

Current theories may be inadequate to elucidate discrete generation cycles in aseasonal insects

Y. B. Srinivasa and K. Muralimohan

Insects have either discrete or continuous generations. Discrete generations (DG) are widespread among insects with restricted breeding seasons (or seasonal insects), while continuous generations are usual among tropical insects with unrestricted breeding seasons (or aseasonal insects). However, there are interesting instances of DG even among aseasonal insects¹⁻⁴. The mechanisms that regulate DG among aseasonal insects have been understood largely through theories that are yet to be thoroughly tested by hard data. Also, it appears that the existing theories may not suffice to explain DG among aseasonal insects, which we attempt to highlight through this note. We use information available on *Opisina arenosella* (Walker) (Lepidoptera: Oecophoridae) and *Artona catoxantha* Hamps. (Lepidoptera: Zygaenidae), both aseasonal insects with DG^{1,4} to substantiate our opinion.

How discrete generations?

Ceteris paribus (a Latin phrase meaning 'all other things being the same') populations tend towards continuous generations. Let us consider that a dispersing group of moths arrives on a fresh patch of perennial resource within a short span of time and starts laying eggs such that the resultant population has a definite age-structure. In absence of any 'regulation', this population will develop continuous generations over time. This can be explained in the following manner. There are four stages in the life cycle of a moth – egg, larva, pupa and adult. As the population moves from one stage to another – egg to larva, larva to pupa and so on, individual variations in time taken to complete each stage start accumulating in the population. Hence, as the population moves from one stage to another and from one generation to another, the availability period of each succeeding stage increases continuously (availability period of a stage is the time for which the population contains individuals representing that stage within a generation). Simultaneously, it would increase over-

lap between the availability periods of successive stages, which cannot be noticed after the point when generations lose their discreteness and become continuous. Therefore, if DG is to be the norm in the moth, periodic constraints should reduce the availability period of at least one of the stages from what would be expected in the absence of the constraint. The extent of reduction should be such that the mean availability dates of any two successive stages remain distinct. In situations where data on temporal variation in the density of only one particular stage are available, the extent of reduction should be such that population peaks are distinct and separated by a distance of one generation time.

Among temperate insects, all but one stage are eliminated by the winter after every one or two generations, which drives discreteness in the following spring and summer generations. Lest all stages hibernate through the winter, populations should have continuous generations. Although the reason behind 'selection' favouring a particular stage to pass through the winter is not understood, its effects on the population are commonsensical – reduction in population size and production of discrete generations. Together, they might enhance opportunities for resource build-up (of, say, plants), because harvest cycles are intermittent when generations are discrete. This can have numerous repercussions in the temperate, where resources are limited. With this outlook, it could be of some worth to examine if natural selection favours DG in these insects, because, till date, it is expected to be a passive outcome of strong temperate seasonality.

In the case of aseasonal insects with DG, which is the focus of this note, the influence of seasons in regulating DG is ruled out. Hence, understanding the mechanisms that govern DG in these insects has been of considerable interest to population ecologists. It is thought that DG can be produced among aseasonal insects by the action of natural enemies^{1,5}, or by inter-stage interactions in the host population^{3,6-8}, or incidentally^{9,10}.

Natural-enemy hypothesis

Mathematical models have shown that a parasitoid with half or one-and-a-half times the host life cycle can bring about stable DG in the host populations^{1,5,11}. A rise in the host population can lead to a rise in the population of its parasitoids. If the parasitoid life cycle is half that of its host, parasitoids would emerge in large numbers half a host generation later, reduce host numbers and produce host troughs. A reduction in host numbers should lead to crashes in the parasitoid population, which would allow the host to build up once again. This pattern will produce peak numbers of the host separated by a time of one host generation. Here, the parasitoid would undergo alternating boom and bust cycles, and their peaks are also separated by one host generation. Similar pattern unfolds when the parasitoid life cycle is 1.5 times that of the host. But, when it is as long as the host (or twice or thrice and so on) or extremely small (<0.5 times the host life cycle), models reveal stable host-parasitoid interactions that dampen host peaks and produce continuous host generations. In order to promote discrete generations, it is also essential that there is moderate degree of density dependence in the natural enemy population, i.e. parasitization and host densities should not be linearly related; linearity accentuates stable host-parasitoid interactions and continuous generations. In addition, for discrete cycles to be generated, distribution of the parasitoid across the host patch should be such that hosts do not escape parasitization; continuous generations are promoted when aggregation increases in the parasitoid population. The parasitoid should occur in substantial numbers such that it can influence the age-structure of the host population; sporadic and rare ones would be of no consequence. And, the host should also occur in high densities; host peaks become indistinct when their numbers are low.

