley et al. in review). An important conclusion stemming from this work, is that the way in which parasitoids relate to hosts is central in the dynamics of the system. Important issues are, for instance, when is parasitoid attack produced (egg, larvae, pupae or adults), whether hosts are killed immediately or are left to develop (idiobiosis or koinobiosis), and if and to what degree are host and parasitoid diapause related. In this paper, we extend our previous findings (Corley et al. in review) by looking into the dynamic effects of synchronic host-parasitoid prolonged diapause in systems with random search. We do so by modifying the classical Nicholson-Bailey model, which offers an important theoretical advantage to study potentially stabilising mechanism as it is reportedly unstable for all combination of parameters (Nicholson and Bailey 1935).

Methods

For host-parasitoid interactions in seasonal environments, the model developed by Nicholson and Bailey may be seen as the cornerstone work (Edelstein-Keshet 1987, Dwyer 1995, Doebeli 1997). The model, which describes how a single parasitoid interacts with a single host species in the simplest possible way, has been well studied. The model has a feedback between the per head rate of change of each population and its previous density, which is the feature responsible for its equilibrium (Murdoch 1994). This equilibrium, is however unstable, leading to unbounded - fluctuations as, in fact, there are no stabilising mechanisms in it. Thus, the populations described by the Nicholson-Bailey model are by definition, typically unregulated (Murdoch 1994). To study the dynamic consequences of host prolonged diapause, we modified the classical Nicholson-Bailey model to include the effects of a delay in adult emergence occurring in a fraction of the host population. Mathematically, the modification consists in adding a term, which represents a delay in the emergence of adults. We assume that the diapausing pattern shown by the host population, affects in an equal manner the parasitoid population (Tauber et al. 1986) and extends itself up to three years in time, as has been described for insect populations (Debouzie and Menu 1992, Menu et al. 2000). The equations for our model are:

$$Nt=\alpha rN_{t-1}\exp(-aP_{t-1}) +(1-\alpha)\sigma_1\beta rN_{t-2}\exp(-aP_{t-2})+(1-\alpha)(l-\beta)\sigma_2 rN_{t-3}\exp(-aP_{t-3})$$

(eqn. l)

$$Pt=\alpha N_{t-1}(1-\exp(-aP_{t-1})) +(1-\alpha)\sigma_1\beta N_{t-2}(1-\exp(-aP_{t-2}))+(1-\alpha)(l-\beta)\sigma_2 N_{t-3}(1-\exp(-aP_{t-3}))$$

where N and P stand for the densities of host and parasitoid respectively, a is the "area of discovery" or parasitoid searching efficiency, r is the host population growth rate (Nicholson and Bailey 1935), a represents the proportion of the population that emerges during time t-1, whereas (1-α) represents the remaining proportion of adults emerging from eggs laid a year before (in t-2) and is the proportion of the population with prolonged diapause that emerge from eggs laid two years before. An additional term, defined by (1-β), is the fraction of the (1-α), which extend diapause for even another year; eggs laid in (t-3). Both fractions, (1-α) and (1-β), are multiplied each by a survival parameter σ_1 and σ_2, respectively which represents the probability of surviving such state. Note that prolonging diapause in some developmental stage, entails an extra risk of mortality. In other words, for both host and parasitoid, the population of adults emerging in time t is the arithmetic sum of those eggs laid in the precedent period plus an extra number corresponding to those eggs laid in two even previous periods and surviving through this state.

The model was analyzed using the symbolic-numerical package Mathematica® and additional simulations were performed with a program written in C++ programming language.

