# The value of three cereal aphid species as food for a generalist predator

T R I N E   B I L D E  and  S Ø R E N   T O F T
Department of Zoology, University of Aarhus, Denmark

**Abstract.** The value of the cereal aphid species *Metopolophium dirhodum* (Wlk.), *Sitobion avenae* (F.) and *Rhopalosiphum padi* (L.) as prey for the linyphiid spider *Erigone atra* (Bl.) was assessed. Fecundity of females was determined for spiders fed on eight experimental diets: three single-species aphid diets, a mixed diet of all three aphid species, three mixed diets with each aphid species in combination with fruit flies *Drosophila melanogaster* (Meig.), and pure *D. melanogaster* as a high quality comparison diet. The development and survival of first-instar juveniles fed on three diets of single aphid species, and on a diet of Collembola were compared with those subjected to starvation. Prey value for adult females was assessed by egg production, hatching success and offspring size.

In pure diets all three aphid species were of low value to the spiders, causing a rapid decline in egg production and supporting no growth of significance of first-instar juveniles. No difference in value of aphid species of single-species aphid diets was found in the fecundity experiment, while a ranking of aphid species of *M. dirhodum* > *R. padi* > *S. avenae* was revealed in the survivorship experiment. A mixed-aphid diet was not found to be advantageous compared with single-species aphid diets, and no advantage of including aphids in mixed diets with fruit flies was found. *Metopolophium dirhodum* and *R. padi* were neutral in mixed diets, while a diet of *S. avenae* and fruit flies caused reduced egg production compared with the pure diet of fruit flies, revealing a toxic effect of *S. avenae* on the spider. The value-ranking of aphid species in mixed diets was similar to that of single-species diets. A similar ranking of aphid species was found for different fitness parameters (fecundity of adult females and development of juveniles).

A ranking of aphids by offspring size of mothers on aphid-only diets was *S. avenae* > *M. dirhodum* > *R. padi*. All aphid-fruit fly diets resulted in larger offspring than a diet of only *D. melanogaster*, with the overall largest offspring being produced on the diet of *M. dirhodum* and fruit flies.

**Key words.** Aphids, diet-dependent offspring size, *Erigone atra*, fitness, food quality, *Metopolophium dirhodum*, mixed-species diets, *Rhopalosiphum padi*, single-species diets, *Sitobion avenae*, spider, toxic prey.

## Introduction

Generalist arthropod predators form a community of natural enemies that may have a significant impact on aphid population growth in cereal fields (e.g. Edwards *et al.*, 1979; Chiverton, 1987). Spring-breeding species of generalist

Correspondence: Trine Bilde, Department of Zoology, University of Aarhus, Building 135, DK-8000 Århus C, Denmark. E-mail: trine.bilde@biology.au.dk

predators disperse into the fields early in the season, when they feed on prey other than aphids and initiate reproduction prior to the arrival of the aphids in the fields later in the growth season. Predation by generalist predators may slow down the exponential growth of aphid populations and lower their ultimate peak population size. Spiders are some of the most abundant predatory arthropods in agroecosystems, and cereal aphids have been found to constitute a large proportion of their diet (Nyffeler, 1982; Nentwig, 1983; Sunderland *et al.*, 1987; Alderweireldt, 1994). If they are a major food source, cereal

aphids would be expected to be valuable prey for its predator, who in turn would be expected to show preference for this prey in order to affect the prey population size. The value of prey species and their availability are major factors determining predation rates. The value (or quality) of a prey results from the joint effects of the prey's content of nutrients, energy and eventual noxious substances on predator performance. It can be assessed by how well it is tolerated by its predator (Bilde & Toft, 1997a; Toft, 1996) in combination with its effects on predator fitness parameters such as egg production, growth rates and survival (Bilde & Toft, 1994; Toft, 1995; Sunderland *et al.*, 1996b; van Dijk, 1996; Marcussen *et al.*, 1999). Studies on consumption rates and fitness parameters of arthropod predators have indicated that the cereal aphid *Rhopalosiphum padi* (L.) is of low value to several species of spiders and carabid beetles (Bilde & Toft, 1994, 1997a; Toft, 1995). Optimal foraging theory predicts that prey of low quality should be rejected by the predator if better prey is available (Stephen & Krebs, 1986). Predation rates on *R. padi* would thus depend on availability of alternative prey.

*Erigone atra* (Bl.) is a small ($\approx$ 2–3 mm) sheet-web spider of the family Linyphiidae. It has two generations per year with breeding periods in early spring and summer (De Keer & Maelfait, 1988a). It is one of the most common spider species in European cereal fields and has repeatedly been reported to feed on cereal aphids (Sunderland *et al.*, 1986a, b, 1987; Sopp & Chiverton, 1987; Janssens & De Clercq, 1990). Alderweireldt (1994) found aphids to constitute 39% of total prey items caught by *E. atra* with the spider consuming 26% aphids of its total diet. *Erigone atra* has a mixed prey catching strategy; it builds small sheet webs which capture prey, but may also chase prey outside the web (Alderweireldt, 1994). Cereal aphids are vulnerable to be caught both in spider webs and by spiders hunting outside the web, as a significant proportion of the aphid population (20–50%) walk from plant to plant or drop to the soil surface (Griffiths *et al.*, 1985; Sunderland *et al.*, 1986a; Sopp *et al.*, 1987). In the study reported here, the food value of the cereal aphid species *Metopolophium dirhodum* (Wlk.), *Sitobion avenae* (F.) and *R. padi* to the spider *E. atra* was evaluated in single-species and mixed-species diets.

## Materials and methods

Adult females and males of *E. atra* were collected as aeronauts in the field on 14 and 16 October 1997. These spiders belong to an autumn generation that normally hibernates before reproducing in spring. When taken to the laboratory and fed, the spiders readily initiate reproduction. Females and males were kept together and standardized on a diet of *D. melanogaster ad libitum* for 3–4 days. Fertile females were assigned subsequently to the experimental treatments after producing one egg sac. Throughout the experiments, spiders were kept in cylindrical plastic tubes with a bottom of moist plaster-of-Paris mixed with charcoal. The pre-experimental standardization and all subsequent experiments were carried out at 20°C and a LD 16 : 8 h photo cycle.