Here, it is crucial that the adult lifespan of the host and the parasitoid is only a small fraction of their respective life cy-

cles. In the models⁵, it has been assumed that adults live for less than half the time taken to complete their respective life cycles (2/9 and 2/5 for the host and parasitoid respectively). An increase in the reproductive lifespan of the hosts and the parasitoids has been shown to promote continuous generations. Consider a situation where the life cycle and adult longevity are the same. In the host, a female will lay her last egg when the first has completed its life cycle, thereby leading to complete overlap of all the developmental stages and continuous generations. In case of the parasitoid, adult periods as long as the life cycle will play against crashes in parasitoid population following host crashes, thus allowing the parasitoids to survive through the 'host dearth period'. In simple words, if the life cycle of the parasitoid is 0.5 times that of its host, equal adult longevity will put-off boom and bust cycles among parasitoids, dampen host peaks by promoting stable host-parasitoid interactions and result in continuous generations.

On the other hand, a parasitoid that follows host DG should tend to have longer adult periods. As parasitoids parasitize only a particular stage of the host, they face periods of dearth and abundance of the preferred host stage within each DG of their host. Such a situation might favour a short life cycle (to maximize the number of generations per host generation) and long adult periods (to survive through the host dearth period) among those that follow host DG. Therefore, such parasitoids may be viewed to be the consequence of adaptation to host

generation cycles, and, that they will be unable to contribute to host DG.

In the light of the above discussion, we verified total life cycle and adult longevity of the major parasitoids of *Opisina* and *Artona*. Both species are defoliators of coconut palms. *Opisina* in India^{12,13} and Sri Lanka¹⁴, and *Artona* in Indonesia¹⁵, frequently build large destructive populations. A time series shows that *Opisina* has five DG in a year, each lasting 65–75 days on an average⁴. Developmental period of *Artona* ranges from 33 to 36 days, while adults live for up to a week¹⁵.

Opisina and *Artona* serve as hosts for a variety of parasitoids. In a comprehensive study that recorded 19 DG of *Opisina*⁴, the major parasitoids were *Meteoridea hutsoni*, *Brachymeria* spp. and *Goniozus nephantidis*¹⁶. The remaining parasitoids did not contribute to parasitization of more than 5% of the host population at any time during any generation¹⁶. Interestingly, the major parasitoids have adult periods at least as long as their life cycle (Table 1). Even in case of *Artona*, none of the ten major parasitoids¹⁵ has an adult period that is shorter than its life cycle (Table 1). The life histories of the most frequently associated parasitoids of *Opisina* and *Artona* have life cycles that are shorter than that of their hosts, and adult periods that are at least as long as their life cycles, which suggests that the parasitoids might be following host DG; they might not contribute to host DG. The evidences can raise doubts on the natural-enemy hypothesis as an explanation for DG among *Opisina* and *Artona*, although the two species have been taken

as examples while explaining the natural-enemy hypothesis¹.

According to the models^{1,5}, parasitoids that produce host DG should themselves undergo short-term boom and bust cycles, which must be favoured only in strong dispersers that usually tend towards being sporadic. Therefore, such parasitoids may not produce stable host DG. Among persistent parasitoids, persistence should itself promote stable host-parasitoid interactions by strengthening the density dependence between the host and parasitoid, and result in continuous generations. Moreover, continuous availability of hosts should be constructive to the persistent parasitoids, especially when the host is aseasonal. The theory is based on simultaneous occurrence of several parameters in the parasitoid – 0.5 or 1.5 times the host life cycle coupled with short reproductive phase, non-aggregated distribution across its host patch, occurrence in high densities and moderate density dependence. Practically, it is extremely difficult for all the conditions to be consistently acting, such that stable host DG are produced; a let-off in any will promote continuous host generations. Factors like density and distribution can be extremely variable in the tropics as they are easily influenced by several other factors; they cannot be assumed to have a sustained influence on the host population. Moreover, the theory holds well when the host occurs in high densities, which adds volatility to the host-parasitoid relationship; relaxation of any condition governing the parasitoid responsible for host DG can have drastic effects on the host peaks and troughs. It

