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Pace of life of insect natural enemies

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Abstract. Analyses of data from the literature clearly indicate that the developmental rates of insect natural enemies that feed on aphids and coccids differ and reflect that of their prey. An attempt to factor out the various confounding factors has been criticized as facile. Here it is argued that as the rates of development of both parasitoids and predators that feed on aphids and coccids differ similarly, and the most likely process underlying this pattern is the same, the evidence for the rates being adaptive rather than phylogenetically constrained is too strong to be ignored.

Key words. Aphids, coccids, constraints, foraging behaviour, natural enemies, pace of life.

INTRODUCTION

Detailed analyses of the rates of development at different temperatures of aphid and coccid eating ladybirds indicate that the difference in their rate of development is not due to differences in body size, nor food quality, lower temperature thresholds for development or a phylogenetic constraint, but in the number of day degrees they require to complete their development, which in the case of coccid eating ladybirds is 3 times greater than that required by similar sized aphid eating ladybirds (Dixon et al. 2013). Studies on *Drosophila* and fish indicate that the rate of development in these organisms is genetically controlled (Cruz do Nascimento et al. 2002, Devlin et al. 1994, 2001). Therefore it is subject to selection. The only study on the effect of artificial selection on life-history traits of ladybirds was done in an attempt to breed *Hippodamia convergens* with shorter developmental times in order to facilitate their production for biological control. After five generations of selection the developmental time was reduced by 18%, and no associated effects on adult weight, fecundity or longevity were recorded (Rodriquez-Saonia & Miller 1995). The implication of this is that the reason why coccid eating ladybirds do not develop as fast as aphid eating ladybirds, which appear to be at the upper bound of the rate of development in ladybirds (Dixon 2000) is the former have been selected to develop slowly.

A likely explanation for this is that it is advantageous for coccid eating ladybirds to forage and consequently develop more slowly than aphid eating ladybirds (Dixon et al. 2011). It is suggested in the latest general book on the ecology and behaviour of ladybirds, however, that the above conclusions have been too facilely drawn (Hodek et al. 2012). It is risky to generalize, especially as in this case the data is seriously limited in terms of its coverage of the various tribes of ladybirds and there is little that I can do about it other than encourage others to work on ladybirds belonging to other tribes and so broaden the data base. Nevertheless, simplifying complex situations and identifying patterns, even though weakly supported, hopefully serves to provoke others to attempt to refute them.

In support of the above generalization, although the marked differences in the pace of life of these two groups of ladybirds differ from the size dependent metabolically determined rate of development well documented for mammals, it is similar to that recorded for closely related similar sized mammals that have different "life styles". This variation in the tempo of life around the primary axis of the fast-slow continuum associated with body size is accounted for in terms of mortality patterns, particularly juvenile mortality, with high mortality rates resulting in the evolution of species with fast rates of development and low mortality rates with slow rates of development.

That is, there is a trade-off between reproduction and survival, which is well supported by empirical data. The assumption is that achieving a high rate of growth is easiest when resources are abundant and in such circumstances species with high rates of reproduction should be favoured (Sibly & Brown 2007, Dobson 2007). Ectothermic animals, especially insects, have been less well studied in this respect. Interestingly aphid eating ladybirds show all the features of species exploiting an abundant resource: fast development, high reproductive rate and short adult life, whereas the coccid eating ladybirds have the features of species exploiting a scarce resource: slow development, low reproductive rate and long adult life. However, if length of adult life is measured by the rate of senescence, rather than its duration, then the overall pace of life of aphid feeding ladybirds is fast, even in terms of mortality, whereas that of coccid feeding species is slow. This leads one to question the assumption that this difference in pace of life is a consequence of a trade-off between reproduction and survival (Dixon 2000).

Not only do coccids develop more slowly, they are less common and occur in smaller and less compact colonies than aphids (Borges et al. 2006, 2011, Dixon 2000). Therefore, the expectation is that a ladybird that is a specialist predator of coccids is likely to experience periods of starvation more frequently than those that specialize on aphids. Coccid eating ladybirds are generally more difficult to rear and experiment with than aphid eating species. Interestingly however, ladybirds, like some other insects, show growth polymorphism (Schönrogge et al. 2000, Thomas et al. 1998, Mishra & Omkar 2012) in which the sibling larvae of at least a few species of aphid eating ladybirds develop at different rates and by the end of the third instar it is possible to identify those that will continue to develop fast or slow (Dixon et al. 2015).