The aphid species *M. dirhodum*, *S. avenae* and *R. padi* tested in the experiments are the most abundant cereal aphids in Europe (Vickerman & Wratten, 1979). Wild type *D. melanogaster* were used as a standard comparison prey, as fruit flies are readily accepted by the spiders and are of relatively high quality (Toft, 1995; Bilde & Toft, 1997a). The fruit flies used in the experiments were reared on instant *Drosophila* medium (Formula 4–24 Plain, Carolina Biological Supply; Burlington, NC, U.S.A.) mixed with crushed dog food (Techni-Cal maintenance®, ) to assure a high nutritional quality of the flies (C. Kristensen and S. Toft, unpublished data). The aphid species were reared on wheat seedlings (mixed cultivars) in laboratory cultures. In a survival experiment of juvenile *E. atra*, the collembolan *Isotoma tigrina* (Nicolet) was used as comparison prey. The Collembola were obtained from a laboratory culture reared on instant *Drosophila* medium and baker's yeast.

### Egg sac production, number of young, and hatchling size

Fertile females were assigned evenly to one of eight prey treatments: (1) *M. dirhodum*, (2) *S. avenae*, (3) *R. padi*, (4) *M. dirhodum* + *S. avenae* + *R. padi*, (5) *D. melanogaster*, (6) *D. melanogaster* + *M. dirhodum*, (7) *D. melanogaster* + *S. avenae*, (8) *D. melanogaster* + *R. padi*. Diets 1–4 are termed the aphid-only diet groups and diets 5–8 the 'fruit fly diet groups'. Replication was 13–14 females in each diet group. A few spiders died during the experiment so sample sizes varied between 10 and 14 in the final analyses. The experiment was terminated after 2 months.

Only egg sacs produced after females were assigned to diet treatments were included in the analyses, reference to egg sac number one thus refers to the first egg sac produced during the experiment.

Spiders were watered and fed live prey in excess two or three times per week, so prey were always available. As *S. avenae* and *M. dirhodum* are larger species than *R. padi*, the spiders were fed predominantly first- to third-instar nymphs of these two species, whereas predominantly late instar or adult *R. padi* were given. The spiders were checked daily for production of egg sacs. When an egg sac was produced, the female was transferred to a new plastic tube and a new male was added to prevent the females from running out of sperm. Fewer males than females were available, so throughout the egg production experiment males were shifted continuously between females. Egg sacs were kept under experimental conditions until hatching. Emergence date and number of hatchlings were recorded. Egg sacs were always dissected to record undeveloped eggs, embryos and larvae so that total egg number and hatching success could be determined. Hatched young were preserved in alcohol for later measurements of size, to detect effects of maternal diet on offspring size. Cephalothorax length of the longest part and width of the widest part of the hatchlings were measured with an ocular micrometer under a dissecting microscope. If fewer than 10 spiderlings were produced per egg sac, all spiderlings were

measured, otherwise 10 randomly chosen spiderlings were measured.

### Hatching success

Hatching success was recorded as the proportion of fully developed young that emerged from the egg sac. Whereas all eggs hatched and spiderlings emerged synchronously in the first three or four egg sacs, development of spiderlings in the following egg sacs appeared variable; some emerged while others were still in the larval stage or were developing embryos within the egg sac. It is not known whether larvae or embryos would have completed development, as the egg sacs were dissected after emergence of the first spiderlings. If this phenomenon was due to a laboratory artefact, the hatching success of eggs was underestimated, as these larvae and embryos were categorized as not-hatched. Consequently, hatching success was analysed both from the proportion of fully developed young that emerged from the egg sac, and from the sum of developed eggs, larvae and fully developed young. At the end of the experiment, females on fruit fly diets still produced egg sacs, but few of these hatched. A large proportion of eggs showed some degree of development, apparently some of the eggs were fertilized but of low quality. The spiders probably produced more egg sacs than they would in the field, and it may be those egg sacs that did not hatch or only partly hatched. It is doubtful whether infertility of late egg sacs was due to senescence of males or of the females themselves. Toft (1995) had one male per female and experienced a similar reduction in fertility of egg sacs with time, and De Keer & Maelfait (1988b) also found a reduced viability of late egg sacs.

### Survival and development of juveniles of E. atra

Spiderlings of mothers fed a monotypic diet of *D. melanogaster* were used to exclude maternal diet effects on the performance of offspring. Spiderlings from the first egg sac produced by nine *E. atra* females were transferred to individual tubes immediately after hatching. Subsequently, the spiderlings were assigned randomly to one of five diet treatments, so an equal number of young from each of the nine mothers was represented in the treatments. The diet treatments were: *M. dirhodum*, *S. avenae*, *R. padi*, *I. tigrina*, and complete starvation. As Collembola of the family Isotomidae are known to constitute an important prey group for linyphiid spiders (e.g. Alderweireldt, 1994), *I. tigrina* was included in the experiment as a potentially high quality prey for comparison instead of *D. melanogaster*, because first-instar *E. atra* are too small to handle fruit flies as prey.

Spiderlings were fed live prey in excess two or three times per week. Mainly first- and second-instar nymphs (in *R. padi* second- and third-instar nymphs) of aphids were given in order to homogenize prey sizes across treatments. Deaths and moults were recorded in daily inspections.

