IDEAS AND PERSPECTIVES

Natural enemy specialization and the period of population cycles

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Abstract

The dynamical consequences of multiple-species interactions remain an elusive and fiercely debated topic. Recently, Murdoch and colleagues proposed a general rule for the dynamics of generalist natural enemies: when periodic, they exhibit single generation cycles (SGCs), similar to single species systems. This contrasts markedly with specialists, which tend to show classic (longer period) consumer–resource cycles. Using a well-studied laboratory system, we show that this general rule is contradicted when we consider resource age-structure.

Theory demonstrates how specialist natural enemies can introduce delayed regulatory mechanisms, which may either destabilize an equilibrium or lengthen the period of oscillations. These oscillations typically possess a period many times longer than that of a consumer generation (Beddington *et al.* 1975; Lauwerier & Metz 1986; Rohani *et al.* 1994). They are referred to as multi-generation cycles (MGCs). Addressing this issue in their recent article, Murdoch *et al.* 2002 stated that 'models of a specialized consumer, tightly coupled to a resource population so that each controls the dynamics of the other, show longer-period, true 'consumer–resource cycles'' (Murdoch *et al.* 2002). This is caused by an intimate link between natural enemy reproduction/survival and prey abundance. They argued that a weakening of this link through the availability of alternative prey species, as with generalist natural enemies, may result in a more 'stable' system, either with steady-state dynamics or with shorter period SGCs (Murdoch *et al.* 2002). The principal conclusion of their study is that generalist predators may be modelled using single-species models.

Despite the intuitive appeal of the theory, there are a number of scenarios in which its conclusions remain untested. Here, we present data and modelling analyses of a laboratory system in which generalist natural enemies show pronounced MGCs, while specialists show single generation cycles. Our findings contradict Murdoch *et al.'s* 2002 theory because of the presence of strong feedbacks between different prey stages, which lead to a weakening of the predator–prey coupling.

Our system of interest centres on the dynamics of the Indian meal moth *Plodia interpunctella* and its ichneumonid parasitoid *Venturia canescens*. Laboratory experiments have shown how moth populations, cultured in isolation, exhibit generation cycles via density-dependent competition for limited resources (Begon *et al.* 1995; Bonsall & Hassell 1998; Sait *et al.* 2000). In these systems, there are significant interactions among different host stages, with direct competition between larvae, and egg cannibalism by large larvae is prominent (Bjornstad *et al.* 1998; Briggs *et al.* 2000).

Theory would predict that the addition of the parasitoid should increase the period of the fluctuations because it is a specialist, yet cultures of the host and parasitoid both exhibit rigid SGCs (Sait *et al.* 2000; Fig. 1a). This finding remains unaffected if a different host species (*Ephestia kuehniella*) is used (White & Huffaker 1969).

To obtain a detailed understanding of the mechanisms generating these dynamics, we have employed a stage-structured model of this system (see Appendix; Briggs *et al.* 2000). In particular, we are interested in discovering the general conditions required for observing MGCs in specialist consumer dynamics. Our explorations reveal egg cannibalism by late instar larvae as the key parameter; when the cannibalism rate is low, egg survival is high and parasitoids can attack a significant fraction of larvae. This scenario gives rise to classic MGC consumer–resource

dynamics, with parasitoids experiencing 'feasts and famines'. If cannibalism is substantial, however, we observe SGCs (Fig. 1b) and find parasitism rates to be surprisingly low (despite very high attack rates). High cannibalism rates dramatically reduce the number of larvae (and subsequently, the number of adults) in the current generation cohort, leading to reduced cannibalism and large larval numbers in the next generation.

It is tempting to assume that our findings are the result of parasitoids being dynamically unimportant, because the host alone exhibits SGCs. This is not the case, however, and we present different lines of argument to counter this view:

(1) Although the inclusion of parasitoids does not increase the cycle period, it substantially accentuates the amplitude of the cycles while dramatically suppressing host density (Begon *et al.* 1995). Contrast the impact of the parasitoid in this case with that of another specialist natural enemy, a pathogen, which has almost no effect on the dynamics and abundance of the host (Sait *et al.* 1994; Sait *et al.* 2000; Bjornstad *et al.* 2001). Like the parasitoid, the pathogen exhibits age-specific infection rates but fails to significantly subdue host density because of the compensatory interactions between the invulnerable age-class (Bjornstad *et al.* 2001).

