FLORAL NECTAR AFFECTS LONGEVITY OF THE APHID PARASITOID *APHIDIUS ERVI* AND ITS HYPERPARASITOID *DENDROCERUS APHIDUM*

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ABSTRACT

In this study, the potential consequences of making a three- or four-trophic level system more complex by adding floral resources was studied in the laboratory for a range of plant nectar sources, the aphid parasitoid *Aphidius ervi* and its hyperparasitoid *Dendrocerus aphidum*. Parasitoids exposed to flowering buckwheat survived 4-5 times longer than those in the control (water only) and 3-4 times longer than those provided with phacelia, alyssum or coriander. Hyperarasitoids provided with buckwheat survived 5–6 times longer than those in the control and 3-5 times longer than those on the other flowering plants. Buckwheat, phacelia, alyssum and coriander can therefore enhance the 'fitness' of *A. ervi* without benefiting its aphid host, which does not feed on nectar. However, the 'fitness' of the hyperparasitoid may increase relatively more than that of the parasitoid, depending on the nectar source.

Keywords: biological control, longevity, *Acyrthosiphon pisum, Aphidius ervi, Dendrocerus aphidum, Phacelia tanacetifolia, Lobularia maritima, Coriandrum sativum,* floral nectars, resource subsidies, trophic cascades, trophic levels.

INTRODUCTION

Indirect interactions between populations of different species can be important in structuring natural communities. Such interactions are mediated either by changes in population densities or in the behaviour of species that are not directly connected. Such indirect effects are likely to have a major influence on structuring herbivore-parasitoid communities. When floral resources such as nectar are added to agro-ecosystems to enhance biological control (Gurr et al. 2004; Lavandero et al. 2005), the possible consequences of the addition of this resource on the 'antagonists' of the biological control agent are usually ignored. Potentially, a three-trophic level 'cascade' (Muller & Godfray 1999) can be disturbed by such an interaction.

It is not uncommon to have high rates of hyperparasitism in some insect communities (Volkl 1992; Holler et al. 1993; Hajek 2004). Despite this, it has been suggested that the overall impact of hyperparasitism on the population dynamics of aphids and their parasitoids is probably limited, due to the generally low fecundity of the hyperparasitoids (Mackauer & Volkl 1993). However, this fundamental aspect of insect community dynamics has largely been neglected (Comins & Hassell 1996). If floral resources provided to enhance parasitism, and therefore pest population suppression, improve the fitness of the parasitoid's own natural enemies, this would challenge some existing community-ecology theories (Hassell 2000), and impact on the theory and practice of conservation biological control (Gurr & Wratten 2000). There is preliminary evidence that floral resource subsidies (Tylanakis et al. 2004) may indeed favour the fourth trophic level, but information comes only from one empirical field-based study (Stephens et al. 1998). In that work, significantly higher numbers of parasitoids of a lacewing predator

were captured in yellow pan traps near an added nectar source, in that case flowering buckwheat, *Fagopyrum esculentum* (Moench), in an apple orchard.

A better understanding of how parasitoids and hyperparasitoids exploit floral subsidies will not only give important information about how life history-omnivory (Polis & Strong 1996) may influence community structure but can also assist in the design of more efficient biological control strategies via ecological engineering (Gurr et al. 2004).

Aphids are a valuable model system for testing ideas about community interactions (Muller & Godfray 1999). The aim of this work was to measure the effects of a range of plant nectars on the longevity of *Aphidius ervi* (Haliday) (Hymenoptera: Braconidae) and its hyperparasitoid, *Dendrocerus aphidum* (Rondani) (Hymenoptera: Megaspilidae) compared with water controls. *Aphidius ervi* is an endophagous parasitoid of various macrosiphine aphid species of economic importance, including the pea aphid (*Acyrthosiphon pisum*) (Harris) (Homoptera: Aphididae). *Dendrocerus aphidum* is an idiobiont ectoparasitoid: 'a parasitoid which prevents further development of its host'. The larva develops as a solitary hyperparasitoid on pre-pupal and pupal stages of aphidiine wasps and other hymenopteran parasitoids inside mummfied aphids (Walker & Cameron 1981).

MATERIALS AND METHODS

Insect rearing

Pea aphids were reared in the laboratory on potted plants of broad bean (*Vicia faba* L. cv. Cole's Dwarf). A clonal culture was started with one female aphid being confined on one leaflet using a clip cage as described by Noble (1958). When the first 5-8 progeny had been produced, the female was discarded to ensure that the progeny and future colony were clonal and free of parasitoids. The resulting progeny were reared on broad bean plants in Perspex cages (64×45×40 cm) with a nylon mesh door. The colony was maintained continuously as parthenogenetic females at 20±4°C and RH 60–70% with a photoperiod of 16:8 h light:dark. Light intensity was 122 µmol/m^2/s.