### Statistical analyses

The rate of egg sac production was analysed with repeated measures ANOVA. The number of eggs per egg sac was also analysed with repeated measures ANOVA, with log $(x + 1)$-transformed data to improve sphericity. The assumption of sphericity was tested (Mauchley's test), but only fulfilled once; then a univariate test was performed, otherwise multivariate tests were applied. Repeated measures ANOVA would also be the appropriate analysis for analysing hatching percentages of successive egg sacs, but it cannot cope with the missing values that appear when hatching success decreases with egg sac number; a large part of the data set is then excluded from the analysis. Hatching success (arcsine-transformed) was therefore analysed using a two-way ANOVA, with diet and egg sac number as main effects. Egg sac number was coded as an ordinal factor to analyse for effects of maternal age. Hatching time of egg sacs was analysed using a two-way ANOVA, with diet treatment and egg sac number (ordinal factor) as main effects. Size of young was analysed using a compound nested ANOVA, with the mothers nested under treatment in order to account for maternal effects apart from the experimental diet. Adjusted means of cephalothorax length, width, and length : width ratio were calculated as least squares means, which are predicted values across the levels of a categorical effect. Survival data were analysed with log-rank tests (cf. Pyke & Thompson, 1986). The significance level $\alpha = 0.05$.

## Results

### Egg sac production

Overall, there were significant differences among diet treatments in the number of egg sacs produced (ANOVA, log-transformed data, $F = 35.98$, d.f. = 7, $P < 0.001$). Females on aphid-only diets produced only two or three egg sacs each, whereas females on fruit fly diets produced 10–12 egg sacs (Fig. 1). No difference in egg sac number was found within the aphid-only diet groups (ANOVA, $F = 0.35$, d.f. = 3, $P = 0.78$). Within fruit fly diet groups, spiders fed *D. melanogaster* + *S. avenae* produced fewer egg sacs than spiders in the three other treatments (ANOVA, $F = 3.69$, d.f. = 3, $P < 0.05$; pairwise comparisons, Fishers LSD, $P < 0.05$). Neither *D. melanogaster* + *M. dirhodum* nor *D. melanogaster* + *R. padi* differed from the pure *D. melanogaster* treatment. Thus, *M. dirhodum* and *R. padi* were neutral additions to the *D. melanogaster* diet, whereas *S. avenae* had a negative effect. No difference was found in the rate of egg sac production within the aphid-only diet groups (repeated measures ANOVA of dates of laying egg sacs 1–3; time × treatment, $F = 1.01$, d.f. = 6, $P = 0.43$). Within the fruit fly diet groups, a significant interaction was found, indicating that egg sac production rate differed between treatments (egg sacs 1–7, time × treatment, $F = 1.77$, d.f. = 18, $P < 0.05$, cf. Fig. 1). Initially, spiders in the *D. melanogaster* + *R. padi* diet group produced egg sacs at a similar rate as *D. melanogaster* + *S. avenae*-fed spiders, but
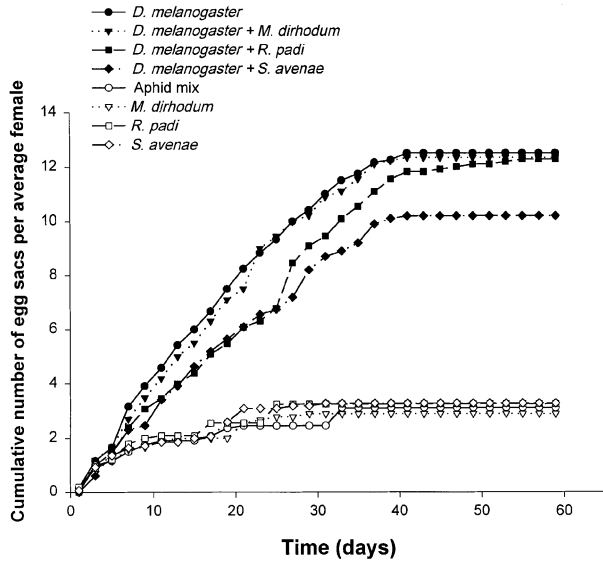
**Fig. 1.** Egg sac production by the average female *Erigone atra* on eight diet treatments. The asymptotic levelling off is due to the decreasing fraction of females that produced egg sacs towards the end of the experimental period.

with time they caught up with the egg-laying rate of spiders in the other two fruit fly diet groups.

*Number of eggs per egg sac*

An overall analysis of the first three egg sacs showed differences between diet treatments in number of eggs per egg sac (repeated measures ANOVA, $F = 3.45$, d.f. $= 7$, $P = 0.01$; Fig. 2a). Within the aphid-only diet groups, no difference between diets was found ($F = 1.96$, d.f. $= 3$, $P = 0.16$); egg numbers declined in successive egg sacs (univariate test, $F = 80.80$, d.f. $= 2$, $P < 0.001$); the rate of decline was the same in all treatments (interaction: diet $\times$ egg sac number, $F = 1.63$, d.f. $= 6$, $P = 0.17$). Analysing the first seven egg sacs of the fruit fly diet groups, there was both a significant diet effect ($F = 3.88$, d.f. $= 3$, $P < 0.05$) and a decline in egg numbers with time ($F = 4.04$, d.f. $= 6$, $P < 0.01$), but no significant interaction, implying a similar rate of decline across diet treatments. A lower number of eggs per egg sac was laid by the *D. melanogaster* + *S. avenae*-fed spiders compared to the other fruit fly diet groups (contrast, egg sacs 1–7, $P < 0.01$). No diet effect was found when the *D. melanogaster* + *S. avenae* diet group was excluded from the analysis ($F = 0.67$, d.f. $= 2$, $P = 0.51$). Total egg numbers per average female are shown in Fig. 2b. Clearly, the spiders fed *D. melanogaster* + *S. avenae* produced fewer eggs than spiders on a pure *D. melanogaster* diet, with the *D. melanogaster* + *M. dirhodum* and *D. melanogaster* + *R. padi* groups showing the same tendency. Overall, there was no positive effects on egg production of mixing aphids with fruit flies but a negative effect on spiders fed *D. melanogaster* + *S. avenae*.
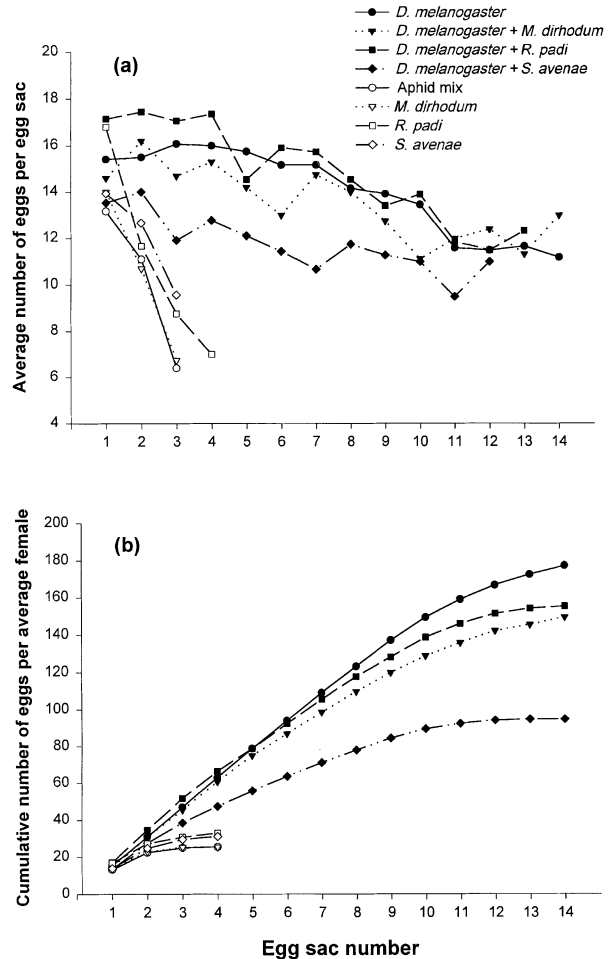


