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Reproductive behaviour and fitness trade-offs in the aphid parasitoid *Diaeretiella rapae* (Hymenoptera: Aphidiidae)

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Abstract

Parasitoids are fascinating insects that lay eggs in or on the body of their hosts where parasitic immatures grow and develop by exploiting the fixed resources available in a host. This study investigated host-parasitoid interaction between the cabbage aphid *Brevicoryne brassicae* and its parasitoid *Diaeretiella rapae*. The research explored the reproductive decisions made by *D. rapae*, and how these decisions affect its fitness and pest suppression ability.

The haplodiploid nature of reproduction in *D. rapae* imposes strongly contrasting outcomes of mating and oviposition decisions that directly affect population sex ratio. This study found that parasitoid fitness is the integral outcome of lifetime mating and oviposition behaviours. Poor host-parasitoid synchronisation was found in an uncontrolled/open system in spring in New Zealand; a low female/male ratio and a significant number of erroneous male-male mating pairs were detected in this D. rapae population. Adult emergence occurred only during the light period, with males emerging before females (protandry). Light triggered both mating and oviposition in D. rapae. Female D. rapae preferred to mate before oviposition, which allowed them to produce female-biased offspring. Females were found to allocate more time for choosing their mates whereas males were more active during mating and selected their mates quickly. Females mated once (monandrous), while males mated multiple times (polygamous) and became sperm depleted after their third mating. The monandrous and polygamous nature of D. rapae changed the female-biased sex ratio to a highly male-biased operational sex ratio, resulting in mating interference. Several factors including age, body size, mating status and previous mating experience affected mate selection behaviour in males and females. Female D. rapae emerged with developed eggs and did not require additional food to mature their eggs (autogenous), however, it took about two days for all their eggs to mature (weakly synovigenic). The nutrients acquired during the larval stage (by feeding on host resources) and during adult stage (by feeding on 10% honey solution) both affected individual fitness. Parasitoids lived longer after feeding on honey solution and this effect was more pronounced in females than in males. Female D. rapae fed on honey also carried their eggs longer without resorbing them. Females preferred to oviposit in larger hosts than in smaller ones, despite stronger defensive behaviour of the larger hosts. Females also preferred the larger hosts for ovipositing fertilised eggs that resulted in larger female offspring; the females that emerged from larger hosts lived longer and produced more offspring than those emegered from smaller hosts. Female oviposited multiple eggs per host (superparasitism) after repeatedly attacking their hosts. This resulted in two to eight parasitoid larvae developing in a host, but only one adult emerged from each (solitary parasitoid). Female *D. rapae* produced more female offspring when hosts were limited, and the number of males only increased when host density was higher. Females oviposited more unfertilised eggs when competing with conspecifics, which allowed them to conserve their fertilised eggs for future oviposition.

Thus, the study suggests that strong intrasexual competition and intersexual selection exist during mating and oviposition in *D. rapae*. This study provides comprehensive information on interactions between cabbage aphid and *D. rapae* which can be used to develop effective biological control programmes for cabbage aphid and other aphid species using *D. rapae* or other parasitoids. Release of honey-fed, mated and 1-day old females in early morning and on sunny days would be most effective and result in quicker suppression of aphid populations. Raising females in low competition situations with large size hosts (5-7 day old) could help in producing efficient and female-biased broods in insectaries.

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Preface

A thesis is presented on reproductive behaviour and fitness trade-offs in aphid parasitoid *Diaeretiella rapae* (Hymenoptera: Aphidiidae). The thesis is comprised of four main parts – General Introduction, experimental chapters (Chapters 1-13), General Discussion and Conclusions, and an Appendix (Appendices 1-3). The experimental work was carried out at Massey University, Palmerston North, New Zealand.

I am the author of each section and chapter, and the first author on published papers from this research. The co-authors of the published papers are my PhD supervisors. I designed the initial experiments, executed the experiments, analysed the results and discussed findings of each chapter. The supervisors gave their inputs in finalising the experiments, helping with statistical analyses, providing comments on the results, and reviewing the drafts in terms of language and clarity.

Various aspects of reproductive, mating and oviposition behaviour of *D*. *rapae* are presented in **Chapters 1-13**. Each Chapter is presented as a standalone paper with its own Introduction, Methods, Results, Discussion and References, and as a result, there is some repetition between the Chapters. The numbering of figures and tables restarts at the beginning of each Chapter.

The thesis begins with a **General Introduction**, which covers the background information and literature relevant to the species used in the research, as well as theories related to reproductive fitness and rationale for this research. **Chapter 1** investigates parasitism and mating strategies of *D. rapae* in a wild population (uncontrolled conditions), identifying some problems in oviposition and mating in *D. rapae*, for example, erroneous male-male mating. All other studies in this thesis were carried out in the laboratory at controlled temperature, humidity and light period. **Chapter 2** looks at the emergence pattern and diurnal variations in mating and oviposition activities of *D. rapae*. Sexual receptivity, courtship and mating behaviour of emerged adults are reported in **Chapter 3**. Sexual selection in *D. rapae* is studied in **Chapter 4**. The effect of multiple matings on sperm transfer and on the fitness of males and females is investigated in **Chapter 5**.

I looked into general biology and the importance of adult food availability for longevity and reproductive potential of *D. rapae* in **Chapter 6**. Since *D. rapae* is a haplodiploid species, a newly emerged female has a valid choice between ovipositing unmated or after mating. I investigated the fitness consequences of this choice in Chapter 7. Further, I examined the effects of age, and mating and oviposition delay on overall fitness of *D. rapae* in Chapter 8.

The general host searching, handling and oviposition behaviours of *D. rapae* are described in **Chapter 9**. **Chapters 10** and **11** investigate the preference–performance hypothesis in host selection, and the effect of host selection on reproductive fitness. Although *D. rapae* is a solitary parasitoid and only one adult emerges per host, the females can lay more than one egg per host (superparasitism). **Chapter 12** examines the consequences of superparasitism for fitness, and checks experimentally whether or not female *D. rapae* can discriminate between unparasitised and already parasitised hosts. The last **Chapter 13** deals with reproductive strategies of *D. rapae* females when they are competing for hosts and when more than one conspecific female are foraging together.

The findings from all the chapters are discussed in General Discussion and Conclusions in a broader context of reproductive fitness, biological control and evolution. The Appendix 1 includes phylogenetic work on *D. rapae*. Some additional information on superparasitism that could not be included in published paper (Chapter 12) is reported in Appendix 2. Abstracts of the full papers published in journals, or abstracts published in conference proceedings which arose from this research are given in Appendix 3.

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