(2) As presented in Fig. 1c, our conclusion that the specialist can exhibit SGCs remains unaffected even when parasitism rates are increased almost until the entire system is on the brink of eventual extinction.

(3) The recent work of Bjornstad *et al.* (2001) has demonstrated how *Venturia* plays a pivotal dynamical role in this interaction by increasing the system's dimensionality. Using time series methods, they showed that the
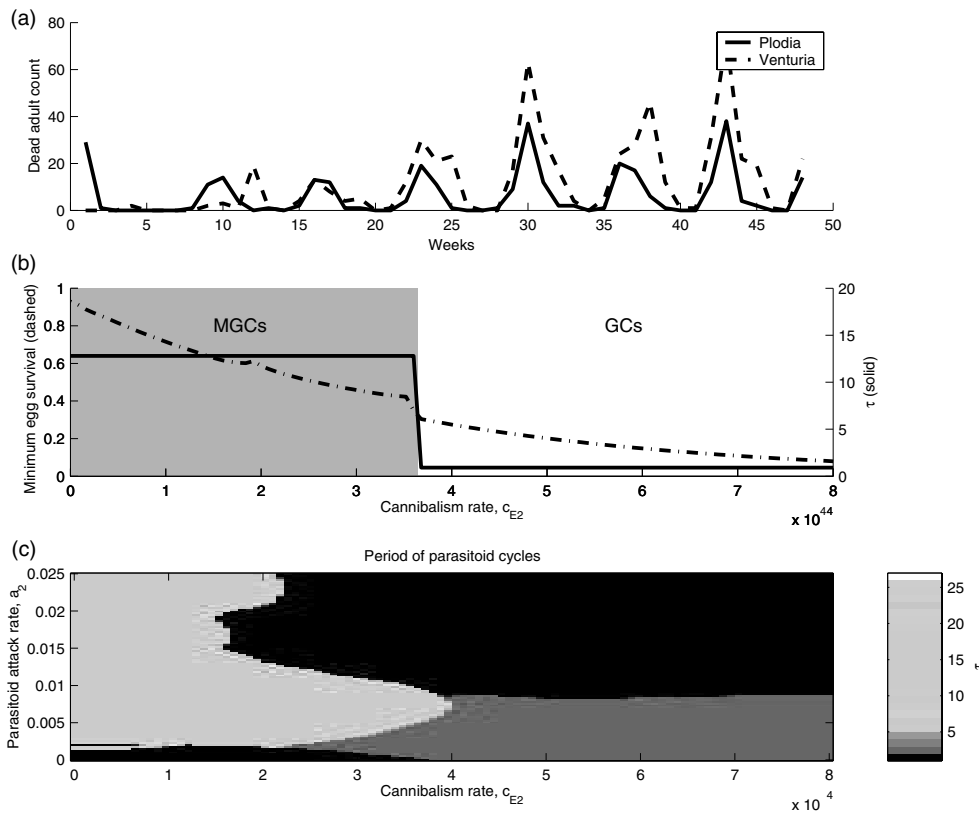