Results

Our modification of the classical model is unstable for all possible values of α and β (Figure la), even for different survival values after prolonging diapause (Figuresl b and c) However, prolonged diapause promotes population persistence, through and oscillatory behaviour, for a combination of parameters (Figure 2). Such persistence is possible only if prolonged diapause is extended to at least three seasons (this is, $\beta < 1$). It is possible, that the density dependent mechanism promoting such persistence, is, as in metapopulation models, a sort of "immigration" (Murdoch 1994, Corley et al. in review, Figure 3). The difference is that in our case the "immigration" of an out of phase small number of individuals to an otherwise extinguishing system, is not on spatial axis, following spatial heterogeneity as in the metapopulation models, but responds to the temporal asynchrony produced by prolonged dipauase. A "refuge effect" occurs in the part of the host population entering diapause that has escaped parasitism at the time when oviposition took place. This would be due to the fact that for systems with synchronic phenologies, host larvae entering diapause have already either undergone parasitism or have escaped it, as by then the "window" for parasitism has expired.

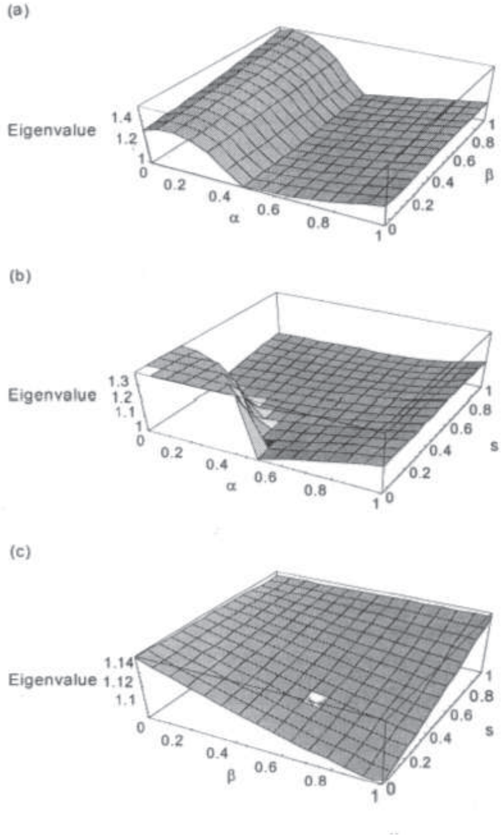

Figure 1. Three dimensional plot showing the instability for all values of α and β (a), and as function of the survival parameter $s=\sigma_1=\sigma_2$ (b & c). All eigenvalues of the Jacobian matrix are larger than 1 in absolute value (see Appendix). Area of discovery is fixed as a=0.008 whereas r=2. For plot (a) both survival parameters $\sigma_1=\sigma_2=0.1$, for plot (b), $\beta=0.2$ and for plot (c), $\alpha=0.9$.

According to our model, at any time t, there is a relatively small contribution of those individuals emerging from eggs laid three years back in time (H_{t-3} and P_{t-3}) to the total numbers of both populations (H_t and P_t) which prevents system extinction (Figures 2 and 3). Moreover, as can be seen in Figure 2, there is a trade-off between parameters determining how many individuals enter prolonged diapause and their survival. In addition, Figure 3 shows that such contribution appears out of phase with respect to the other two population fractions (t-2 and t-1; Partial Auto-Correlation Function PACF for t-1 and t-2=+0.63; and PACF for t-1 and t-3=-0.41, both significant ($p < 0.05$); longer lags are non-significant).

