Prey preference and egg production of the carabid beetle *Agonum dorsale*

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Abstract

In order to elucidate whether the aphid *Rhopalosiphum padi* is low quality food for the carabid beetle *Agonum dorsale*, as it has previously been found to be for cereal spiders, we performed a series of experiments using fruit flies *Drosophila melanogaster* as a standard alternative prey ('control prey'): 1) Prey preference, 2) Aphid consumption for satiated and starved beetles, 3) Egg production on different diets and 4) Preference experiments with fruit flies coated with a taste of different prey types. Other alternative prey types used were earthworms and sciarid midges, all potential prey in the field. *A. dorsale* has a low preference for aphids compared to fruit flies. Apparently there is an upper limit to the consumption of aphids independent of hunger and much below the beetles' total food demand. Egg production on a pure diet of aphids is lower than on a pure diet of fruit flies; it is extremely low on a pure diet of earthworms; the highest fecundity is found on a mixed diet. As fruit flies coated with a taste of aphids or sciarid midges are less prefered than flies covered with a taste of fruit flies there may be a chemical factor, acting through taste, involved in determining prey preference.

Introduction

The carabid beetle *Agonum dorsale* (Pont.) has repeatedly been cited as one of the top ranking species among the polyphagous predators that contribute to the reduction of aphid population growth in cereal fields (Sunderland, 1975; Sunderland & Vickerman, 1980; Bryan & Wratten, 1984; Griffiths *et al.*, 1985). An implicit assumption in these statements is that the aphids are also a highly prefered prey to the predator. A recent finding (Toft, in press) that the aphid *Rhopalosiphum padi* L. is low quality food to cereal spiders, that are also thought to be important in aphid suppression (Sunderland *et al.*, 1987), made us speculate whether similar relations might exist between aphids and other groups of polyphagous predators, especially carabids. Other studies have pointed out the possibility that a demonstrable impact on aphids is not necessarily associated with a high preference for aphids. Thus, Dennis *et al.* (1990; 1991), for example, found that the staphylinid *Tachyporus hypnorum* (Fabr.) prefers mildew to aphids, but still has an impact on the latter.

In order to elucidate whether aphids are low quality food for *A. dorsale*, as for the spiders, we performed a series of laboratory experiments to measure the preference of *A. dorsale* for *R. padi* relative to some other prey types, both natural alternative prey types and laboratory fruit flies *Drosophila melanogaster* (Meig.), which are used as a standard alternative prey ('control prey'). Fruit flies were chosen for this because they are readily obtainable from laboratory cultures, they are apparently highly preferred by most polyphagous predators (Toft, in press), and small dipterans are known to make up a substantial part of the beetles' diet. In the study of Sunderland (1975) aphids formed 46%, Diptera 25% and earthworms 7% of the meals of *A. dorsale*; whether drosophilids are eaten in the field is unknown.

The ultimate measure of prey quality is the prey's contribution to fitness components of the predator, like fecundity. Therefore egg production of females exposed to different prey types may be used as an indicator of prey quality and a correlation between preference and prey quality is to be expected.

Finally we have made a preliminary attempt to identify the causes of differences in preference for various prey types. We here report on two simple experiments in which *D. melanogaster* were coated with a mush of squashed other prey. If a chemical constituent of the prey is involved we expect that the preference for fruit flies coated with a taste of other prey would decrease if the other prey is less preferred than fruit flies.

Materials and methods

In all experiments the aphid used as prey is *Rhopalosiphum padi* obtained from laboratory culture. The fruit flies were wild type *Drosophila melanogaster*. All preys were killed by freezing before being offered in the experiments. The earthworms used, mainly *Lumbricus terrestris* L., were collected in the field, killed by freezing and grounded, thus offered in minute pieces.

By offering the prey animals dead we wanted to isolate the nutritional quality aspect of prey selection. We assume that a less preferred prey will always be taken rarely in the field, whereas field consumption of a highly preferred prey will depend on the prey's ability to escape or other defence mechanism. In order to apply the results to the field situation it is then necessary to consider also the predator's capture efficiency as well as other aspects of prey profitability, e.g. prey toughness (or predator handling time). Since some prey types may be obtained primarily by scavenging (Sunderland, 1975) our results may apply directly to the natural situation.