**Fig. 2.** (a) Average number of eggs laid in successive egg sacs by *Erigone atra* on eight diet treatments. (b) Cumulative number of eggs laid as a function of egg sac number by an average *Erigone atra* female on eight diet treatments. For clarity SE is not shown. The asymptotic levelling off is due to the decreasing fraction of females that produced high numbers of egg sacs.

*Hatching success*

For the first three egg sacs hatching success was high (70–100%) and no difference was found among the eight diet treatments (two-way ANOVA, egg sacs 1–3, $F = 0.43$, d.f. $= 7$, $P = 0.87$). Hatching success then declined at a steady rate to 30–60% in egg sac 7, approaching 0–20% in later egg sacs. No effect of diet treatment on hatching success was found when analysing the four fruit fly diet groups separately for egg sacs 1–7 (diet, $F = 0.17$, d.f. $= 3$, $P = 0.91$). Hatching success declined with successive egg sac number ($F = 10.05$, d.f. $= 6$, $P < 0.001$), but no interaction was found, indicating that hatching success decreased at a similar rate in all treatments. Repeating the analysis on the sum of developed eggs, larvae, and young gave a similar result, with no diet effect (egg sacs 1–7, $F = 0.05$, d.f. $= 3$, $P = 0.98$), but a significant decrease in

hatching success with egg sac number ($F = 6.67$. d.f. $= 6$, $P < 0.001$).

The number of spiderlings produced per average female represents the reproductive success on a diet (Fig. 3b). No differences in the production of spiderlings were found within the aphid-only diet groups (ANOVA, total number of young produced, $F = 1.44$, d.f. $= 3$, $P = 0.24$). Within the fruit fly diet groups, the lowest number of young per female was found in the *D. melanogaster* + *S. avenae* group (ANOVA, total number of young produced, $F = 3.0$, d.f. $= 3$, $P < 0.05$; contrast *D. melanogaster* + *S. avenae* vs. *D. melanogaster*, $P < 0.05$), because of a lower number of eggs per female produced in this group (Fig. 2).

Hatching time in days from egg laying to emergence of young from the egg sac increased with successive egg sac number from 13.16 days $\pm$ 1.10 (mean $\pm$ SE) in egg sac 1 to 15.14 $\pm$ 0.21 in egg sac 6 (two-way ANOVA, all diet treatments, egg sacs 1–3, $F = 10.34$, d.f. $= 2$, $P < 0.001$). No difference was found between diet treatments ($P = 0.88$) and no diet $\times$ egg sac number interaction ($P = 0.82$), implying that hatching time increased with egg sac number at the same rate in all treatments. When analysing egg development time in the first six egg sacs of the fruit fly diet groups separately, a similar result was found; hatching time increased with egg sac number ($F = 16.42$, d.f. $= 5$, $P < 0.001$), with no effects of diet ($P = 0.92$) or interaction ($P = 0.70$).

*Offspring size*

The length and the width of the cephalothorax of first-instar offspring of females from the eight diet treatments are shown in Fig. 4. The length of the cephalothorax decreased with egg sac number (egg sacs 1–3) in all diet treatments (compound nested ANOVA with mothers nested under treatment, egg sacs 1–3; $F = 11.63$, d.f. $= 140$, $P < 0.001$), but seemed to stabilize from egg sacs 3–6 in the fruit fly diet groups (Fig. 4a). Separate effects of diet ($F = 25.55$, d.f. $= 7$, $P < 0.001$) and of mother ($F = 10.74$, d.f. $= 87$, $P < 0.001$) on the length of the cephalothorax were significant, implying both experimental (diet) and other maternal factors determining spiderling size. There was a highly significant difference between the fruit fly and the aphid-only diet groups (contrast, fruit fly diet groups vs. aphid-only diet groups, $P < 0.001$; Fig. 4b); these two groups were subsequently analysed separately.

