WAY OF LIFE OF APHID EATING LADYBIRDS

ANTHONY F. G. DIXON[1],* AND JEAN-LOUIS HEMPTINNE[2]

[1] School of Biological Sciences, University of East Anglia, Norwich, UK
[2] Laboratoire Évolution and Diversité Biologique, Université de Toulouse, Toulouse, France
* Corresponding author: a.f.dixon@uea.ac.uk

ABSTRACT

Ladybirds have attracted attention from ancient times and continue to do so. There appears to be three phases in the way ladybirds have been viewed over time, which can be represented in the form of models.

Keywords: aphids; ladybirds

Model 1 Reverence

This model of the population dynamics of ladybirds resulted from our ancestors in ancient times revering ladybirds. Like rats in the orient, ladybirds were associated with an abundance of food. In the case of ladybirds, it is an indirect association with an abundance of food as ladybirds attack aphids infesting crops. Due to the short period for which colonies of aphids last and the delay in the response of the ladybirds to aphids it looks as if they cause the decline in the abundance of aphids, particularly those on crops, and the commonest species of ladybird is most likely to have been a predominantly red species (*Coccinella septempunctata*), which resulted in them being called "birds of our Lady" or the equivalent in other western countries. This thinking retarded the development of ladybird ecology and possibly continues to do so, as they are "flagship" species for organic produce.

This is a classic case of confusing cause and effect. At that time there was also no appreciation that ladybirds belong to a very large group of insects (Coccinellidae) and are not all conspicuously coloured red, in spite of the name of this group, or feed on aphids. It is also the case that currently little or nothing is known about most of the more than 6,000 species described worldwide. Just like the unsolved problem in physics, Dark Matter, this lack of knowledge is discerned by its magnitude, which indicates there is far more for us to learn about ladybirds than currently known.

Model 2 Realization

This model is based on an increase in understanding of ladybird ecology, which came with the realization that for ladybirds, like all other insects, selection favours the fittest and therefore the population dynamics of their prey is likely to be important. Aphid reproduction is very dependent on the quality of plants as a source of food, which is very variable in space and time, with the time for which it is available very short, which results in aphid colonies developing very quickly and then rapidly decreasing in abundance, even in the absence of natural enemies, which is referred to as boom and bust or patch dynamics. Appreciation of this resulted in the "egg window" concept (references in Dixon 2000), which is the phenomenon by which ladybirds lay their eggs at a time during the development of an aphid colony such that there is sufficient time for their larvae to complete their development before the aphids disappear. That adult ladybirds differ greatly in size, which affects the area they can forage and the number of aphids they need to consume per unit time to be able to mature eggs, with the egg window being later in the increase of aphids for large than small ladybirds, which enables two species of ladybirds to exploit a colony (Dixon 2007). These studies clearly reveal that it is the abundance of aphids that determines the abundance of aphid eating ladybirds not vice versa. However, for coccid eating ladybirds there is a classical biological control success in the form of *Rodolia cardinals* that needs to be considered as its introduction into California resulted in a great reduction in the abundance of the scale insect (*Iceryia purchasi*) that severely reduced the yield of citrus there. The difference between the aphid and coccid eating ladybirds is that the former develops more slowly than their prey, whereas the latter develop much faster. This led to the development of the generation time ratio (GTR) concept that states that natural enemies that develop faster than their prey are more likely to control their abundance than those that develop more slowly, which has considerable empirical and theoretical support in terms of its consequence for their fitness (references in Dixon 2000).

Model 3 Reductionism

This model of ladybird population dynamics involved a dramatic shift from studying individual species to considering the patterns and processes shaping the way of life of aphid eating ladybirds in general. That is, adopting a reductionist approach. Although, there was a tendency in the