Preliminary preference experiments. In this experiment ten females of *A. dorsale* were offered a choice of three prey types: Aphids, fruit flies and earthworm. Experimental beetles were collected in the field and kept in the refrigerator for a few days until three days before the experiment. For these three days they were starved but otherwise kept under the experimental conditions and exposed to the normal diurnal cycle. Ten beetles were placed individually in petri dishes supplied with moist filter paper. Each beetle was given 20 aphids, 5 fruit flies and pieces of earthworm, approximately equal amounts of each prey type were offered. The experiment was run in darkness at room temperature (c. 20 °C) and beetle activity was observed in red light. Though the species is normally night active, the beetles immediately become active when placed in darkness. The order in which the beetles consumed the prey and the amount consumed was recorded for

two hours.

Aphid preference and consumption in relation to hunger. Satiated predators are expected to be more selective in their choice of prey than hungry ones. Thus, even if satiated predators would not aggregate at patches with high aphid densities, hungry ones might do if few other preys are available. To see if preference and consumption depends on hunger the consumption of aphids and fruit flies by satiated and starved beetles was measured over three hours when offered in pure and mixed diets. The beetles were kept on a diet of cod roe and the day before the experiment they were supplied with surplus fruit flies to ensure satiation of the beetles at the start of the experiment.

The experiment consisted of three series in which each individual beetle was supplied with a) 12 fruit flies, b) 15 aphids, and c) 10 fruit flies and 10 aphids, respectively. These amounts were all surplus amounts for the 3 hour experimental period. There were 20 replicates in each series with equal numbers of each sex. The experiment was run in darkness at room temperature (c. 20 °C) with each individual in a petri dish with moist filter paper. The experiment was repeated with the same beetles after they had been starved for seven days at 20 °C.

Effect of diet on egg production. Egg production was measured over 5 weeks on four groups of beetles held on one of the four diets: Pure diets of each of the prey types a) fruit flies, b) aphids, c) earthworm, and d) a mixed diet of these three. Food was renewed every second day with surplus amounts; they were run at room temperature (c. 20 °C) and the natural daily rhythm was followed. The experiment was started with animals collected in the field at about the beginning of the egg-laying period (13 May 1993).

There were 10 replicates in each diet with 1 female and 1 male in each. Each pair of beetles was placed in a petri dish (14 cm diam.) with moist sand and the eggs or larvae were counted directly on the surface every second day. This procedure caused a minimum of disturbance to the parent beetles. As the eggs were removed after being counted, the larvae must have come from overlooked or buried eggs. Dicker (1951) found eggs from *A. dorsale* inside small lumps of soil on the back of strawberry leaves. If this egg-laying habit is used also when eggs are laid in soil, a substantial number of eggs may have been overlooked. However, this should have no influence on the relative number of eggs recorded for the treatments. The large

size of the petri dishes should prevent any substantial influence of cannibalism among hatched larvae.

Coated prey experiments. These experiments were performed with fruit flies as the basic food source in all cases. Besides one experiment in which fruit flies were given a taste of the aphid *R. padi*, a second similar experiment used the sciarid midge *Bradycera paupera* (Tuom.), also obtained from a laboratory culture. Sciarid midges are common near the ground in cereal fields and may be important alternative preys for many polyphagous predators (though not the species used here, which was chosen because it is easily bred). Experiments with wolf spiders (Toft, in press) show, that these animals have a lower preference for the sciarids than for fruit flies, though sciarids are preferred to aphids. For the present experiment we therefore predicted a reduction in preference to sciarid-coated fruit flies compared to control-coated flies.

Preparation of coated prey: Some hundred milligrams of aphids (or sciarids) were obtained from laboratory cultures, killed by freezing for about an hour, and grounded in a mortar with a small amount of water. This produced a mush into which freshly killed fruit flies were soaked, so that after drying they were completely covered with a layer of aphid (or sciarid) tissue (aphid/sciarid coated flies). To ascertain that the hypothesized change in preference of the beetle was not simply a result of the change in surface properties of the coated fruit flies, the control flies were treated with a fruit fly mush prepared in the same way (control-coated flies). Beetles were starved for two days before the experiments.

