

Limited Predation Capacity by Generalist Arthropod Predators on the Cereal Aphid, *Rhopalosiphum padi*

Trine Bilde and Søren Toft

*Department of Zoology, University of Aarhus, Building 135, DK-8000
Århus C, Denmark*

ABSTRACT

Predatory species that are considered beneficial in the limitation of cereal aphids might be expected to display a high preference for aphids. Experiments with several potential generalist aphid predators have revealed a low preference for the aphid *Rhopalosiphum padi* and a low tolerance limit to the consumption of aphids. In these experiments, the limited tolerance of some carabid beetles and linyphiid spiders to *Rhopalosiphum padi* is demonstrated. Twenty four h food consumption (mg dw mg^{-1}) of two prey types, *R. padi* and *Drosophila melanogaster*, was determined in both satiated and starved predator individuals. In most cases the feeding capacity for aphids was found to be consistently lower than for fruit flies. Aspects of the natural control of a pest that is of low preference and is not well tolerated by its predators are discussed.

INTRODUCTION

In organic agriculture, there is great interest in maximizing the number of natural control agents of aphids. This can be done either by increasing the predator population in general or by improving conditions for especially efficient aphid predators, if such species exist. In classical biological control, an efficient predator is expected to show a high specificity for its prey and to respond to changes in density of the prey (Riechert & Lockley, 1984). A stable interaction between predator and prey populations is achieved by density-dependent predation on the prey, where both the feeding behaviour and the density of the predators are important factors (Riechert & Lockley, 1984). For understanding

the feeding biology of a predator, preference for and capacity for feeding on its prey types are key factors.

A number of polyphagous carabids, e.g. *Agonum dorsale* (Pont.), have been reported to be efficient in aphid predation (Sunderland, 1975; Sunderland & Vickerman, 1980; Bryan & Wratten, 1984; Griffiths *et al.*, 1985). Experiments with *Agonum dorsale* revealed a significantly lower preference for the aphid, *Rhopalosiphum padi* (L.), compared with the fruit fly, *Drosophila melanogaster* (Meig.), and egg production on a pure diet of *R. padi* was significantly lower than on a pure diet of fruit flies or on a mixed diet (Bilde & Toft, 1994). However, aphids seem to make a positive contribution to the fitness of the predator, since the highest egg production was found on a mixed diet.

Low preference for aphids compared with fruit flies has also been found in the carabid, *Bembidion lampros* (Hbst.) (Flemming Sørensen pers. comm.), and in *Harpalus rufipes* (Deg.) which displays a low preference to cereal aphids in comparison with fruit flies and different types of weed-seeds (Jørgensen & Toft, 1997).

Cereal spiders are also thought to be important in aphid suppression (Sunderland *et al.*, 1987; Alderweireldt, 1994a). Experiments with the linyphiid spider, *Erigone atra* (Bl.), showed that females given a pure aphid diet had the lowest egg production and a lower number of young per egg sac than females given fruit fly or mixed diets (Toft, 1995). No spiderlings fed only aphids developed beyond the first instar. As with *A. dorsale* the mixed diet resulted in the highest spider fitness.

Preference and feeding experiments in two species of wolf spiders revealed similar results. *Pardosa amenitata* (Clerck) showed a lower preference for *R. padi* than for fruit flies; spiderlings on a pure aphid diet never survived the first moult in contrast to spiderlings fed fruit flies. Starved juveniles of *P. prativaga* (Koch) never consumed more than one aphid per 24 h irrespective of hunger state, while consumption of fruit flies increased dramatically with hunger (Toft, 1995).

In summary, several experiments have demonstrated that aphids are both of low palatability and, in pure diets, of low quality to a range of generalist predators which have been considered important in aphid predation (Edwards *et al.*, 1979; Sunderland *et al.*, 1987; Chiverton, 1986). The result is a limitation on the amount of aphids that the predators can tolerate at a time which in turn limits the predation capacity.

In contrast to aphids, it seems that fruit flies are a highly preferred prey on which some ground beetles and spiders can reach satiation (Bilde & Toft, 1994; Toft, 1995). If a predator reaches satiation on a diet of a certain prey type, the daily amount consumed can be defined as the daily food demand of the predator. The amount of aphids consumed relative to the food demand expresses the tolerance of the predator to the aphid.

In an attempt to elucidate the feeding capacity for *R. padi* among some generalist predators from cereal fields, we conducted an experiment determining the tolerance limits of a range of predators to *R. padi* compared with their food demand.