past to study mainly the few that feed on aphids on crops, because it was easier to obtain the necessary funding, nevertheless Hemptinne et al. (2021), were able over a period of 30 years to study many more species of ladybirds and establish a phylogeny for them, which enabled a more critical analysis of ladybird life histories. This revealed that biomass production is fundamental for understanding the ecology of these ladybirds. The exponent for the relationship between egg mass and adult mass for 45 species is 0.7137 (SE 0.0532) (Hemptinne et al. 2021), which is close to the 0.768 predicted by metabolic theory (Brown et al. 2004). Biomass production in their case, however, is for a very wide variety of eukaryotes with markedly different life histories, which differ greatly in shape and in biomass by more than 20 orders of magnitude. There is also a lot of scatter around this relationship, whereas the relationship for the investment in biomass production in ladybirds is for a group of ladybirds the mass of which differs by only one order of magnitude and they all have a similar hemispherical shape. More importantly, the relationship between biomass production in terms of ovariole number × egg mass and adult mass, a widely used measure of biomass production (Church et al. 2021), for the same 45 species of ladybirds has an exponent of 1.1943 (SE 0.0428), which is not less than 1, which is also the value reported earlier by Stewart et al. (1991) based on considerably fewer species. That is, the pattern in the relationship between log biomass production and log adult mass for ladybirds does not conform with that predicted by metabolic theory. Thus, it is important to determine the process(es) that underly the relationships between adult mass, egg mass and reproductive investment, which are fundamental components of their life history strategies.

Studies on *Coccinella septempunctata*, *Harmonia axyridis* and *Harmonia dimidiata*, indicate that the duration of the egg stage might be a constraining factor if predation on eggs is an important determinant of the interspecific decrease in egg size with increase in adult size (negative allometry) in this group of insects (Hironori and Katsuhiro 1997; Agarwala and Dixon 2017). Although there are very few life tables for ladybirds, they support the above in that the percentage loss of eggs is much higher than that of early stage larvae (e.g. Dixon 2000, Fig. 6.1). The recent paper by Church et al. (2021) supports the above implication that there is a negative relationship between egg size and ovariole number for a very wide range of insects. Unfortunately, they do not consider biomass production other than to state that ovariole number × egg mass is often used as a measure of biomass production.

The results in the papers of Agarwala and Dixon (2017) and Osawa and Ohashi (2008) indicate that the eggs of big species take longer to hatch than those of small species. This is confirmed by the results for *Coccinella septempunctata* and *Harmonia dimidiata*, but more importantly it is not proportionally so. Assuming cell size is the same in all ladybirds and that cell division during incubation occurs at regular intervals, starting with 1 then 2-4-8-16 cells etc., it is clear egg hatch time cannot be proportional to egg weight with large eggs taking less time to hatch per unit weight than small eggs.

Clearly if larvae are relatively small at hatching then they will take longer to reach maturity, which will again increase the risk of cannibalism or predation. There is some empirical support for a longer development time for such larvae in Stewart et al. (1991), but it is mainly based on the literature and although the conditions are likely to have differed slightly in terms of temperature, as they were all recorded close to 20 °C, in terms of food quality and availability they are likely to have differed.

It is also important to consider, like Sloggett and Matthias (2008), what the reserves in ladybird eggs are used for, which could account for some of the variation in the relationship between egg mass and adult mass. Ferrer et al. (2016) report that hatchling larvae of *Adalia decempunctata* survive for longer without food than those that hatch from similar sized *Adalia bipunctata* eggs, which implies the fat reserves in the eggs of the former are greater than in those of the latter. It is also likely that the proportion of the protein reserves in an egg needed for producing the cuticle of a small hatchling is likely to be more than for a large hatchling. In addition, the ovarian dynamics of the above two species differ in their response to starvation in terms of the resorption of oocytes and resumption of oogenesis when fed, which is faster in the generalist (*A. bipunctata*) than the specialist (*A. decempunctata*) (Ferrer et al. 2010). In addition, there are ladybirds, like *Harmonia axyridis*, which unlike most other ladybirds that lay their eggs prior to peaks in aphid abundance (egg window references in Dixon 2000), appear to synchronize their attack with peaks in aphid abundance (Hironori and Katsuhiro 1997) and act as top predators by exploiting aphids that will shortly rapidly decline in abundance and also the abundant immature stages of other insect predators (Dixon 2000). Thus, the scatter around the relationship between egg mass and adult mass is likely to reflect differences in the life-history strategies of the species.