The experiments were run in darkness at 20 °C with beetles in individual petri dishes supplied with moist filter paper. Five beetles were given 10 control-coated fruit flies only, five other beetles were given 10 aphid (or sciarid) coated fruit flies, finally 20 beetles were offered 5 aphid/sciarid coated and 5 control-coated fruit flies. The number of flies eaten were recorded after 3 h. The experiment with sciarid-coated flies was run for 20 h; however, most feeding took place within the first hours, probably due to the fact that the beetles were starved, and the relative amounts of the food categories eaten did not change by prolonging the experiment. We therefore present data for 3 h consumption only.

Table 1. Preference experiment with *A. dorsale* given a choice between fruit flies and the aphid *R. padi*, indicated as numbers and dry weight eaten during 2 h by hungry beetles (N = 10)

	D. melanogaster	*R. padi*
Mean no ±s.d.	4.100±1.729	7.000±4.190
Mean dw mg ±s.d.	1.312±0.553	0.339±0.203

Results

Preference. The beetles show a significant preference for fruit flies compared to aphids measured on a dry weight basis (Table 1; Wilcoxon matched pairs test, $p = 0.007$). Our observations under red light showed that the beetles visited the earthworm crumbs even less often than aphids, indicating a somewhat lower preference for earthworms than for aphids. However we were unable to measure the amounts of earthworm eaten with any degree of accuracy. From observations it was uncertain whether the beetles consumed the earthworms to any extent or only licked juices. We therefore present only the amount of aphids and fruit flies consumed (Table 1).

Preference and consumption vs. hunger. Figure 1a shows the mean consumption in no. of each prey type based on the results for both sexes. In the consumption of fruit flies (pure diet) there is a significant difference depending on whether the beetles were starved or not (ANOVA; $p < 0.001$). It makes no difference whether fruit flies are given in a pure or mixed diet ($p = 0.199$). In the consumption of aphids (pure diet) there is no difference between satiated and starved beetles ($p = 0.245$), but there is a significant difference between pure and mixed diets ($p < 0.001$); in the mixed diet consumption of aphids is reduced.

Sex had a significant influence on the consumption of fruit flies, ($p < 0.001$) but not on the consumption of aphids, ($p = 0.346$). The females had a greater consumption of fruit flies than the males, perhaps because they are generally larger.

Figure 1b shows the mean consumption in mg dry weight for each of the two prey types. Notice that consumption of fruit flies in all situations is far above consumption of aphids. The results for pure diets show a hunger effect in the consumption of fruit flies, but not in the consumption of aphids. On a mixed diet the satiated beetles hardly consume any aphids; consump-
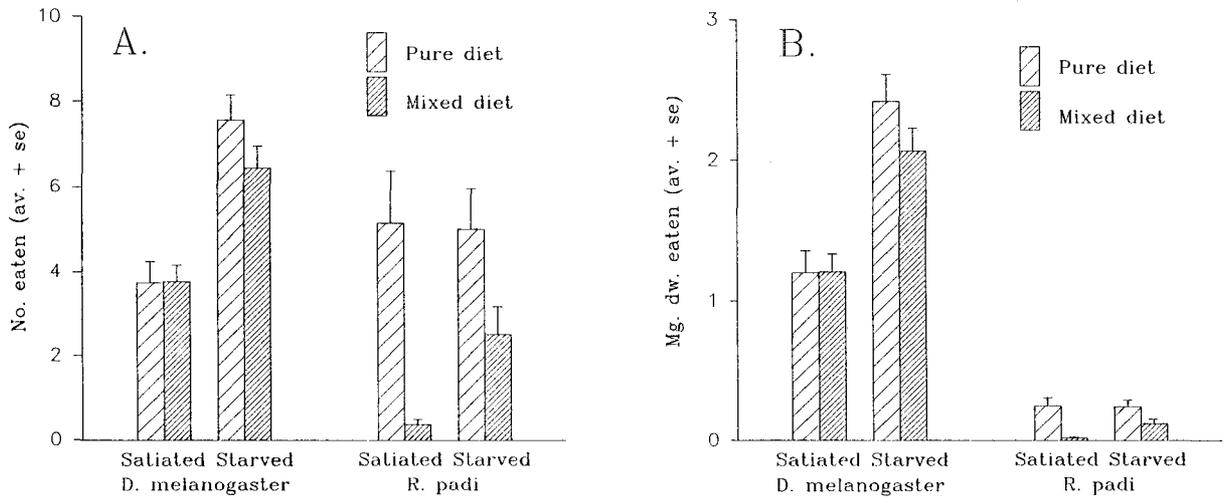
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Fig. 1. Consumption of fruit flies D. melanogaster and the aphid R. padi by satiated and starved A. dorsale in pure and mixed diets. N = 20 in all treatments.