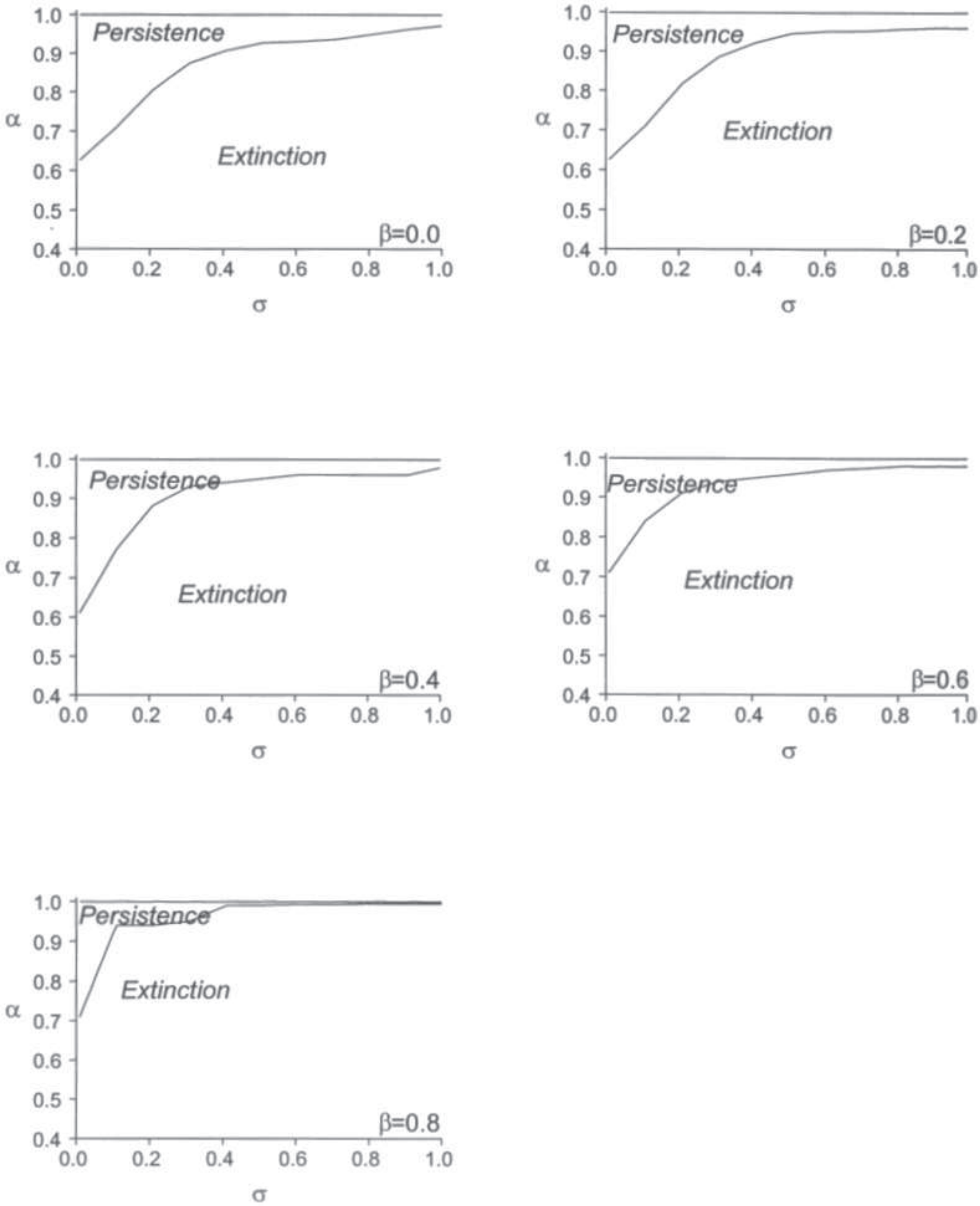

Figure 2. Regions of parameter space for the modified Nicholson-Bailey model where persistence of the system occurs. Again, area of discovery ís fixed as a=0.008 whereas r=2.