Figure 1 (a) Weekly data from *Plodia–Venturia* laboratory populations show cycles with a period of approximately one host generation. (b) and (c) Increasing the rate of late instar egg cannibalism shifts the host–parasitoid dynamics from true consumer–resource cycles, with a period of several parasitoid generations, to single generation cycles (SGCs). Panel (b) illustrates the reduction in minimum egg survival and the transition from multi-generation cycles (MGCs) to SGCs as the rate of egg cannibalism (c_{E2}) is increased. Panel (c) shows the period of parasitoid cycles scaled with the parasitoid development time (τ) as both the rate of egg cannibalism and the rate of late instar parasitism (a_2) are increased. Simulations are based on the *Plodia* delay-differential equation model of Briggs *et al.* (2000) with asymmetric larval competition and egg cannibalism (see Appendix). Parasitism is included via a nonlinear attack function with rates on late instar larvae greater than on early instar larvae. The host development time is 36 days and the parasitoid development time is 20 days. Simulations are inoculated with 10 adult hosts and two adult parasitoids are added after 30 weeks.
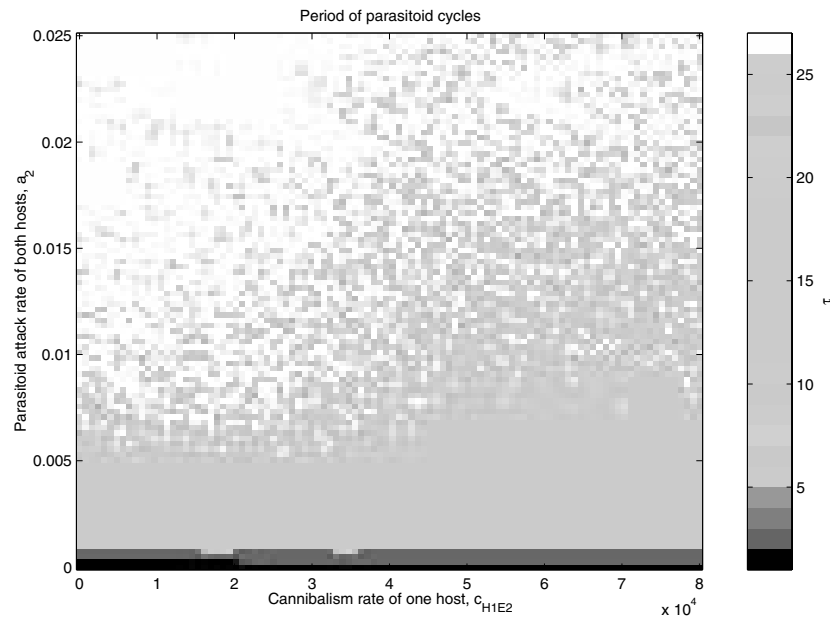
Figure 2 An additional host species promotes multi-generation cycles. In the presence of *Ephestia*, *Venturia* is effectively a generalist. Intriguingly, we no longer see, as in Fig. 1, the transition from MGCs to SGCs as the rate of egg cannibalism is increased. We plot the period of parasitoid cycles scaled with the parasitoid development time (τ) as the egg cannibalism rate in one host (c_{H1E2}) and the parasitoid attack rate on the late instar larvae of both hosts (a_2) are varied. As parasitoid attack rate increases, there is a transition from SGCs to MGCs (with a period exceeding 10 parasitoid generations; light grey shading) and eventually, parasitoid extinction (white shading). Simulations are based on the model used in Fig. 1 with an additional host species which differs only in life-history parameters and the rate of egg cannibalism (fixed at 0.00004 day^{-1}). The life-history parameters are those for *Ephestia cautella* taken from Gordon & Stewart (1988). We also assume that the two host species do not compete directly, i.e. that there is only apparent competition, and that the system is inoculated with both species present. The development time for the second host is 34 days.

host–parasitoid system we are studying contains five density dependent lags, while the host alone populations are characterized by only three such time-delays. The parasitoid not only modifies the existing time delays of the host but introduces two additional delays specific to the trophic interaction between prey and parasitoid. The main conclusion of their study was that the observed increase in dimensionality is indicative of strong coupling between *Plodia* and *Venturia*.

(4) For some combinations of parameter values, host alone populations settle to an equilibrium and SGCs are only observed with the addition of parasitoids, echoing Godfray & Hassell (1989) classic work.

Our explanation for these findings is that such systems are subject to strong tension between within-resource (interactions among host age-classes) and consumer–resource (interactions between hosts and parasitoids) forces. The dynamics are determined by which of these factors exerts a greater influence. While parasitoids can excite SGCs when host alone populations are stable, their dynamical influence is limited in the face of strong within-host feedbacks.

This system also contradicts Murdoch *et al.'s* 2002 theory when additional host species are incorporated into the model (see Appendix). In the presence of alternative hosts, the parasitoid effectively behaves like a generalist natural enemy. We explored the consequences of adding *Ephestia* to the *Plodia–Venturia* interaction, assuming no direct competition between the two moth species (an example of 'apparent competition'; *sensu* Holt & Lawton 1993; Bonsall & Hassell 1997). We also assume no preferential parasitism.