tion of both prey types increases with hunger, but for aphids stays below the pure diet level.

On a pure diet the consumption of fruit flies is approx. 5 times greater than the consumption of aphids for satiated beetles, while it is 10 times greater for starved beetles. On a mixed diet the consumption of fruit flies is approx. 67 times greater than the consumption of aphids for satiated beetles and 17 times greater for starved beetles.

Diet vs. egg production. For the statistical analysis the variances were homogenised with a logarithmic transformation (Bartlett's test). Results are shown in Table 2. There is a significant diet effect on the number of eggs (ANOVA; $p < 0.001$). In a subsequent pairwise comparison (Fisher's LSD test, cf. Day & Quinn, 1989) there are significant differences between diets of aphids and fruit flies ($p = 0.039$), aphids and mixed diet ($p < 0.001$), fruit flies and earthworm ($p = 0.005$), fruit flies and mixed diet ($p = 0.012$) and between earthworm and mixed diet ($p < 0.001$).

The experiment evaluates earthworms a low quality food for A. dorsale. It also places the aphids well below fruit flies, but first of all points to a great advantage of the mixed diet compared to the best pure diet (fruit flies).

Is preference determined by prey taste? The results appear in Table 3. In experiment 1 it is obvious from the choice situation that giving fruit flies a taste of aphids decreases the palatability of the fruit flies to A. dorsale,

Table 2. Influence of diet on egg production in A. dorsale. Figures indicate no. of eggs plus larvae per female. Different letters indicate a significant difference between the diets. N = 10 in all treatments

Diet	Mean no±s.d.
1. *R. padi*	1.000±1.247 a
2. *D. melanogaster*	2.900±2.558 b
3. Earthworm	0.500±0.707 a
4. Mixed	5.600±2.716 c

which shows a clear preference for the control-coated fruit flies (paired t-test, $p < 0.001$). However, it is also seen, by comparing the two no choice groups that total consumption is reduced when the fruit flies get a taste of aphids. Such a reduction in food consumption is not obvious with the sciarid-coated flies (experiment 2), though also here the choice experiments demonstrate a clear difference in preference (paired t-test, $p < 0.001$). As expected, coating fruit flies with a sciarid taste decreases preference.

Discussion

The results of the preference experiments show that to A. dorsale aphids are ranked well below fruit flies as food. Probably, earthworms are even less attractive. It is interesting that a substantial part of this predator's

Table 3. Consumption experiments with *A. dorsale* in single diet and preference situations. Food items were dead fruit flies coated with a mush of fruit fly (control-coated), aphid, or sciarid tissue. Figures indicate number of food items eaten in 3 h

	N	Pure diet mean±s.d.	N	Mixed diet mean±s.d.
Experiment 1				
Control-coated flies	5	7.60±1.56	20	3.80±1.25
Aphid-coated flies	5	5.50±2.60	20	1.53±1.49
Experiment 2				
Control-coated flies	5	4.00±1.84	20	2.55±1.61
Sciarid-coated flies	5	3.90±2.92	20	0.98±0.92

food consists of low preference prey types (aphids and earthworms together constitute 53% of meals; Sunderland, 1975). Diptera also forms a substantial proportion of meals of *A. dorsale*. Sciarid midges can be imagined as one of the main dipteran prey types in the cereal fields; our results indicate a low preference for these too.