Although the prey of aphid eating ladybirds is usually abundant, especially when they are laying eggs, and also there is a tendency for the colonies of aphids they attack initially to increase in size, this is not always the case, and the older larval stages can experience a severe shortage of food that can result in high levels of cannibalism and intra-guild predation. As size is a major determinant of the outcome of an interaction between these predators it is clearly advantageous for them to grow and develop as fast as possible while aphids are abundant, which initially puts them at an advantage when food becomes scarce. However, although in general aphid colonies are ephemeral and initially increase in size this is not always the case and so it may be advantageous if the offspring of ladybirds differ in their ability to survive periods when food is scarce. When food is abundant all the larvae are equally likely to survive, but when scarce it is those that develop slowly that are most likely to survive. Therefore, in the case of coccid eating ladybirds the general scarcity and low productivity of their prey might mean it is advantageous for these ladybirds to develop slowly.

The data on ladybirds strongly indicate that the pace of life of coccid eating species is generally slower than that of aphid eating species and that a similar phenomenon, "growth polymorphism", occurs within at least some species of aphid eating ladybirds. The basis for this generalization, however, has been challenged and to strengthen or refute it requires the collection of information on other tribes of ladybirds and more importantly other groups of natural enemies, and to address the evolutionary question: why?

Growth polymorphism

The frequency distribution of the duration of development recorded for larvae that hatched from batches of eggs laid by young adults of *Adalia bipunctata* and reared under similar conditions is unimodal (Dixon et al. 2015). It is, however unknown to what extent the ratio of fast to slow developers is dependent on rearing conditions, mode of inheritance and whether the mothers, based on their experience, can influence the ratio. As it is possible to select ladybirds for faster development (Rodriquez-Saonia & Miller 1995) it is likely that these differences in the rate of development are inherited. In this context it would be interesting to know whether the ratio differs, and the extent to which it differs between species, and whether the differences are associated with the population dynamics and/or structure of the particular aphid colonies that the different ladybirds attack. Interestingly the unimodal distribution recorded by Dixon et al. (2015) is skewed to the left indicating there are proportionally more fast than slow developers, which is what one would expect if most of the colonies of aphids in which this species of ladybird lays its eggs thrive, whereas if they lay their eggs generally in colonies in which the aphids do not become abundant then the expectation is that the distribution would be skewed to the right. Generalizing, based on the little information we have for aphid eating ladybirds, the expectation is that the frequency distributions for aphid eating species are likely to be skewed to the left and those for coccid eating species skewed to the right, because as stated above their prey are generally less common and occur in smaller and less compact colonies than aphids, which implies that their larvae are more likely to experience periods of food shortage.

The ability of larvae that develop at different rates to survive periods of food shortage has been tested using larvae of aphid eating ladybirds. Surprizingly, the percentages of fast and slow developing fourth instar larvae that survive when fed 0.5, 1 or an excess of aphids per day do not differ (Dixon et al. 2015). Like the larvae of *Cheilomenes sexmaculatus* and *Propylea dissecta* (Mishra & Omkar 2012) the slow developing larvae of both sexes of *Adalia bipunctata* take longer to complete their development than the fast developing larvae when fed 1 or an excess of aphids per day (Dixon et al. 2015). Although the weights of the fast and slow developing fourth instar larvae differ at the beginning of the instar they do not differ in weight at the end of this instar when fed 1 aphid per day, and the slow developers achieve 90% of the weight of the fast developers when fed an excess of aphids each day.

That is, during the course of the fourth instar the slow developing larvae, in spite of their lower body weight at the beginning of this instar, can either achieve the same final weight or they nearly do so. During the fourth instar the male larvae of both fast and slow developing strains consume the same amount, whereas the females of the fast developing strain consume more aphids than the slow developing larvae. There is no difference in the adult weight of the fast and slow individuals when as fourth instar larvae they are reared on 1 aphid per day. However, when reared on an excess of aphids per day the adult weights of the fast developing individuals are greater than those of the slow developing individuals. Developing slowly when food supply is restricted therefore, does not appear to be costly in terms of adult weight/ fecundity (Stewart et al. 1991). When food is abundant however, there are costs associated with developing slowly: they develop into small adults. This brings one back to the ratio of fast to slow developers. If food is always abundant then developing slowly is disadvantageous but when food is scarce slow development does not appear to be advantageous or disadvantageous.

There are also marked differences in the time for which the slow and fast developing larvae can survive when fed 0.5 aphids/day, with the fast developing larvae surviving for 9.8 ± 0.5 days and slow developing larvae 17±1.3 days. That is, when food is scarce and larvae are starving slow developing fourth instar larvae can survive on little food on average for nearly twice as long as fast developing larvae.