Within the aphid-only diet groups, significant effects of diet ($F = 32.12$, d.f. $= 3$, $P < 0.001$) and of mother ($F = 12.79$, d.f. $= 44$, $P < 0.001$) were found, as well as a decrease of cephalothorax length with egg sac number ($F = 14.40$, d.f. $= 56$, $P < 0.001$). Offspring from mothers fed *R. padi* and *M. dirhodum* had lower cephalothorax length than offspring from *S. avenae* and mixed-aphid diet (Fig. 4b). A ranking of diets after offspring cephalothorax length revealed *S. avenae* = mixed aphids > *M. dirhodum* > *R. padi* (contrast analyses, all $P < 0.001$ except *S. avenae* vs. mixed aphids, $P = 0.86$).

For egg sacs 1–6 of the fruit fly diet groups, highly significant effects of diet ($F = 8.48$, d.f. $= 3$, $P < 0.001$), mother
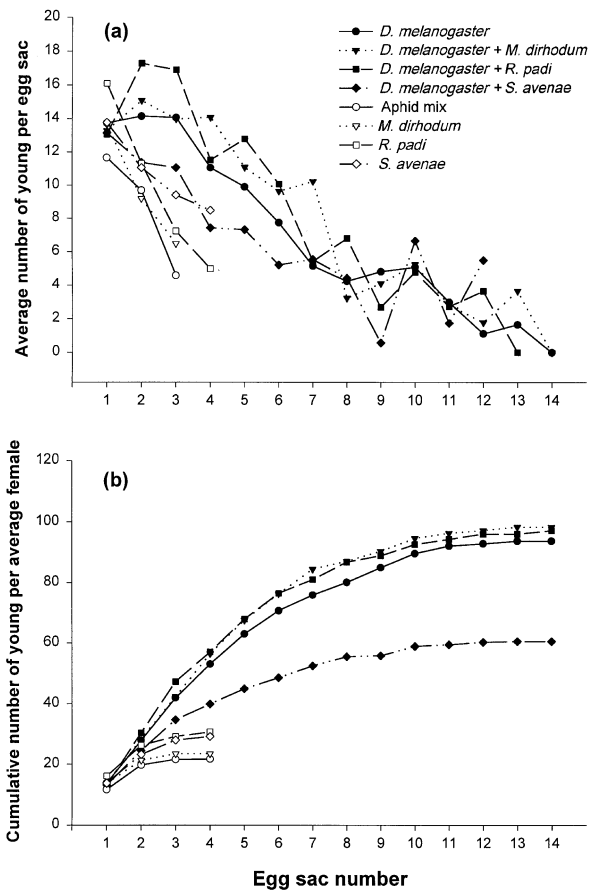


**Fig. 3.** (a) Average number of young hatched from successive egg sacs laid by *Erigone atra* on eight diet treatments. (b) Cumulative number of young hatched per average female from successive egg sacs laid by *Erigone atra* on eight diet treatments. For clarity SE is not shown.

($F = 8.83$, d.f. $= 43$, $P < 0.001$), and successive egg sac number ($F = 10.64$, d.f. $= 171$, $P < 0.001$) were found. Generally, the combination diets of aphid + fruit flies resulted in offspring with longer cephalothoraces than the pure *D. melanogaster* diet (contrasts, *D. melanogaster* + *M. dirhodum* vs. *D. melanogaster*, $P < 0.001$; *D. melanogaster* + *R. padi* vs. *D. melanogaster*, $P < 0.05$; *D. melanogaster* + *S. avenae* vs. *D. melanogaster*, $P = 0.052$). Offspring from the *D. melanogaster* + *M. dirhodum* diet group were larger overall than those from the two other aphid supplementation diet groups (contrasts, $P < 0.001$), which did not differ from each other (*S. avenae* + *D. melanogaster* vs. *R. padi* + *D. melanogaster*, $P = 0.61$). A ranking of *M. dirhodum* > *R padi* = *S. avenae* > *D. melanogaster* was revealed in the fruit fly diet groups.

Cephalothorax width apparently decreased with egg sac number within the aphid-only diet groups, but not in the fruit fly diet groups (Fig. 4a). For all diet groups, the overall analysis on egg sacs 1–3 revealed highly significant main effects (diet, $F = 6.56$, d.f. $= 7$, $P < 0.001$; mother, $F = 6.52$, d.f. $= 87$, $P < 0.001$; egg sac number, $F = 6.09$, d.f. $= 140$,

(a)



(b)