In direct contrast to the theoretically predicted single-species dynamics for such a scenario, we instead observe an increased likelihood of MGCs (Fig. 2). This is because of the differential development rates of the two host species, leading to an extended overall distribution of larval stages that are vulnerable to the parasitoid, comprising consecutive cohorts of *Plodia* and *Ephestia*. The combination of roughly two parasitoid generations per host generation would lead to cycles with a period of multiple parasitoid generations for the total duration of two-host species vulnerability.

The results of Murdoch and colleagues are novel and exciting, but our brief analyses of systems with resource

age-structure suggest that their conclusions may not be universally applicable. Precisely which systems conform to their prediction remains an untapped and rich area for further research.

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REPLY

Results in Rohani *et al.* (2003) are not relevant to the conclusions in Murdoch *et al.* (2002). *Resource*-driven single-generation cycles (SGCs) in lab and model host–parasitoid populations discussed by these authors are not examples of the *consumer*-driven SGCs of Murdoch *et al.* Their models cannot produce consumer SGCs.

'SINGLE-SPECIES-LIKE' CONSUMER (PARASITOID) CYCLES

Murdoch *et al.* (2002) concerns cycles (henceforth consumer or parasitoid cycles) driven by competitive interactions between different-aged cohorts of a *consumer* population, with a period determined by *consumer* development time, T_P (subscripted for parasitoid). These are either single-generation cycles (SGCs) with period between T_P and $2T_P$ or delayed-feedback cycles (DFCs) with period at least $2T_P$. They have been found in two predator–prey models (Persson *et al.* 1998, chapter 11 in Murdoch *et al.* 2003) and a parasitoid–host 'gain' model (Murdoch *et al.* 1992; Briggs *et al.* 1999, chapter 6 in Murdoch *et al.* 2003). They have two prerequisites.

(1) There is roughly constant recruitment to the *resource* population. This suppresses inherent long-period, specialist consumer–resource cycles, and decouples the consumer–resource interaction, allowing the consumer to behave as if it were a single population receiving a constant food supply. Constant recruitment in the predator–prey models comes from a prey refuge, and in the parasitoid–host model from a roughly constant long-lived adult host population. (2) There is competition between different ages or stages in the *consumer* population. Delayed competition yields DFCs; absence of delay gives SGCs. In the predator–prey models, SGCs arise because young predators (fish, *Daphnia*) are

better competitors than adults: until it matures and reproduces, each dominant cohort of young predators suppresses the resource (zooplankton, algae) below the level required for successful reproduction.

In the parasitoid–host model, parasitoid SGCs cannot occur if, as in almost all parasitoids, T_P is less than host development time, T_H. Instead, parasitoid cycles are DFCs with period approximately $2T_P + T_H$ (Briggs *et al.* 1999). Requirements for parasitoid SGCs include: the host has young and old immatures; the parasitoid attacks both but gains more from older hosts (creates inter-cohort competition); and $T_P > T_H$ (Table 1). SGCs arise because a dominant adult parasitoid cohort suppresses all host stages until its offspring mature. They thus require host stage-structure (cf. Rohani *et al.*).

HOST SGCs IN LABORATORY POPULATIONS

In *Plodia* lab populations without parasitoids, each cycle is caused by a dominant cohort of larvae that suppresses survival of all existing cohorts (including via cannibalism of eggs and small larvae). The immediate successor cohort becomes the next dominant one (Briggs *et al.* 2000). The period is over 40 days; *Plodia* development time, T_H, is 36.3 days.

When the parasitoid *Venturia* is added, these *host* SGCs persist and no parasitoid SGCs appear. Cycle period (>40 days) is little changed, and the mechanism driving the cycle remains asymmetrical interactions between different *host* stages, which create pulses of host recruitment (Begon *et al.* 1995; Bjornstad *et al.* 2001). *Venturia* T_P is 20 days; the cycles are self-evidently not parasitoid SGCs. They are not induced by age-dependent interactions in the parasitoid (Begon *et al.* 1995; Bjornstad *et al.* 2001).