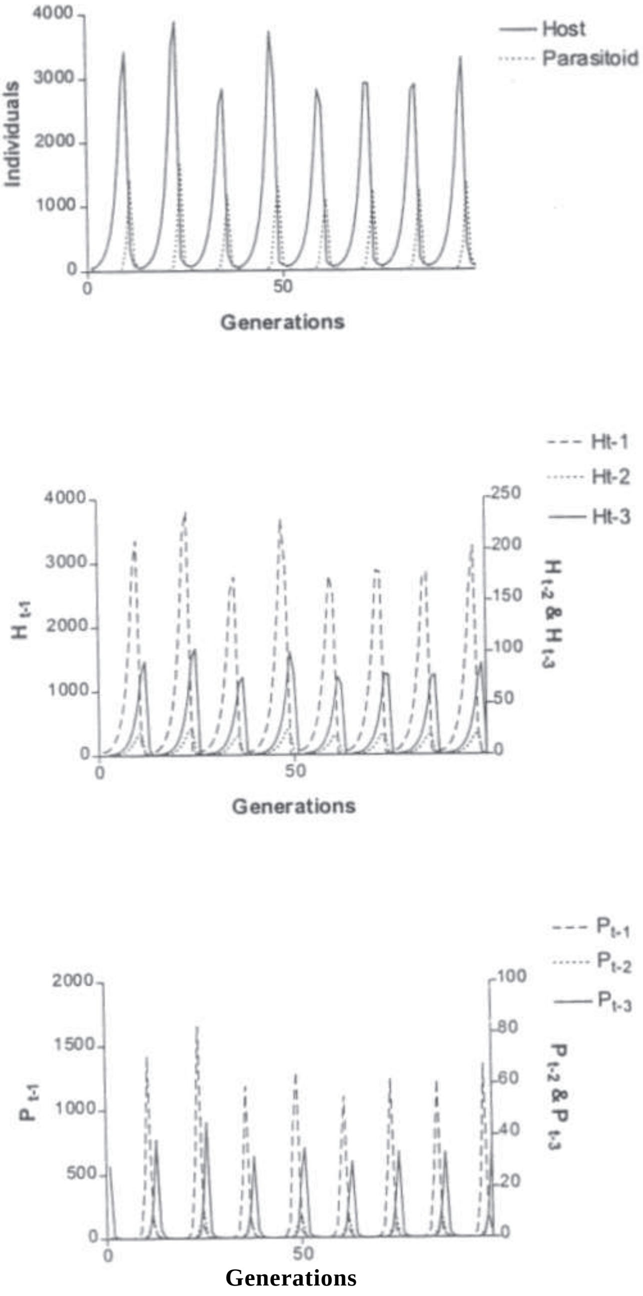

Figure 3. Selected simulations of the Nicholson-Bailey model modified to include host prolonged diapause. The model was built in C++ language and run for 100 generations. Area of discovery is fixed as a=0.008 whereas r=2, β=0.2, α=0.86 and σ_1=σ_2=0.21.

Discussion

Our results show that the unstable conditions predicted by Nicholson and Bailey (1935) for host-parasitoid systems are not reverted by prolonged diapause.

The instability of the Nicholson-Bailey model, has led to an array of research on the biological events promoting stability (see for recent reviews, Dwyer 1995 and Bernstein 2000*)*, which, in turn, have had an influential role on the theoretical framework for the study of predator-prey interactions, Some well known modifications of the classical model promoting persistence are: (a) the incorporation of density dependent resource limitation, where the hosts rate of increase is a function of its density (Beddington et al. 1975); (b) the interference among parasitoids, where female parasitoids avoid each other or common hosts, reducing the speed with which parasitism rises as a function of the number of parasitoids (Hassell and May 1973); and (c) the aggregation of parasitoids, determining partial refuges from parasitism (Hassell and May 1974). Recently, it has been argued that stability is also achieved through genetic variability in the host and parasitoid populations (Doebeli 1997). In all these cases, persistence is a consequence of an ecologically and genetically heterogeneous environment.

Others instead, have shown that regional stability may be acquired by out of phase fluctuating Nicholson-Bailey-type subpopulations (Reeve 1988). Again, stability is a consequence of a spatially heterogeneous environment that leads to a metapopulation structure. Unregulated subpopulations are linked through random movement. In this sort of environment, the stabilising mechanism is, in appearance, immigration, and the density dependence arises from the fact that the number of residents arriving per head into a subpopulation decreases with the number of residents (Reeve 1988).

Two past papers have dealt with diapause in host-parasitoid systems. Hassell et al. (1993), studying the potential effects of global change in host-parasitoid interactions, have shown the importance of asynchronic diapause in the stability of such systems. In their case, the differential development rates promote a heterogeneity in the distribution of parasitism among the hose population which explains population stability. Ringel et al. (1998), in turn, conclude that prolonged diapause can promote stability to a Nicholson-Bailey scenario with aggregation of parasitoid attacks, However this work has several assumptions that we discuss in detail elsewhere (Corley et al. in review).