An interesting and puzzling feature of aphid eating ladybirds is the distribution of their sizes, which for British species is strongly biased towards small species. Those in the size range 2–4 mm make up 70%, 4–5 mm 18% and 7–8 mm 12%. Aphid colonies can be exploited at different times by species of ladybirds of different sizes, first small and then large species. Theory based on the geometry and physiology of ladybirds predicts that a 35 mg ladybird requires 1.5 times more aphids per unit area for oviposition than a 10 mg ladybird (Dixon 2007). This and other predictions in that paper were tested experimentally in cereal fields (Honěk et al. 2008a,b). Adult females of both *Coccinella septempunctata* (dry mass 15.4 mg) and *Propylea quatuordecimpunctata* (dry mass 3.7 mg) were collected at 2–5-day intervals up to the peak in abundance of cereal aphids. These beetles were kept unfed for 24 hours and the number of eggs laid recorded. Both species colonized

the cereal crop simultaneously in the middle of May. As predicted the small *P. quatordecimpuctata* produced proportionally more eggs during the early stages of the aphid infestation, when aphid numbers were still low, than *C. septempunctata*, their investments in reproduction were very similar (ca. 12%) and the larger of these two species laid more eggs per day than the small species.

The preponderance of small species of ladybirds reflect that of the size distribution of aphids, which is right skewed on a logarithmic axis (Dixon 1998; Figs 10.13 and 10.14) and most of the small species of aphids form small colonies on small plants, many of which are annuals that have low carrying capacities. The bigger species live on perennial woody plants in which the depth of the phloem is generally much deeper than in herbaceous plants and because of the way aphids reach the phloem only large species have long enough stylets to reach such depths. The largest British aphid, *Stomaphis quercus* (length 7 mm) feeds on the trunks of oak trees and has a proboscis twice the length of its body, which when not feeding is inverted within its body (Dixon 1998; Figs 4.6 and 4.7). If disturbed, this aphid cannot immediately withdraw its stylets like small species and can take up to 40 minutes, therefore, it is not surprizing that it is pugnaciously defended by wood ants. In addition, the hairs on the leaves of plants, which hinder the movement of small larvae, can also be hook like or produce sticky substances that can ensnare foraging insects. That is, in addition to the ability of aphids to defend themselves by dropping from a plant, kicking and waxing predators, and their great variability in terms of their quality as food, even to the extent of being toxic and that some are even defended by ants (Dixon 1958), aphids occupy a very complex and inhospitable environment for insect predators. It is likely that ladybirds have each adapted to a particular part of this complex environment, which could account for their size distribution being similar to that of their prey. In addition, there are very few specialist ladybirds and the only evidence available is that they are more likely to be habitat than aphid specialists (Ferrer et al. 2016).

In spite of the paucity of information on the ecology of many ladybirds, especially the smallest species, one can ponder on whether there are any advantages in being small or large. Being small not only enables them to attack patches of aphids early in their development but may also enable them to exploit aphids even when they are relatively uncommon or only produce small colonies. Large species, on the other hand, could be at a disadvantage when aphids are generally uncommon, but when abundant they can more effectively exploit the more numerous very large patches of aphids because they can lay more eggs per unit time than small species. Thus, small ladybirds should vary less in abundance and size from year to year than large species. There is some empirical support for the first prediction, as *C. septempunctata* is more frequently recorded in plague numbers than the smaller *A. bipunctata* (Majerus and Majerus 1996). How-ever, in terms of generality this needs to be confirmed for other large ladybirds and that it is not a consequence of them being more conspicuous. In addition, ladybirds are assumed to live for only one year, but it is reported that some individuals of *Harmonia axyridis*, a relatively large species, can live and oviposit for up to three years (Hodek and Honěk 1996). Thus, it would be interesting to know whether length of life in ladybirds is associated with size.

Reductionism has provided a broader understanding and identified some trends, most importantly that the negative allometric relationship between adult size and egg size is a consequence of their similar hemispherical morphology and the relationship between egg size and ovariole number. That is, because of their very similar morphology, their development is similar, which has been a major factor in shaping their way of life.