These results indicate that the advantage of developing slowly when prey is very scarce is that the larvae are able to survive and remain active for longer than fast developing larvae. This would put slow developing larvae at an advantage over fast developing larvae, which as a consequence are likely to eat the moribund fast developing larvae, and/or in surviving for longer are more likely to find the few but now increasing numbers of aphids and so survive to the adult stage. That is, this result provides support for the hypothesis that it is advantageous to develop slowly in those cases when in the latter stages of the existence of an aphid colony prey is extremely scarce. Extrapolating these results to coccid eating ladybirds the general scarcity and low productivity of their prey might mean it is advantageous for all the individuals of these ladybirds to develop slowly and disadvantageous for them to develop fast.

Predator productivity

A model has been developed to determine the optimum rate of development of a predator. In this model the rate of increase in predator biomass is maximized by changing the rate at which the body size of the predator increases. If one assumes that it is increase in predator biomass that is maximized then the model indicates that the optimum growth rate of a predator depends on that of its prey (Dixon et al. 2015).

PARASITOIDS

In addition to ladybirds there are several other groups of predatory and parasitic insects that attack both aphids and coccids. For a better understanding of the pronounced difference in the pace of life of ladybirds attacking aphids and coccids it is important to know whether other insect natural enemies also show similar differences in their pace of life. The analysis of the rate of development of parasitoids of aphids and coccids reveals that the same overall pattern as is well documented for ladybirds also occurs in parasitoids, with those attacking aphids developing much faster than those attacking coccids. In this case, however, it is not currently possible to factor out completely the effect of phylogeny in determining the difference recorded in their rates of development. This is mainly because of the small size of the data set and lack of information on the relatedness of the genera for which there is data, or, put another way how phylogenetically robust is the family Aphelinidae and to what extent do the genera in this family differ phylogenetically. Although limited, the data for parasitoids is generally supportive of the hypothesis that we are dealing with a general phenomenon rather than one restricted to ladybirds (Dixon & Honěk 2014).

The challenge now is not only to obtain more data on parasitoids but also on the other groups of insects that feed on both aphids and coccids, and for other insect predators that feed on prey with very different rates of development. The above study on parasitoids also provides an insight into to why the rate of development of predators is so closely related to that of their prey and supports the prediction of the model developed for predators (Dixon et al. 2015). In this particular case the parasitoid lays an egg inside a young host, which continues to develop, and the parasitoid larva completes its development within the body of that individual host. The well-defined nature of this interaction provides strong evidence that the speed of development of the parasitoid larva relative to that of the host individual is critical in determining the maximum size it can achieve. If the larva developed faster it would quickly over exploit the food supply resulting in it developing into a smaller adult. If a host develops slowly then the parasitoid larva must also develop correspondingly slower than those that develop in fast developing hosts. That is, foraging in this case involves optimizing the trade-off between rate of development and adult size, which determines their fitness. In the case of predators the problem is similar but they have to pursue and catch not one but many individuals and their availability in terms of biomass and the time for which they are available is determined by the speed with which they develop.

CONCLUSIONS

There is no doubt that the insect natural enemies studied that feed on aphids develop faster than those that feed on coccids and this reflects the rate of development of their prey. In addition, there is good evidence that the rate of development is genetically determined and therefore subject to selection. This implies that the rates of development recorded are optimum in terms of the fitness of these particular natural enemies. Currently our understanding of the extent to which life history traits are evolutionarily or phylogenetically conserved is still very rudimentary. The expectation, however, is that future studies, particularly on other groups of natural enemies of aphids and coccids, will provide the information that will enable us to compare the degree to which each life history trait is evolutionarily and phylogenetically conserved.

The argument for evolutionarily conserved rates of development is based on data from the literature for species of *Nephus* and *Scymnus* which each feed exclusively on aphids and coccids, respectively, and belong to a robust tribe of ladybirds, the Scymnini (Dixon 2000), and in the case of the parasitoids species belonging to one family (Dixon & Honěk 2014). The fact that both parasitoids and ladybirds show the same pattern in terms of their rates of development is strong support for the concept that those natural enemies that feed on aphids are all likely to develop faster than those that feed on coccids. Further support comes from the fact that the most likely process underlying this pattern is the same: the optimization of their growth rate. In summary, the evidence for the rates of development of aphidophagous and coccidophagous being adaptive rather than phylogentically constrained is too strong to be ignored.

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