In more recent work, we have shown that prolonged diapause may contribute little to the stability of host-parasitoid systems with aggregation of attacks and that the biological details of the interaction may be important in the final outcome (Corley et al. in review). The modelling framework taking into account random search (no aggregation of attacks), provides additional evidence on the limitations of prolonged diapause in promoting stability for host-parasitoid interactions.

A second finding we report is that, according to our model, there is persistence through an oscillatory dynamics. These oscillations can be abrupt and the host population can achieve an increase from a few individuals to thousands of them in just a few generations. However, in contrast with the classical Nicholson-Bailey model, these oscillations do not amplify but instead are long-lasting.

Prolonged population persistence can prove to be an important attribute describing many natural populations. It is important to note here that, model behaviour in most analyses is focused on an equilibrium concept. Thus stability is the key mathematical concept under study (Briggs et al, 1999). However, as has been noted by Hastings (1999), for many insects, namely pests and other insects affecting crops and other natural systems, such equilibrium approaches may not be appropriate. The reason behind this, is that many populations exhibit outbreaks, which are nothing less than large departures from equilibrium. An additional problem with setting the emphasis on local stability is that the concept may be misleading for biological control practitioners as stability may be brought at the expense of increased population density (Briggs et al. 1999). A final consideration is that long-term persistence is, from a practical standpoint, to some degree equivalent to stability. Many short-lived plant species communities that sustain host populations, as for example many crops and their insect pests may be outlived by the pest-parasitoid interaction. In these cases, long term persistence of the pest-natural enemy interaction is relevant, and thus looking into the transient dynamics may prove to be more informative.

Conclusions

In this paper we extend past findings and provide additional evidence on the fact that prolonged diapause in host and parasitoid coupled populations does not promote local stability. However, we argue that looking into the transient dynamics may offer a different scenario. Prolonged diapause, a feature common to many insect populations, may allow for long term persistence through an oscillatory behaviour. This, may explain the population dynamics of many insects exhibiting outbreaks, living in unpredictable environments. According to our model, persistence through an oscillatory dynamics is long lasting. Oscillations can be abrupt and the host population can achieve an increase from a few individuals to thousands in just a few generations. Persistence is, in this case only the product of a heterogeneous physiology in the host populations.

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Appendix

The equilibrium for each model is found by setting

$$N^* = N_{t-1} = N_{t-2} = N_{t-3} \text{ and}$$
$$P^* = P_{t-1} = P_{t-2} = P_{t-3}$$

Where

$$H = \{\alpha + \sigma_1(1-\alpha)\beta + \sigma 2(1-\alpha)(1-\beta)\}$$

thus for the model,

$$P^* = \text{Log } rH/a$$
$$N^* = P^*/(1-\exp[-aP^*])H$$

The corresponding Jacobian matrix (J) for the model is,

$$\begin{bmatrix} e^{-aP}r\alpha & e^{-aP}r\sigma_1\beta(1-\alpha) & e^{-aP}r\sigma_2(1-\alpha)(1-\beta) & -ae^{-aP}r\alpha N & -ae^{-aP}r\sigma_1\beta(1-\alpha)N & -ae^{-aP}r\sigma_2(1-\beta)(1-\alpha)N \\ 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ (1-e^{-aP})\alpha & (1-e^{-aP})\sigma_1\beta(1-\alpha) & (1-e^{-aP})\sigma_2(1-\alpha)(1-\beta) & ae^{-aP}\alpha N & ae^{-aP}\sigma_1\beta(1-\alpha)N & ae^{-aP}\sigma_2(1-\beta)(1-\alpha)N \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \end{bmatrix}$$

Local stability is insured if and only if all the eigenvalues of the Jacobian matrix are less than 1 in absolute value. For the model, as a function of the relevant parameters, this condition was found numerically using the symbolic-numerical package Mathematica®. Additionally, simulations were performed with a program written in the C++programming language.