Table 1. Developmental time and maximum adult longevity of major parasitoids of *Opisina arenosella* and *Artona catoxantha*

Host	Parasitoid	Development time (days)	Maximum adult longevity (days)
<i>Opisina arenosella</i>	<i>Goniozus nephantidis</i> ²¹	11–14	65
	<i>Meteoridea hutsoni</i> ²²	21–24	21
	<i>Brachymeria</i> spp. ²¹	12–15	53
<i>Artona catoxantha</i> ¹⁵	<i>Apanteles artonae</i>	13–16	30
	<i>Neoplectrus bicarinatus</i>	12	88
	<i>N. maculatus</i>	12	88
	<i>Cadurcia leefmansi</i>	16–24	~21
	<i>Ptychomyia remota</i>	15–22	>21
	<i>Euplectromorpha viridiceps</i>	18–21	32
	<i>Goryphus inferus</i>	13–15	75
	<i>G. rufobasalis</i>	14–15	73
	<i>G. javanicus</i>	14–15	69
	<i>G. fasciatipennis</i>	Not available	72

is also a fact that the parasitoid theory demonstrates that parasitoids ‘can’ produce host DG; it has not been enquired whether they ‘should’ produce host DG. The only empirical evidence to sustain the parasitoid theory comes from a study on the salt marsh planthopper, *Prokelisia marginata*, whose generation cycles are apparently linked to its egg parasitoid, *Anagrus delicatus*². Here, the patterns in population dynamics of the host and the parasitoid agree with the prediction of a model; there is no direct proof that the parasitoid produces host DG. On the whole, it appears that there are reasons to distrust the natural enemy hypothesis as an explanation for DG among aseasonal insects.

Inter-stage competition hypothesis

DG can arise from inter-stage competitions provided individuals in the older age-cohort cannibalize younger ones in a manner that the younger age-cohort goes missing with certain periodicity^{3,6-8}. The situation is also associated with periods of resource crunch³. However, inter-stage competition leading to host DG may be applicable only in confined experimental set-ups, where the test insect shows pronounced cannibalism. Under field situations, it may be exaggerated to expect systematic mortality of younger larvae, such that the host has stable DG. Evidence supporting the theory comes from a study on the long-term population dynamics of *Epilachna vigintioctopunctata* in Indonesia³. Patterns obtained agree with the predictions of a model that host DG are driven by cannibalism of eggs and young grubs by individuals in older age-cohorts; yet again, there is no direct experimental support.

Except for a rare remark on cannibalism of eggs and young larvae by older larvae¹⁴, cannibalism has not been reported in *Opisina*, and has never been observed during several years of culturing at the Department of Entomology, University of Agricultural Sciences, Bangalore. Cannibalism has not been reported in *Artona* too¹⁵. Lack of cannibalism and presence of a perennial food source outrightly weakens the inter-stage competition theory. In the earlier described study involving *Opisina*⁴, there were no periods of resource crunch in any of the 19 DG. Additionally, resource exhaustion has been associated with adult dispersal, not cannibalism, in *Opisina* and *Artona*¹⁵.

Incidental factors like insecticide application can cause DG by removing the exposed stages of a population^{9,10}. However, as this is a temporary phenomenon, and, as DG in *Opisina* are reported from populations that were not treated with insecticides⁴, we have not considered this hypothesis for the present discussion. Overall, there are indications that the three existing hypotheses may not suffice to explain DG in *Opisina*.

Can there be other options?

We propose an indirect but simple method by which one can narrow down on the factor that might regulate DG in an aseasonal insect before verifying the same. The aim here is to identify the stage that is constrained, which would make it easy to identify the constraint afterwards. The aim would be consistent with the existing theories because a parasitoid parasitizes a particular stage of the host, and, cannibalism eliminates only a particular age-cohort.