(c)
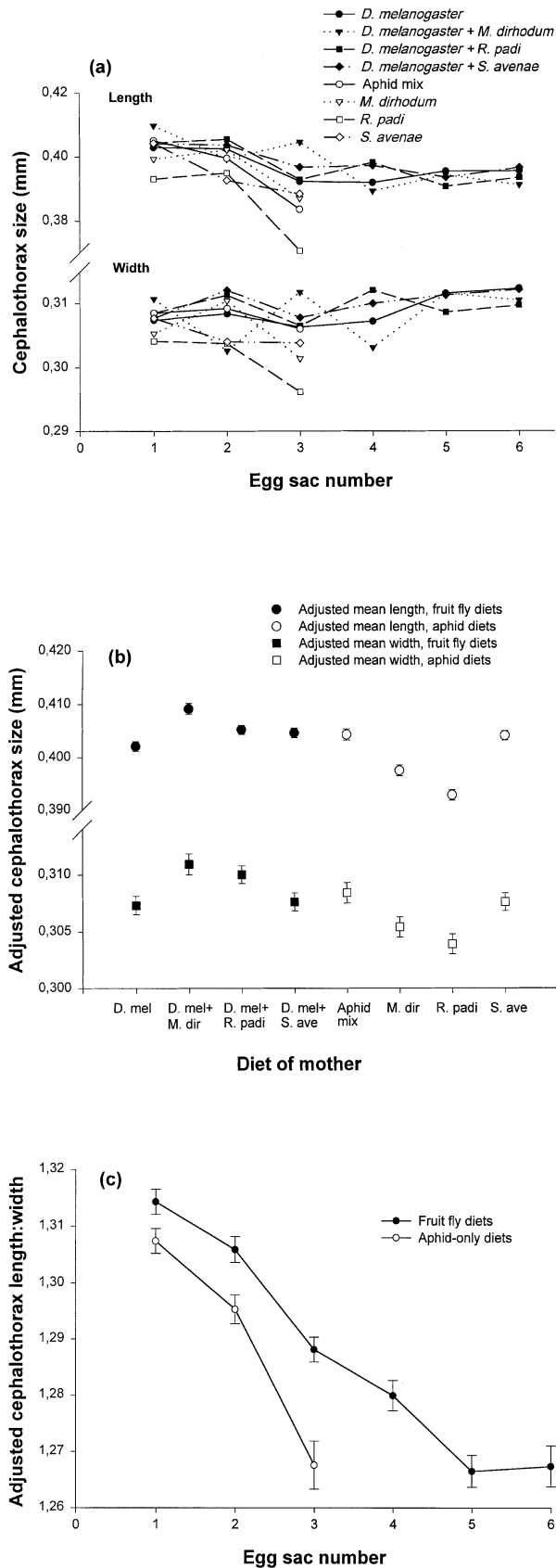
$P < 0.001$). Offspring from the fruit fly diet groups were wider than those from the aphid-only diet groups (contrast, $P < 0.001$). Analysing the aphid-only diet groups separately, the main effects were significant (diet, $F = 5.62$, d.f. $= 3$, $P < 0.001$; mother, $F = 7.32$, d.f. $= 44$, $P < 0.001$) and cephalothorax width decreased with egg sac number ($F = 5.60$, d.f. $= 56$, $P < 0.001$); a similar ranking of aphid diets by width as by length was found (Fig. 4b). In the fruit fly diet groups, significant effects of diet (egg sacs 1–6, $F = 4.44$, d.f. $= 3$, $P < 0.01$), mothers ($F = 6.12$, d.f. $= 43$, $P < 0.001$) and egg sac number ($F = 6.77$, d.f. $= 171$, $P < 0.001$) were found. Overall, addition of aphids to fruit flies resulted in larger offspring (Fig. 4b). A ranking of *M. dirhodum* $= R$ *padi* $> S.$ *avenae* $= D.$ *melanogaster* was revealed in the fruit fly diet groups.

Offspring of all diet groups apparently changed shape with egg sac number. In the aphid-only diet groups, cephalothorax length was reduced at a higher rate than cephalothorax width, while in the fruit fly diet groups, length but not width was reduced with egg sac number. The length : width ratio, shown as adjusted least squares means across treatments in Fig. 4c, thus declined with egg sac number in both diet groups (two-way ANOVA, egg sacs 1–3, effects of diet, $F = 2.82$, d.f. $= 7$, $P < 0.01$; and egg sac number, $F = 62.07$, d.f. $= 2$, $P < 0.001$). A steeper decline was found in the aphid-only diet groups than in the fruit fly diet groups (interaction diet $\times$ egg sac, $P < 0.01$).

In summary, dietary mixing of aphids and fruit flies seemed to increase offspring size relative to the pure diet of *D. melanogaster*, with addition of *M. dirhodum* resulting in the largest offspring. *S. avenae* and the mixed-aphid diet resulted in largest offspring size within the aphid-only diets. Changes in the length : width ratio of cephalothorax revealed effects of maternal age on offspring size and shape. Maternal effects other than experimental diet on offspring size was also revealed.

### Survival and development of juveniles of E. atra

Survival was relatively high on diets of *M. dirhodum* and *R. padi*, lower on *S. avenae*, and poor on the collembolan diet (Fig. 5). Significant overall diet effects were revealed (log-rank test, $P < 0.001$). No difference in survival was found between *M. dirhodum* and *R. padi* (pairwise log-rank comparisons, the significance level $\alpha = 0.05$ corrected with sequential Bonferroni adjustment (Rice, 1989), $P = 0.22$), whereas survival on the *S. avenae* diet was significantly lower than

**Fig. 4.** (a) Average size (cephalothorax length and width) of first-instar spiderlings hatched from successive egg sacs laid by *Erigone atra* on eight diet treatments. For clarity SE is not shown. (b) Mean $\pm$ SE cephalothorax length and width adjusted for egg sac-number of first-instar spiderlings produced by *Erigone atra* on eight diet treatments. (c) Mean $\pm$ SE cephalothorax length : width ratios adjusted for diet treatment of first-instar spiderlings hatched from successive egg sacs laid by *Erigone atra* on fruit fly diets and aphid-only diets (four diets combined in each line).
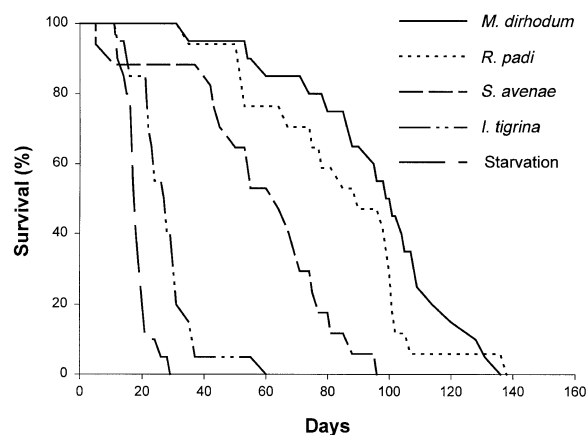
**Fig. 5.** Survivorship curves for hatchlings of *Erigone atra* fed single-species diets of the aphid *M. dirhodum*, *R. padi*, *S. avenae*, the collembolan *Isotoma tigrina* and a starvation control.

