

A. F. G. Dixon, *Insect Predator–Prey Dynamics. Ladybird Beetles and Biological Control*

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Although ladybirds are currently perceived as harbingers of good tidings and much work has been done on their biology and their potential use in biological control, Dixon stresses the point that we still lack rigorous analyses of the dynamics of their interactions with prey species. According to him, the reason is that ladybirds are mainly regarded as a tool for reducing aphid numbers rather than “organisms attempting to maximise their fitness”.

With that idea in mind, the author produces a penetrating review of our knowledge on Coccinellidae based on the incredible amount of data he gathered during his whole career on that group and on a thorough analysis of the available literature. Following a synthesis of their basic biology, he debates size variation within and between species relating this to ways of maximizing their population rate of increase. He confirms that sexual size dimorphism is linked to differences in mating and reproductive constraints on males and females. Cocciphagous and aphidophagous ladybirds exhibit clear differences in development rate and fecundity. Aphidophagous ladybirds possess higher values of fecundity and more rapid developmental rates than cocciphagous ones, development of aphidophagous species being strongly influenced by temperature. Tradeoffs appear clearly between fecundity and longevity. According to Dixon, these differences between the two groups are not linked to differences in food quality of the prey but are determined by natural

selection. Coccids develop quite slowly compared to aphids and this is reflected in the dynamics of their predators. Surprisingly, most cases of successful bio-control programs using ladybirds were reported for coccidophagous beetles. This is paradoxical regarding predictions based on their population attributes but is probably owing to the high specificity of cocciphagous ladybirds. Dixon dedicates an important chapter to foraging behaviour, with a clear distinction between adults and larvae. For him, foraging behaviour provides the essential data needed in modelling prey-coccinellid interactions. It appears to be clear that prey abundances and presence of conspecifics are the main cues used by adults for their choice of oviposition. Larvae are much more constrained by choices made by their mothers. Cannibalism is a part of ladybird normal foraging behaviour. Field and laboratory data showed that cannibalism decreases when prey density increases. In that context, laying eggs in clusters as done by most aphidophagous species may be interpreted as a case of intrabrood altruism as cannibalism should increase the survival probability of some members of the brood.

Dixon stresses that most prey–predator theory and models were established using parasitoids but parasitoids have simpler life history than predators, which lead to oversimplification of current models. In parasitoids, only adult females are searching for hosts. In contrast, coccinellids also seek prey as juveniles. This increases the complexity of modelling as search rates and handling times vary with the stage of development. Moreover, in aphid–ladybird systems, prey has a shorter development time than predators. In consequence, optimum oviposition strategy is likely to be determined by expectation of future prey abundances.

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This generation time ratio conditions the potentiality of suppressing the prey and explains many failures in biological control. Study on intraguild predation among Coccinellidae is limited by our poor knowledge of the preferred biotope, even of the commonest ladybirds. The main data available in the literature were obtained in the laboratory, in agrosystems or in anthropic systems. Most studies referred to additive vs. non-additive effects of predators in a biological control context. Non-additive and antagonist effects seem the rule but far more data need to be gathered on natural systems.

The last chapter is devoted to biological control. Dixon wonders why so few studies contributed directly to biological control programs and proposes to practitioners a list of desirable and easily measurable traits a biological control agent should have. He reports that on 155 attempts to control aphids using coccinellids,

only one succeeded, far less than the 53 successes to control coccids on 613 assays. He underlines however, that the use of ladybirds can result in conflict between conservationists and biological control practitioners, but this is far less controversial than the extensive use of pesticides. In his book, except for a paragraph on biological control of invasive species in nature reserves, Dixon hardly touches on conservation issues, and one would expect in such a book a more extensive review on newly invasive species such as *Harmonia axiridis*, or on the state of knowledge of coccinellids' roles in ecosystem functioning. This was obviously not the aim of the author, who mainly focuses on predator–prey relationships bringing together scattered data on models readily applicable in other situations. Dixon indeed concludes his book by saying that if the ideas developed therein prove to be general, there will be less need to record the fall of every apple.