Aphid mummies were collected from lucerne fields, then put singly into 600 µl gelatine capsules and kept in a transparent polystyrene box (20×10×5 cm) under the above conditions. A mummy in this context is a dead aphid containing a parasitoid larva, pupa or adult and it usually has a papery texture. When parasitoids or hyperparasitoids emerged, they were identified using the keys of Mertins (1985). An *A. ervi* colony was established using 10 males and 10 females, which were presented with second-instar pea aphids. The culture was subsequently maintained under the same rearing conditions that were used for the aphids (see above).

A colony of *D. aphidum* was established from individuals (*A. ervi* or *A. eadyi* (Stary) (Hymenoptera: Braconidae)) emerging from parasitised pea aphids which had been collected as mummies from lucerne fields. Ten males and ten females of *D. aphidum* were reared on newly-formed mummies (containing aphid parasitoid pupae, which form approximately 9 days after oviposition by *A. ervi* (Walker & Cameron 1981)) and were maintained under the conditions described above. The identification of *A. ervi* and its parasitoids was confirmed by Dr J. Berry of Landcare Research, Auckland, New Zealand, in April 2004, and key identification characters were recorded for future reference.

Flowering plants as nectar sources

Phacelia (*Phacelia tanacetifolia* Bentham cv. Balo), buckwheat (cv. Katowase), alyssum (*Lobularia maritima* L. cv. Carpet of Snow) and coriander (*Coriandrum sativum* L. cv. Slowbolt) were assessed for their ability to enhance the fitness and efficacy of *A. ervi* and *D. aphidum.* Candidate plant species were grown in a greenhouse with 16:8 h light:dark and were sown at 2-week intervals to ensure that flowers were continuously available for laboratory experiments.

Experiment 1: Effect of flowers on *A. ervi* longevity

Selected flowering plant species were tested against a water control. For each treatment, a well-watered flowering, rooted shoot of the plant was utilised, to maximise quality and quantity of nectar available to the wasps. The flowering shoots were carefully inserted

into a transparent polycarbonate jar (120 mm tall and 85 mm in diameter) through a bottom opening, which was then sealed with foam around the shoot. The top of the jar was removed and covered with fine nylon mesh. The jar was attached to a vertical wooden stake fixed to the plant pot. A sealable small hole was cut into the wall of the jar to introduce parasitoids when required. Similar cages were used for water treatments with damp dental rolls provided on the mesh top of the cage. For each treatment and control there were seven replicates. A randomised block design was used.

One newly-emerged female and one male of *A. ervi* were used per cage. Longevity of the parasitoids was recorded for all treatments. The test was conducted at 20±4°C and 16:8 h light:dark. Survival was recorded every 24 h.

Experiment 2: Effect of flowers on *D. aphidum* longevity

The same flowering plant species, control and cage design as Experiment 1 were used. For each treatment and control there were seven replicates. A randomised block design was used (see above). One newly-emerged female and male *D. aphidum* were used per cage. Longevity of the hyperparasitoids was recorded for the treatments and control. Survival analysis was recorded every 24 h.

Data analysis

Survival analysis was used to compare the effect of the food resources on the longevity of *A. ervi* and *D. aphidum* by using a Kaplan-Meier estimate of the survival function (Lavandero et al. 2005).

RESULTS

Survival in the controls was 3-4 days for *A. ervi* females and 2-3 days for males. Survival with buckwheat was 12-20 and 8-16 days for females and males, respectively. For phacelia the equivalent data were 6-15 and 6-10 days, coriander 7-17 and 6-15 days and alyssum 7-16 and 5-14 days. Parasitoids exposed to buckwheat survived, on average, 4–5 times longer than those in the control and 3–4 times longer for the other flowering plants than the control. Survival curves differed significantly between treatments (log-rank=103.11, P<0.001; Wilcoxon (Breslow)=95.51, P<0.001; Tarone-Ware=99.52, P<0.001; Wilcoxon (Peto-Prentice)=95.03, P<0.001) (Fig. 1).