MATERIALS AND METHODS

Field sampling

Polyphagous predators used for the experiments were species of Linyphiidae (Araneae) (*E. atra*, *Oedothorax apicatus* (Bl.)) and Carabidae (Coleoptera) (*A. dorsale*, *Calathus fuscipes* (Gz.), *Calathus melanocephalus* (L.), *Pterostichus melanarius* (Ill.)), collected from a winter wheat field at Kalø, Denmark, from May to August 1994. Most were collected below pieces (25 x 12.5 cm) of wooden planks laid out in the field to serve as hiding places for the animals during inactive periods. The animals were weighed on arrival at the laboratory.

Laboratory procedure

Food consumption measurements took place under constant experimental conditions in a room with a 16L:8D cycle and a temperature of 20°C. Spiders were kept in glass tubes with a moistened 1–2 cm pad of plaster of Paris with charcoal; while beetles were placed in plastic petri dishes with a piece of moist cotton wool.

Animals were fed to satiation with fruit flies for 1–2 days before the first determination of food consumption (satiation consumption). Then spiders and beetles were starved for 7 days under the experimental conditions and food consumption was determined once more (starvation consumption). In all cases feeding rate was determined as food consumption over 24 h. The prey used in the experiments was wild type fruit flies, *Drosophila melanogaster*, and the cereal aphid, *Rhopalosiphum padi*, both obtained from laboratory cultures.

Spiders were offered live prey in excess numbers while beetles were offered freeze killed prey; small beetles received a certain number of prey while larger beetles were offered a weighed (wet weight) sample. On all feeding dates a counted and/or weighed sample of prey was dried in a vacuum oven at 60°C for at least 2 days and then weighed, in order to convert numbers or fresh weights of prey to dry weights. At the end of the experiment food remains were collected and their dry weight obtained as above. Food consumption in mg dw was then determined by subtracting the dried food remains from the dry weight of food offered.

Presentation of results

In order to account for variation in food consumption caused by size differences, the weight specific feeding rate is presented (mg dw consumed mg⁻¹ live weight predator), except for *C. melanocephalus* where the absolute food consumption is used, as these beetles were not weighed.

RESULTS

Food consumption of satiated and 7-day starved beetles and spiders is presented in Table 1. As there were no differences in food consumption between males and females in any of the beetles (ANOVA, $p > 0.05$), sexes were not treated separately.

TABLE 1

	Mean weight-specific food consumption (mg dw mg ⁻¹ ± SD (N))			<i>R. padi/D. mel</i> (%)
	<i>D. melanogaster</i>	<i>R. padi</i>		
<i>A. dorsale</i> ♂+♀ satiated	0.093 ± 0.059 (44) ^{A*}	0.021 ± 0.025 (33) ^A		22
	0.166 ± 0.058 (35) ^{B*}	0.124 ± 0.081 (23) ^B		74
<i>C. fuscipes</i> ♂+♀ satiated	0.053 ± 0.032 (23) ^A	0.035 ± 0.034 (30) ^A		66
	0.109 ± 0.055 (23) ^{B*}	0.057 ± 0.041 (30) ^B		52
<i>C. melanocephalus</i> ¹ satiated ♂+♀	1.258 ± 0.370 (13) ^A	1.229 ± 0.648 (13) ^A		98
	2.745 ± 0.797 (13) ^{B*}	1.639 ± 1.085 (13) ^A		60
<i>P. melanarius</i> ♂+♀ satiated	0.063 ± 0.039 (14) ^{A*}	0.036 ± 0.037 (10) ^A		57
	0.119 ± 0.029 (14) ^{B*}	0.064 ± 0.018 (9) ^A		53
<i>E. atra</i> ♀ satiated	0.338 ± 0.042 (6) ^{A*}	0.054 ± 0.049 (13) ^A		16
	0.627 ± 0.177 (6) ^{B*}	0.035 ± 0.034 (12) ^A		5
<i>O. apicatus</i> ♀ satiated	0.166 ± 0.103 (58) ^{A*}	0.041 ± 0.045 (30) ^A		25
	0.465 ± 0.241 (47) ^{B*}	0.047 ± 0.040 (30) ^A		10

¹Mean absolute food consumption mg dw ± SD in *C. melanocephalus*.

^{A,B}Different letters indicate significant differences in consumption between satiated and starved groups of each species given the same prey type (ANOVA, $p < 0.05$).

*Indicates a significantly higher consumption of *D. melanogaster* than *R. padi* (ANOVA, $p < 0.05$).

In *A. dorsale*, consumption of aphids was lower than consumption of fruit flies both in satiated and starved beetles. Aphid consumption in starved beetles was significantly higher than in satiated beetles. In satiated *C. fuscipes* and *C. melanocephalus* there was no significant difference in consumption of the two prey types; in starved animals consumption of aphids was lower than consumption of fruit flies. Consumption of aphids was higher in starved than in satiated *C. fuscipes*; in *C. melanocephalus* there was no difference. Both satiated and starved *P. melanarius* have a lower consumption of aphids than of fruit flies; there was no difference in consumption of aphids between satiated and starved animals.