**Table 1.** Index of diet quality. The aphid species *M. dirhodum*, *R. padi* and *S. avenae* were ranked (1 = best, 3 = worst) by their contribution to each fitness parameter measured in *Erigone atra* fed single-species aphid diets and mixed-species aphid-fruit fly diets.

|  | *M. dirhodum* | R. padi | S. avenae |
|---|---|---|---|
| Aphid-diets |  |  |  |
| Eggsacs | 2 | 2 | 2 |
| Eggs | 2 | 2 | 2 |
| Hatching success | 2 | 2 | 2 |
| Survival | 1.5 | 1.5 | 3 |
| Percent moulting | 1 | 2.5 | 2.5 |
| Σ scores | 8.5 | 10 | 11.5 |
| Aphid-fruit fly diets |  |  |  |
| Eggsacs | 1.5 | 1.5 | 3 |
| Eggs | 1.5 | 1.5 | 3 |
| Hatching success | 2 | 2 | 2 |
| Σ scores | 5 | 5 | 8 |
| Overall ranking | 1 | 2 | 3 |

on the two other aphid diets ($P < 0.001$). Survival of the Collembola-fed spiders was better than that of starved spiders ($P < 0.001$) but lower than *S. avenae*-fed spiders ($P < 0.001$). Although many spiders survived for several months (Fig. 5), none developed beyond the second instar. Of the aphid-fed spiderlings, 80.0% on the *M. dirhodum* diet, 47.0% on *R. padi*, and 52.9% on the *S. avenae* diet moulted to second instar, while no spiders in the *I. tigrina* or starvation treatments went through a single moult (likelihood ratio, $\chi^2$-test, $P < 0.001$). Pairwise comparisons between the three groups of aphid-fed spiders revealed differences in moulting percentages between *M. dirhodum*- and *R. padi*-fed spiders ($P < 0.05$) but not between *M. dirhodum*- and *S. avenae*-fed spiders ($P = 0.07$). Overall, survival revealed a ranking of prey species with *M. dirhodum* > *R. padi* > *S. avenae* > *I. tigrina*. No detrimental effect of prey on survival was found, as mortality in all diet treatments was lower than for the starved controls.

### Ranking of aphid species

The aphid species were ranked by their contribution to each of the measured fitness parameters both in single-species and mixed-species diets (Table 1). The size of offspring was not included in the ranking, as these indirect effects could not be interpreted unequivocally. An overall ranking of *M. dirhodum* > *R. padi* > *S. avenae* was found.

## Discussion

### Egg production

Spiders in the fruit fly diet groups produced significantly more eggs than those in the aphid-only diet groups. The rapid decline in egg sac and egg production in the single-species and mixed-aphid diet groups compared to the fruit fly diet groups, indicates an energy deficiency in the aphid-fed spiders, which

could be due to low consumption rates of aphids as demonstrated in a previous study (Bilde & Toft, 1997a). The low consumption rate of *R. padi* could be caused by feeding deterrents or toxins in the aphid (cf. Toft, 1996). The aphid-fed spiders may have to use their body reserves for production of eggs and cease laying eggs when the energy reserves are depleted. No difference in egg production between the aphid-only diet treatments was found, indicating that the spiders gained no energy from *M. dirhodum* or *S. avenae* either. Mixing of aphid species also had no beneficial effects on egg production. There was no indication of beneficial effects of mixing aphids and fruit flies with respect to egg production. On the contrary, the *D. melanogaster* + *S. avenae*-fed spiders produced egg sacs at a lower rate and with fewer eggs than spiders in the other fruit fly treatments. In summary, these results demonstrate either a negative or, at best, no effect on egg production of mixing aphids with the high quality prey.

### Hatching success

In all diet treatments, hatching success was high for the first three egg sacs, then declined at a steady rate. Hatching success can be interpreted as an indicator of egg quality, which thus remained high in the aphid-only diet groups, although the number of eggs laid declined. Within the fruit fly diet groups, no improvement in hatching success of mixing with aphids was found. In a similar study, hatching success in eggs of *E. atra* was improved significantly when *R. padi* was mixed with fruit flies compared to a pure fruit fly diet (Toft, 1995); in that study, however, a shortage fruit fly diet was used in combination with aphids *ad libitum*. With a pure fruit fly diet, egg production was high but hatching success low, perhaps indicating excess availability of energy but limitation of nutrients (Toft, 1995). The improved hatching success implies that the spiders did extract nutrients from the aphids, despite the small amounts consumed. A decisive difference between the two experiments was probably in the quality of the fruit

flies used. Toft (1995) fed fruit flies reared on plain fruit fly medium while mothers in the present study were fed fruit flies reared on medium with addition of nutrients. It may be that the quality of fruit flies reared on a medium with nutrient additions was improved to such a degree that mixing with *R. padi* could add nothing of significance. A direct comparison of the results of the pure *D. melanogaster* diets fed *ad libitum* in the two experiments reveals a substantially higher egg production, hatching success and total number of young per female on the nutritionally improved fruit flies. *Drosophila melanogaster* reared on plain fruit fly medium was of only intermediate value to the wolf spider *Schizocosa* sp. (Toft & Wise, 1999a), whereas nutritionally improved fruit flies, as used in the present study, were of superior quality (C. Kristensen and S. Toft, unpublished observations). When assessing the value of a prey species to a predator, it appears to be necessary to take into consideration what the prey itself has fed on or been reared on. This may refer to the nutrient composition, as in the above mentioned examples, or to defensive chemicals sequestered from the prey's food. Eisner & Eisner (1991) found that a wolf spider rejected a moth species which had developed on alkaloid-containing host plants or on artificial diets where alkaloid had been added, whereas the moth was readily accepted when reared on an artificial diet containing no alkaloids. Malcolm (1989) found an araneid spider to build disrupted webs after feeding on aphids containing cardenolides derived from the host plant.

When spiders are fed an intermediate value prey (as *D. melanogaster* reared on plain medium), it can be expected that they include low value prey such as *R. padi* in their diet to optimize nutrient composition. This was partly confirmed in a later study, where aphids combined with intermediate quality flies and enriched flies, respectively, were tested as food for a spider (Bilde & Toft, 2000a). Adding aphids to enriched flies did not improve spider performance, whereas adding aphids to intermediate quality flies improved the quality of offspring (Bilde & Toft, 2000a). The low quality prey might thus be excluded from the diet in situations of abundant high quality prey, such as nutritionally improved *D. melanogaster*. Consequently, the value of a prey species such as an aphid, cannot be categorized on an absolute scale, but must be evaluated in the context of alternative prey species and of previous prey consumption (i.e. present nutrient balance) of the predator.