Stable DG are brought about among aseasonal insects when at least one stage in the life cycle is constrained at a certain periodicity, such that availability period of the succeeding stage is reduced. In a simple case let the life cycle, for convenience, be divided into stages of approximately equal durations, individual variation in the time taken to complete each stage be allowed to accumulate in the population, and a particular stage be constrained to produce DG. Here, the availability period of the stage that succeeds the one that is constrained would be the shortest and the availability period of each subsequent stage would be greater than the one previous to it, with the constrained stage having the maximum. The constraint should have a definite periodicity in its occurrence for generating DG. In an actual situation, data on the availability periods of different stages can be recorded through periodic observations and corrected for the difference in the developmental durations between different stages before identifying the stage that is constrained.

We carried out this exercise by re-analysing a published dataset on the age-structure and population density (of egg, early-, mid- and late-larval and pupal stages) of two spatially segregated populations of *Opisina*⁴. The parameters were recorded at fortnightly intervals for a pe-

riod of two years, and data were available for 19 complete generations (the first few samples in one of the locations belonged to an incomplete generation, and hence were not considered; the original article⁴ may be referred to for further details). Here, the number of sample points that contained a particular stage of the insect was averaged over 19 generations and weighted by dividing it by the developmental time of that stage. The resultant is simply called as ‘availability value’. For example, pupae figured in 36 samples and pupae take ~10 days to complete their life cycle, therefore its availability value would be 0.19. Following this method the values for egg, early-, mid-, and late-larval stages are 0.15, 0.14, 0.16 and 0.23 respectively. (Early-, mid- and late-larval stages take approximately 15, 15 and 10 days respectively, for development¹⁷. Table 2 provides the time taken by an individual to complete each stage of its life cycle.) Data on the moth availability period were obtained from another study¹⁸ that traced the emergence and activity periods of moths all through a generation, around the same area where the previous study⁴ was conducted. The moth availability period (35 days)¹⁸ was weighted by its longevity (~9 days) and divided by the sampling interval of the earlier mentioned study⁴ (15 days), in order to make the availability value for moths (0.26) comparable with those of other stages.

There is a clear trend of increase in availability values from egg to moth stage, which suggests that moths are available for the longest duration and the early stages are available for the shortest dura-

Table 2. Number of days taken by an individual to complete each stage of its life cycle [Individuals of *Opisina* were reared at $26 \pm 1^\circ\text{C}$ for two generations; data presented here are the average of 188 individuals that completed their second generation¹⁸.]

Stage	Number of days taken by an individual to complete a stage	
Egg		7.54 \pm 0.77
Larva	Male	37.08 \pm 3.55
	Female	40.50 \pm 3.18
Pupa	Male	10.12 \pm 1.23
	Female	10.82 \pm 1.21
Moth	Male	8.63 \pm 1.84
	Female	8.16 \pm 1.49

tion. If our proposition is correct, then the probability of moths being the constrained stage is high. This is possible because *Opisina* has been recently demonstrated to exhibit protandry¹⁸, and protandry can prevent females that arrive towards the later part of the flight period from contributing to the next generation^{19,20}. This can reduce the availability period for eggs from what it would be if females emerging throughout the flight period were to successfully oviposit. If protandry is a norm in the insect, and the theory on risk to the last arriving females is correct, it may be worthwhile to examine if protandry could generate stable DG in *Opisina*. Indeed, if the moth stage is the one that is consistently constrained to generate DG in *Opisina*, the natural enemy and inter-stage competition hypotheses get disregarded, as moths are neither killed by parasitoids nor cannibalized. Further, it suggests that DG need not be mediated by factors like density, food or natural enemy. Further exploration can yield interesting dividends.

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*Y. B. Srinivasa** is in the Institute of Wood Science and Technology, P.O. Malleswaram, Bangalore 560 003, India; *K. Muralimohan†* was in the Department of Agricultural Entomology, University of Agricultural Sciences, GKVK, Bangalore 560 065 India; †Present address: *Monsanto India Ltd, 5th Floor, Ahura Centre, 96, Mahakali Cave Road, Andheri East, Mumbai 400 093, India.*
*e-mail: ybsrinivasa@gmail.com