Such host–parasitoid systems are unlikely to generate parasitoid SGCs (Table 1). (a) The invulnerable *Plodia* adult

Table 1 Characteristics of and factors promoting two different types of cycles in stage-structured parasitoid–host interactions

Host-driven SGCs	Parasitoid-driven SGCs
Distinctive features	
Pulsed host recruitment	Approx. constant host recruitment
Period approx. one host development time, T_R	Period approx. one consumer development time, T_C
Induced by age-dependent interactions in host	Induced by age-dependent interactions in parasitoid
Promoted by	
Short adult duration in host T_P approx. $0.5T_H$	Long adult duration in host $T_P \geq T_H$
Pseudointerference (density dependence in adult parasitoid search rate)	Pseudointerference in parasitoid search rate suppresses these cycles

is short lived (5.5 days). This favours pulsed host recruitment, the basis of host SGCs but antagonistic to parasitoid SGCs; (b) there is no inter-cohort parasitoid competition; and (c) since $T_P < T_H$, any parasitoid cycles would be DFCs with period approximately $2T_P + T_H$ (here about 80 days).

ROHANI *ET AL.* MODELS

The Rohani *et al.* models lack the prerequisites for parasitoid SGCs and do not produce them. They also assume 'pseudointerference' among searching parasitoids, which would suppress parasitoid SGCs if they were possible: adding pseudointerference suppresses parasitoid SGCs and DFCs in the 'gain' parasitoid–host model (Briggs *et al.* 1999). Simulation results supporting this conclusion and those to follow are given on the *Ecology Letters* web site (see Supplementary Material).

The one-host (*Plodia*) model without *Venturia* shows host SGCs (usually damped) with period 37 days, very close to *Plodia* development time, T_H. They are induced by inter-stage competition. With *Venturia* present, host SGCs with almost exactly the same period (36.5 days) dominate dynamics in the blue regions of Rohani *et al.* (Fig. 1c). *Venturia* merely deepens the host nadir and narrows the peak. These are still *host* SGCs (see Godfray & Hassell 1989), not parasitoid SGCs or DFCs. The period is $1.8T_P$; parasitoids in each peak are not offspring, or F_2, of those in the previous peak; age-dependent parasitoid interactions are not in the model and do not drive the cycles.

Host SGCs persist at 'high' parasitoid attack rate because the skewed ($k = 1$) negative binomial distribution of attacks (Rohani eq. 15) causes *within-adult* parasitoid density dependence (pseudointerference): parasitoid efficiency decreases as parasitoid density increases (Murdoch & Stewart-Oaten 1989); parasitoid–host cycles are suppressed and host SGCs appear (Godfray & Hassell 1989). Host SGCs require short-lived adults (which tends to produce cycles) and T_P approximately $0.5T_H$ (which reinforces that tendency), features of the Rohani *et al.* model.

The two-host model also lacks a mechanism to produce, and has pseudointerference that would suppress, parasitoid SGCs. In the blue regions of Rohani *et al.* (Fig. 2), (1) *Plodia* goes extinct in most of the parameter space and (2) the cycles are *Ephestia* half-generation cycles, which the parasitoid simply tracks. (*Ephestia* alone shows transient SGCs then damped half-generation cycles; see Briggs *et al.* (2000) on half-generation cycles).