In the two spider species, *E. atra* and *O. apicatus*, a similar picture was found with a significantly lower consumption of aphids than fruit flies both in satiated and starved animals, while there was no difference in consumption of aphids between satiated and starved spiders.

In general, aphid consumption of satiated beetles was below 70% of the consumption of fruit flies except in *C. melanocephalus* (98%). When starved, three species of beetles, *C. fuscipes*, *C. melanocephalus* and *P. melanarius*, had a consumption of aphids of 50–60% of the food demand, while *A. dorsale* showed a higher tolerance to aphids (74%). The spiders had a lower relative consumption of aphids than the beetles (5–25%).

DISCUSSION

Our results show a generally lower consumption of aphids than of fruit flies especially in starved predators. There is a tendency of not reaching food demand when fed aphids also in satiated animals; this is significant in four species, *A. dorsale*, *P. melanarius*, *E. atra* and *O. apicatus*. Two species of carabids, *C. fuscipes*, and *C. melanocephalus*, when satiated, reach a consumption of aphids close to food demand. The two linyphiid spiders included in our experiment show an even lower tolerance to the aphid *R. padi* than the beetles. This might indicate that the carabids are more aphidophagous than the spiders.

In *A. dorsale*, we found a significant increase in the consumption of aphids with hunger level, though consumption of aphids was still lower than consumption of fruit flies. This is in contradiction to earlier findings, where aphid consumption did not increase with hunger, and where a much lower tolerance to aphids than found in this experiment was indicated (Bilde & Toft, 1994). *A. dorsale* used in this experiment were collected from April to July, while animals used in the previous experiments were from August/September. It may be possible that the tolerance of the predator to the aphid varies with the season, as beetles in different phases of the life cycle were worked with. The autumn population of *A. dorsale* is the new non-reproductive generation of beetles which, after hibernation, become reproductive in spring.

Another explanation could be different reactions to starvation at different times of the season. In spring and early summer, hunger levels of *A. dorsale* have been found to be very high, decreasing to lower levels in mid summer (unpublished data). If the physiological state of the animal is more geared to cope with high hunger levels in spring, the beetles could be better able to handle and exploit encountered prey.

The finding of a low tolerance limit combined with an apparently low preference in generalist arthropod predators for the cereal aphid *R. padi*, found in earlier studies (Bilde & Toft, 1994; Toft, 1995), in theory would not lead us to expect them to be efficient in natural control of these aphids. Nevertheless, polyphagous predators have been shown to play an important role as natural control agents in the population dynamics of cereal aphids (Edwards *et al.*, 1979; Sunderland & Vickerman, 1980; Chiverton, 1986). Specifically, *R. padi* was the main aphid species in the work of Chiverton (1986). Also *R. padi* has been found to be common in the diets of a range of polyphagous predators (Sunderland & Vickerman, 1980; Chiverton, 1987; Sunderland *et al.*, 1987). A mechanism that could explain a higher predation on aphids than expected is the lack of sufficient alternative prey available to the predators. Shortage of food probably is a frequently occurring situation in the field (Lenski, 1984; Juliano, 1986; Van Dijk, 1986). The hunger level of predators is often assumed to play an important role in the choice of prey, e.g. whether to accept a less preferred prey or not (Stephens & Krebs, 1986). High hunger levels in the field could force the predators to survive on a diet of less preferred prey.

This leads to the question of what happens with predation on a low preferred prey in a field situation where the predators are not food limited. One of the aims in organic farming is to increase the diversity and numbers of natural enemies on cereal pests in order to avoid both the chemicals and the pests. Along with a general increase in diversity there would probably also be an increase in alternative prey types and numbers of alternative prey available to the predators. If the pest is not very well tolerated or preferred by its predators, this could lead to a decreased predation on the pest. Thus, Chiverton & Sotherton (1991) found *A. dorsale* to consume relatively fewer aphids in unsprayed headland plots than in sprayed plots.

If it is a general trend that generalist predators have a low tolerance to cereal aphids, a search for aphidophagous generalists, for which to optimize conditions, is not the right strategy in aphid control. A general increase in the population of generalist predators would increase efficiency in aphid predation (Alderweireldt, 1994b). Thus, Sunderland *et al.* (1986) found aphid predation to be limited by low population densities of the predators. As long as the aphids contribute with energy or nutrients to the diet of the predator, a certain predation on aphids is to be expected (Greenstone, 1979; Waldbauer & Friedman, 1991). A large population of predators, though with a low individual predation on aphids, might have an impact on the ultimate population peak of aphids, if present at the time the aphids colonize the fields.