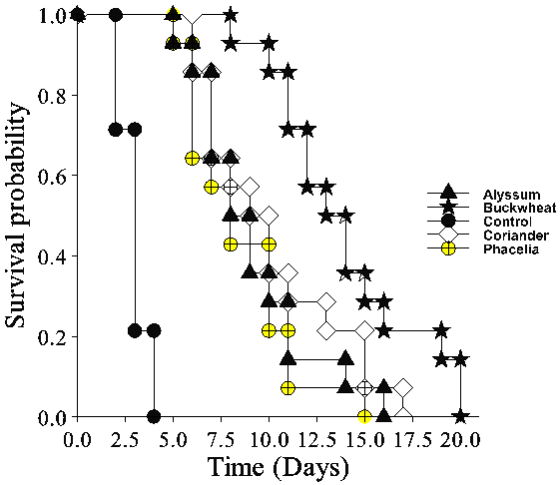

FIGURE 1: Kaplan-Meier estimates of survivorship functions of *A. ervi* given access to water (control), buckwheat, phacelia, coriander or alyssum as floral nectar sources.

Survival times of *D. aphidum* females ranged from 6-12 days and males from 5-10 days in controls, 23-57 and 25-55 days, respectively, with buckwheat, 24-41 and 18-48 days with phacelia, 16-48 and 17-37 days with coriander and 18-36 and 18-27 days with alyssum. Hyperparasitoids exposed to buckwheat survived, on average, 5–6 times longer than those in the control and 3-5 times longer for the other flowering plants than the control. Survival curves differed significantly between treatments (log-rank=127.66, P<0.001; Wilcoxon (Breslow)=112.33, P<0.001; Tarone-Ware=119.769, P<0.001; Wilcoxon (Peto-Prentice)=111.995, P<0.001) (Fig. 2).

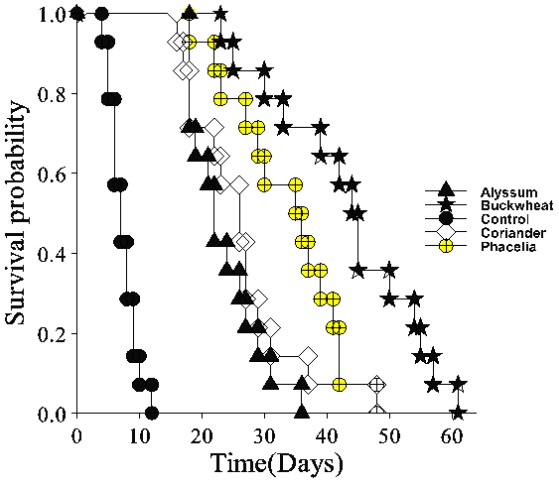

FIGURE 2: Kaplan-Meier estimates of survivorship functions of *D. aphidum* given access to water (control), buckwheat, phacelia, coriander or alyssum as floral nectar sources.

DISCUSSION

The relative complexity of a habitat is determined largely by the number of different structural elements per unit volume (Denno et al. 2002). If habitat complexity confers favourable microhabitats and refuges from predation for natural enemies, top-down effects on herbivores should increase, not only because natural enemies are more abundant but also because antagonistic interactions among them are reduced since complex-structured habitats provide refuges from intraguild predation. Indeed, there is evidence that the selective accumulation of natural enemies in complex habitats coupled with relaxed intra-guild predation intensifies top-down effects and promotes herbivore suppression (Thomas et al. 1991; Dobel & Denno 1994; Denno et al. 2002).

This study demonstrates the importance of flowering plants, as an example of enhancing habitat complexity, for parasitoid survival. Longevity was significantly enhanced by the tested flowering plants under laboratory conditions, indicating that the floral nectar of these species is accessible to the parasitoid and its hyperparasitoid. Floral morphology may also contribute to the relative unsuitability of phacelia, alyssum and coriander for *A. ervi* and *D. aphidum*, as it does for other parasitoid species (H.D. Vattala, unpubl. data).

Buckwheat significantly increased longevity of *A. ervi* and *D. aphidum* compared with the other flowering plants. This was consistent with results of other studies, which have shown buckwheat to have beneficial effects on other natural enemy species (Gurr

& Wratten 2000). Elevated female parasitoid longevity following the provision of the flowering plants supports the theoretical arguments for the importance of omnivory in promoting top-down community regulation by parasitoids (Polis & Strong 1996). Both *A. ervi* and *D. aphidum* were able to use these resources to mature eggs and increase their longevity, increasing their potential life-time fecundity (S.A. Araj, unpubl. data). Survival time can also play an important role, as these two species are synovigenic (i.e. they mature eggs during their life time (Jervis et al. 2001)) so females that live longer should mature more eggs. Although *D. aphidum* produces fewer than half the total number of progeny that *A. ervi* does (S.A. Araj, unpubl. data), *D. aphidum* lived 3 and 2.5 times longer than did *A. ervi* when they were provided with buckwheat and water, respectively. In terms of community dynamics, this suggests that *D. aphidum* with access to nectar could affect top-down trophic cascades and may increase aphid populations indirectly (Boenisch et al. 1997).