Resolution

It is now time to address the fact that little or nothing is known about most of the more than 6,000 species of ladybirds, which clearly indicates there is lot more to learn about ladybirds. For this it might be helpful to ask are there any lessons to be learnt from the studies carried out over the last 60 years? Firstly, predictions based on studies on a few species should not be dismissed as history indicates there is a high probability that they are worthy of serious consideration. Secondly, as incontestably expressed in the motto of The Royal Society "Nullius in verba" predictions need to be tested experimentally and in the case of ladybirds preferably in the field and "physics envy" should not inhibit biologists from doing experiments and developing models the predictions of which can be tested.

Thirdly, very little is known about the ecology of the smallest ladybirds that make up the vast majority of the predatory ladybird fauna. In particular a lack of information about the ecology of their prey, survival of their immature stages in general and ecology of top predators greatly hinders a better understanding of predatory ladybird ecology. The expectation is the future will provide that understanding.

Acknowledgements

REFERENCES

Agarwala BK, Dixon AFG (2017) Negative allometry for egg size in ladybeetles (Coleoptera: Coccinellidae): Trade – off between egg hatch time and size. Curr Sci 113: 2350–2353.

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85: 1771–1789.

Church SH, de Medeiros AS, Donoughe S, Márquez Reyes NL, Extavour CG (2021) Repeated loss of variation in insect ovary morphology highlights the role of development in life history evolution. P Roy Soc Lond B Bio 288: 20210150. doi: 10.1098/rspb.2021.0150.

Dixon AFG (1958) The escape responses shown by certain Aphids to the presence of the coccinellid *Adalia decempunctata* (L.). Trans R Entomol Soc Lond 110: 319–334.

Dixon AFG (1998) Aphid Ecology: An optimization approach. Chapman and Hall, London, UK.

Dixon AFG (2000) Insect Predator – Prey Dynamics: Ladybird Beetles and Biological Control. Cambridge University Press, Cambridge, UK.

Dixon AFG (2007) Body size and resource partitioning in ladybirds. Popul Ecol 49: 45–50.

Ferrer A, Dixon AFG, Gibernau M, Hemptine J-L (2010) Ovarian dynamics and specialization in ladybirds. Ecol Entomol 35: 100–103.

Ferrer A, Dixon AFG, Hemptinne J-L (2016) Habitat or prey specialization in predatory ladybird beetles: a case study of two closely related species. J. Appl Entomol 140: 199–208.

Hemptinne J-L, Lecompte E, Sentis A, Dixon AFG, Magro A (2021) Prey life-history influences the evolution of egg mass and indirectly reproductive investment in a group of free-living insect predators. Ecol Evol. doi: 10.1002/ece3.8438.

Hironori Y, Katsuhiro S (1997) Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. Entomophaga 42: 153–163.

Hodek I, Honěk A (1996) Ecology of Coccinellidae. Kluwer Academic Publishers.

Honěk A, Dixon AFG, Martinkova Z (2008a) Body size and the temporal sequence in the reproductive activity of two species of aphidophagous coccinellids exploiting the same resource. Eur J Entomol 105: 421–425.

Honěk A, Dixon AFG, Martinkova Z (2008b) Body size, reproductive allocation, and maximum reproductive rate of two species of aphidophagous Coccinellidae exploiting the same resource. Entomol Exp Appl 127: 1–9.

Majerus MEN, Majerus TMO (1996) Ladybird population explosions. Br J Entomol Nat Hist 9: 65–76.

Osawa N, Ohashi K (2008) Sympatric coexistence of sibling species *Harmonia yedoensis* and *H. axyridis* (Coleopters: Coccinellidae) and the role of maternal investment through egg and sibling cannibalism. Eur J Entomol 105: 445–454.

Sloggett JJ, Matthias WL (2008) Egg composition and reproductive investment in aphidophagous ladybird beetles (Coccinellidae: Coccinellini): egg development and interspecific variation. Physiol Entomol 33: 200–208.

Stewart LA, Hemptinne J-L, Dixon AFG (1991) Reproductive tactics of ladybird beetles: relationships between egg size, ovariole number and developmental time. Funct Ecol 5: 380–385.