More feeding experiments with a broader range of prey types are needed, though, in order to be able to elucidate feeding behaviour and potential predation on aphids by generalist arthropod predators.

ACKNOWLEDGEMENTS

The studies were funded by a grant from the Danish Environmental Research Programme to the Centre for Agricultural Biodiversity.

References

- Alderweireldt, M. (1994a). Prey selection and prey capture strategies of linyphiid spiders in agricultural fields. *Bulletin of the British Arachnological Society*, **9**, 300-308.
- Alderweireldt, M. (1994b). Habitat manipulations increasing spider densities in agroecosystems: possibilities for biological control? *Journal of Applied Entomology*, **118**, 10-16.
- Bilde, T. & Toft, S. (1994). Prey preference and egg production of the carabid beetle *Agonum dorsale*. *Entomologia Experimentalis et Applicata*, **73**, 151-156.
- Bryan, K.M. & Wratten, S.D. (1984). The responses of polyphagous predators to prey spatial heterogeneity: Aggregation by carabid and staphylinid beetles to their cereal aphid prey. *Ecological Entomology*, **9**, 251-259.
- Chiverton, P.A. (1986). Predator density manipulation and its effects on populations of *Rhopalosiphum padi* (Hom.: Aphididae) in spring barley. *Annals of Applied Biology*, **109**, 49-60.
- Chiverton, P.A. (1987). Predation of *Rhopalosiphum padi* (Homoptera: Aphididae) by polyphagous predatory arthropods during the aphids prepeak period in spring barley. *Annals of Applied Biology*, **111**, 257-269.
- Chiverton, P.A. & Sotherton N.W. (1991). The effects on beneficial arthropods of the exclusion of herbicides from cereal crop edges. *Journal of Applied Ecology*, **28**, 1027-1039.
- Edwards, C.A., Sunderland, K.D. & George, K.S. (1979). Studies on polyphagous predators of cereal aphids. *Journal of Applied Ecology*, **16**, 811-823.
- Greenstone, M.H. (1979). Spider feeding behaviour optimises dietary essential amino acid composition. *Nature*, **282**, 501-503.
- Griffiths, E., Wratten, S.D. & Vickerman, P. (1985). Foraging by the carabid *Agonum dorsale* in the field. *Ecological Entomology*, **10**, 181-189.
- Juliano, S.A. (1986). Food limitation of reproduction and survival for populations of *Brachinus* (Coleoptera:Carabidae). *Ecology*, **67**, 1036-1045.
- Jørgensen, H.B. & Toft, S. (1997). Food preference, diet dependent fecundity and larval development in *Harpalus rufipes* (Coleoptera: Carabidae). *Pedobiologia*, **41**, 307-315.
- Lenski, R.E. (1984). Food limitation and competition: A field experiment with two *Carabus* species. *Journal of Animal Ecology*, **53**, 203-216.
- Riechert, S.E. & Lockley, T. (1984). Spiders as biological control agents. *Annual Review of Entomology*, **29**, 299-320.
- Stephens, D.W. & Krebs, J.R. (1986). *Foraging Theory*. Princeton University Press, Princeton, New Jersey.
- Sunderland, K.D. (1975). The diet of some predatory arthropods in cereal crops. *Journal of Applied Ecology*, **12**, 507-515.
- Sunderland, K.D. & Vickerman, G.P. (1980). Aphid feeding by some polyphagous predators in relation to aphid density in cereal fields. *Journal of Applied Ecology*, **17**, 389-396.
- Sunderland, K.D., Fraser, A.M. & Dixon, F.G. (1986). Field and laboratory studies on money spiders (Linyphiidae) as predators of cereal aphids. *Journal of Applied Ecology*, **23**, 433-447.
- Sunderland, K.D., Crook, N.E., Stacey, D.L. & Fuller, B.J. (1987). A study of feeding by

- polyphagous predators on cereal aphids using ELISA and gut dissection. *Journal of Applied Ecology*, **24**, 907-933.
- Toft, S. (1995). Value of the aphid *Rhopalosiphum padi* as food for cereal spiders. *Journal of Applied Ecology*, **32**, 552-560.
- Van Dijk, Th. S. (1986). How to estimate the level of food availability in field populations of carabid beetles. In *Carabid Beetles, Their Adaptations and Dynamics*. (P.J. den Boer, M.L. Luff, D. Mossakowski & F. Weber, eds.), pp. 371-382. Gustav Fischer, Stuttgart, New York.
- Waldbauer, G.P. & Friedman, S. (1991). Self-selection of optimal diets by insects. *Annual Review of Entomology*, **36**, 43-63.