The MGCs in both models are a mixture of long-period parasitoid–host cycles and short-period host cycles. In the MGCs of the *Plodia–Venturia* model (Rohani *et al.* Fig. 1c), periods of extremely scarce parasitoids and dense hosts undergoing damped SGCs are interrupted by brief parasitoid eruptions (Fig. 1a). A simpler *Plodia–Venturia* model has
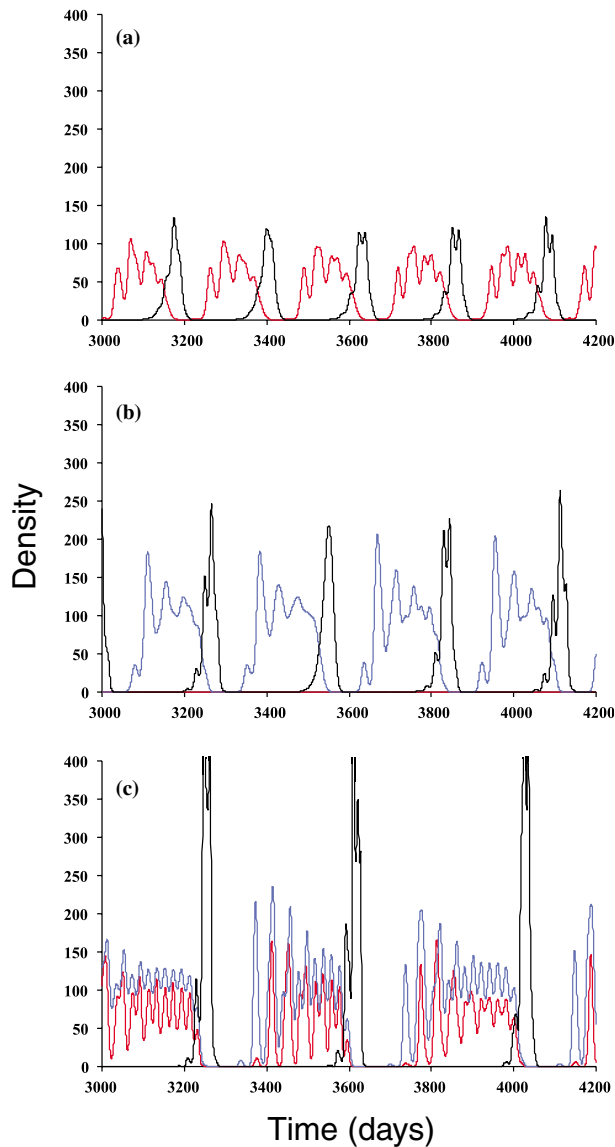
Figure 1 Dynamics in the multi-generation cycle (MGC) regions. (a) One-host system with *Plodia* and *Venturia*, (b) one-host system with *Ephestia* and *Venturia*, and (c) two-host system with *Plodia*, *Ephestia*, and *Venturia*. In each case adult *Plodia* density is shown in red, adult *Ephestia* in blue, and adult parasitoid *Venturia* in black. In each panel, the rates of egg cannibalism are: $c_{E2\_Plodia} = 1 \times 10^{-4}$ and $c_{E2\_Ephestia} = 4 \times 10^{-4}$, and the attack rate on late larvae of both species is $a_2 = 0.005$. All other parameters are set at the default values in Rohani *et al.*

similar dynamics (chapter 5, Murdoch *et al.* 2003), which may be general. The *Ephestia–Venturia* version mainly shows the transient damped host SGCs (Fig. 1b). The *Venturia* + two-hosts version behaves similarly to the one-host models. The two host SGCs are initially synchronous; each host SGC is reinforced; and the more abundant total hosts

induces larger-amplitude and longer-period parasitoid–host cycles (Fig. 1c).

Interestingly, the contrast above between *Plodia* extinction at low values of a_2 and three-species persistence in the MGC region, shows that increased attack rate on older larvae causes coexistence of the two hosts in the face of apparent competition.

GENERALITY

Murdoch *et al.* (2002) claim that single-species-like cycles should be seen in generalist consumers because, *inter alia*, the recruitment rate of their combined resource species is likely to be independent of the abundance of the consumer or any one resource species. Consumer SGCs or DFCs in specialists would not refute this claim: they are expected when the conditions in Table 1 (defined by three specialist consumer–resource models) are met. Murdoch *et al.* found 3 examples.

A compelling counter-example would be a *generalist* consumer with inter-cohort competition and appropriate resource recruitment, which nevertheless shows consumer–resource cycles. Such a species should not be a *de facto* specialist in the population studied or the resource in a specialized consumer–resource interaction. Murdoch *et al.* (2002) found two apparently generalist species, carabid beetles, that cycled with marginally long periods, and these merit additional attention.

ACKNOWLEDGMENTS

SUPPLEMENTARY MATERIAL

The following material is available from http://www.black wellpublishing.com/products/journals/suppmat/ELE/ELE461/ELE461sm.htm

Figure S1 Diagrams of models discussed in text.

Figure S2 Simulations of the models in Rohani *et al.*

Figure S3 A negative binominal parasitism function in the gain model stabilizes the parasitoid single generation cycles.

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