Careful selection of the flowering species for use must be made since there can be negative impacts of poor management decisions in the field, such as herbivore population enhancement (Baggen & Gurr 1998) or fourth-trophic level effects (Stephens et al. 1998) from planting inappropriate resource subsidies. More effective conservation biological control may be achieved by the provision of selective floral resources and it will also provide a better understanding of the ecological consequences of increasing biodiversity at the field level.

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REFERENCES

Baggen LR, Gurr GM 1998. The influence of food on *Copidosoma koehleri* (Hymenoptera: Encyrtidae), and the use of flowering plants as a habitat management tool to enhance biological control of potato moth, *Phthorimaea operculella* (Lepidoptera: Gelechiidae). Biological Control 11: 9-17.

Boenisch A, Petersen G, Wyss U 1997. Influence of the hyperparasitoid *Dendrocerus carpenteri* on the reproduction of the grain aphid *Sitobion avenae*. Ecological Entomology 22: 1–6.

Comins HN, Hassell MP 1996. Persistence of multi-species host-parasitoid interactions in spatially distributed models with local dispersal. Journal of Theoretical Biology 183: 19-28.

Denno RF, Gratton C, Peterson MA, Langellotto GA, Finke DL, Huberty AF 2002. Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. Ecology 83: 1443–1458.

Dobel HJ, Denno RF 1994. Predator-planthopper interactions. In: Denno RF, Perfect TJ ed. Planthoppers: their ecology and management. Chapman and Hall, New York. Pp. 325-399.

Gurr G, Wratten SD 2000. Biological Control: Measures of Success. Kluwer Academic Publishers, Dordrecht. 444 pp.

Gurr GM, Wratten SD, Altieri MA 2004. Ecological Engineering for Pest Management. CSIRO, Melbourne. 256 pp.

Hajek AE 2004. Natural enemies: an introduction to biological control. Cambridge University Press, Cambridge, England. 394 pp.

Hassell MP 2000. Host-parasitoid population dynamics. Journal of Animal Ecology 69: 543-566.

Holler C, Borgemeister C, Haardt H, Powell W 1993. The relationship between primary parasitoids and hyperparasitoids of cereal aphids: an analysis of field data. Journal of Animal Ecology 62: 12-21.

Jervis MA, Heimpel GE, Ferns PN, Harvey JA, Kidd NAC 2001. Life-history strategies in parasitoid wasps: a comparative analysis of 'ovigeny'. Journal of Animal Ecology 70(3): 442-458.

Lavandero B, Wratten S, Shishehbor P, Worner S 2005. Enhancing the effectiveness of the parasitoid *Diadegma semiclausum* (Helen): movement after use of nectar in the field. Biological Control 34(2): 152-158.

Mackauer M, Völkl W 1993. Regulation of aphid populations by aphidiid wasps: does parasitoid foraging behaviour or hyperparasitism limit impact? Oecologia 94: 339-350.

Mertins JW 1985. Hyperparasitoids from pea aphid mummies, *Acyrthosiphon pisum* (Homoptera: Aphididae), in North America. Entomological Society of America 78: 186-197.

Muller CB, Godfray HCJ 1999. Indirect interactions in aphid-parasitoid communities. Research in Population Ecology 41: 93-106.

Noble MD 1958. A simplified clip cage for aphid investigations. Canadian Entomologist 90: 760.

Polis GA, Strong DR 1996. Food web complexity and community dynamics. American Naturalist 147: 813-846.

Stephens MJ, France CM, Wratten SD, Frampton C 1998. Enhancing biological control of leafrollers (Lepidoptera: Tortricidae) by sowing buckwheat (*Fagopyrum esculentum*) in an orchard. Biocontrol Science and Technology 8: 547-558.

Thomas MB, Wratten SD, Sotherton NW 1991. Creation of island habitats in farmland to manipulate populations of beneficial arthropods: predator densities and emigration. Journal of Applied Ecology 28: 906-917.

Tylanakis JM, Didham RK, Wratten SD 2004. Improved fitness of aphid parasitoids receiving resource subsidies. Ecology 85: 658-666.

Volkl W 1992. Aphids or their parasitoids: who actually benefits from ant-attendance? Journal of Animal Ecology 61: 273-281.

Walker GP, Cameron PJ 1981. The biology of *Dendrocerus carpenteri* (Hymenoptera: Ceraphronidae), a parasite of *Aphidius* species, and field observations of *Dendrocerus* species as hyperparasites of *Acyrthosiphon* species. New Zealand Journal of Zoology 8: 531-538.