With respect to the consumption of fruit flies there is a hunger effect, where starved beetles have a greater food demand than satiated beetles. This hunger effect does not manifest itself in the consumption of aphids. Apparently there is an upper limit to the consumption of aphids independent of hunger and much below total food demand. This phenomenon has not previously been shown for a carabid beetle, but agrees with findings for cereal spiders (Toft, in press). Over a given period of time *A. dorsale* seems to tolerate only a certain amount of aphids, which may indicate its tolerance limit to a presumed defensive system of the aphids. The coated-prey experiments show that some chemical factor in the prey, acting through taste, forms part of such a defensive system. Nakamuta (1984) showed that the body fluids of aphids stimulate feeding in *Coccinella 7-punctata*; it can be hypothesized that the same factors may serve as feeding deterrents against *A. dorsale*.

The consumption of aphids was found to be much lower than food demand, as determined by consumption of fruit flies. This is not a simple effect of the beetles' low preference. One can imagine an increase in consumption of a food type in response to low quality (compensatory response), provided the food is without deterrent substances. We interprete the reduction in consumption as evidence of the existence of a deterrent system.

The existence of a limit to aphid feeding may explain why *A. dorsale*, though seemingly perfectly able to climb cereal plants (Vickerman & Sunderland, 1975), does not do this in the field to any significant extent (Griffiths *et al.*, 1985). By climbing the plants, the beetles would encounter an abundant food supply in aphid colonies. However, if the tolerance limit to the aphid is low, this food source is unexploitable. By staying on the soil surface the beetles probably expose themselves to a more diverse food source; at the same time the beetles may reach their aphid tolerance limit by preying on aphids on the ground (cf. Sopp *et al.*, 1987).

Dennis *et al.* (1990, 1991) suggested that aggregation of *T. hypnorum* in areas of high aphid densities might reflect attraction to rich mildew growth on the honeydew close to aphid aggregations rather than to the aphids themselves. Such an explanation is unlikely to hold for carabids and other predator groups that has also been found to aggregate around aphids (Bryan & Wratten, 1984), unless other insects like small Diptera and other potential alternative prey are also attracted to honeydew; to our knowledge, though, such a phenomenon has not been demonstrated.

Generally there is accordance between preference to and egg production on the different diets. The highest egg production is found on a mixed diet. Probably a pure diet is nutritionally too one-sided in the long term. *A. dorsale* has a higher reproduction on a pure diet of fruit flies than on a pure diet of aphids and also shows a clear preference to fruit flies compared to aphids. Egg production on the earthworm diet was extremely low. This could indicate that consumption of worms in nature is not very profitable. It is not known whether *A. dorsale* preys on live earthworms in the field or rather scavenge dead worms. It is surprising that egg production on the mixed diet is larger than that of the sum of the three pure diets. Separate experiments are needed to determine the relative contribution of aphids and earthworms to the increased fecundity of the mixed diet.

Our results demonstrate that *R. padi* is not a highly prefered prey for *A. dorsale*. This result accords with similar findings for cereal spiders (Toft, in press). The question therefore arises to what extent this applies also to other species and groups of polyphagous predators. Our results are also relevant to considerations concerning the prospects of improving the predator limitation of aphids. If preference for aphids is generally low among polyphagous predators, a significant reducing effect on the aphids in the field may indicate that the

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predators are experiencing severe shortage of alternative prey.

Results of Chiverton & Sotherton (1991) indicate that this may actually be so. These authors found by dissection of *A. dorsale* females, that egg production was higher in beetles from unsprayed headlands than in beetles from sprayed headlands. Also in the sprayed headlands aphids made up a larger proportion of the stomach contents of these beetles. On the basis of such results one might wonder about the consequences of increased biodiversity of agricultural fields. If the spectrum of alternative prey to polyphagous predators widens and the amount of food available through non-aphid sources increases, it can be anticipated that relative predation on aphids (functional response) will decrease, since some of the alternative prey are likely to be more prefered than aphids. This can be counteracted of course by an eventual increase in the number of predators in the field which is likely to take place at the same time.

Acknowledgements

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