### Survival of young

The survivorship experiment revealed a ranking of aphids with *M. dirhodum* over *R. padi* and *S. avenae*. Although survival of spiderlings fed *R. padi* was similar to those fed *M. dirhodum*, a higher proportion of spiders on the *M. dirhodum* diet moulted; however, none of the aphid species tested supported any growth of significance. Under similar experimental conditions with an excess of isotomid Collembola and *D. melanogaster*, *E. atra* completed development to maturity in only 18 days (De Keer & Maelfait, 1988b). The fact that 80% of the *M. dirhodum*-fed spiders moulted,

indicates that they gained slightly more from this species than from the other two aphid species. The lowest survival was found on *S. avenae*; this species also proved to be low quality prey to hatchlings of the linyphiid spider *Lepthyphantes tenuis*, which survived only 14 days, with only 2% of spiders completing two moults on a single-species diet of *S. avenae* (Sunderland *et al.*, 1996a). In a survivorship experiment (Toft, 1995), where first-instar *E. atra* fed *R. padi* were compared with a group of starved spiders, spiders on *R. padi* survived less than half as long as they did in the present study, whereas survival of starved spiders were approximately the same. One difference between the two studies was temperature, which was 16°C in the early study and 20°C in the present study; from the temperatures, better survival would have been expected in the earlier study. Another major difference was in the quality of the fruit flies of the mothers' diet. Toft (1995) fed intermediate quality fruit flies, whereas mothers in the study reported here were fed nutritionally improved fruit flies. The difference in survival (50% survival at ~25 days compared to ~ 90 days in the study reported here) might be ascribed to the diet of the mothers.

The finding that the collembolan *I. tigrina* was of lower quality than the aphids in the survival experiment was unexpected, because the spiders seemed to feed much more readily on the Collembola than on the aphids. The Collembola seemed to be highly palatable, but was of no food value to the spiders. Apparently, the Collembola lacks feeding deterrents, leading to high consumption rates, but no benefit for the spider. *Isotoma tigrina* may contain chemical substances with negative post-ingestive effects; these are then consumed readily with the Collembola.

### The size of offspring

Effects of maternal diet on the size of the offspring were revealed. Whereas no positive effects of feeding on aphids in either single-species or mixed-species diets were found on egg production and hatching success, combined *M. dirhodum*-fruit fly and *R. padi*-fruit fly diets increased the size of offspring size in comparison with the pure fruit fly diet. Although *S. avenae* in combination with fruit flies had negative effects on egg production, as a single-species diet this aphid resulted in larger offspring than the other two aphid species. Toft (1995) also found effects of maternal (*E. atra*) diet on offspring size, with larger offspring produced on a mixed diet of *R. padi* and *D. melanogaster* than on a pure diet of *D. melanogaster*, and the smallest offspring on a single-species *R. padi* diet. These results were consistent with the finding of improved hatching success and increased production of young on the *R. padi*-fruit fly diet compared with the single-species fruit fly diet, and demonstrated overall beneficial effects on spider performance of mixing the aphid with fruit flies (Toft, 1995). It is hypothesized that positive effects of mixing aphids with fruit flies was not found in the study reported here because the fruit flies had been improved nutritionally, so that the aphids could not contribute further. So why are positive effects of aphids on the size of offspring found? Considering aphids as

poor quality food, increasing size of offspring can be seen as a response that improves chances of survival of offspring in a habitat with low quality of available food. Size is a phenotypic factor that affects fitness parameters such as survival (Wallin *et al.*, 1992; Tanaka, 1995) and fecundity (Gilbert, 1984; Juliano, 1985; Honek, 1993). By increasing the size of the offspring, fitness may be maximized in a stressed environment, but then a trade-off with egg production would be expected (Solbreck *et al.*, 1989; Gilbert, 1990; Stewart *et al.*, 1991). All mixed aphid-fruit fly diets actually did result in a lowered total output of eggs, although only the *S. avenae* + *D. melanogaster* diet was significantly different from the pure *D. melanogaster* diet.

### Effects of maternal age

The length and width of the cephalothorax were generally correlated isometrically, but the relationship between them changed with maternal age. The causes of the change are unknown, as are the consequences for juvenile survival. Hatching time also increased in successive egg sacs from ≈ 13 to 15 days; the latter is the value reported by Van Praet & Kindt (1979), although they neglected maternal age. De Keer & Maelfait (1988b) found that eggs of *E. atra* were not viable after the fourth egg sac, although females produced up to 10 egg sacs. Viability of eggs decreased with the age of the mother in a carabid beetle (Nelemans, 1987). The reproductive potential of *E. atra* may be limited even under favourable food conditions, so that eggs in excess of the number possible under normal conditions decrease in quality or become sterile.

### Effects of aphid species

In mixed diets with fruit flies, the effects of added *M. dirhodum* and *R. padi* were neutral, whereas inclusion of *S. avenae* had a negative effect on egg production. This is an interesting result because it reveals a 'toxic' effect of the aphid in the sense that inclusion of the aphid in the diet reduces the fitness of the spider. In earlier experiments on food consumption, *M. dirhodum* and *S. avenae* have generally been of higher palatability for the predators than *R. padi* (Bilde & Toft, 1997b; Jørgensen & Toft, 1997). Differences in palatability would lead to variable amounts of the different aphid species consumed by the predator, and may thus cause differences in intake of toxins from the aphids. In the case of *R. padi*, which has an extremely low palatability to spiders (Toft, 1995; Bilde & Toft, 1997a), a low rate of consumption would lead to a low rate of intake of possible toxins. If *S. avenae* is of higher palatability to spiders than *R. padi*, they would consume a larger amount of this species and toxic effects might be revealed. In growth experiments with the wolf spider *Schizocosa* sp. on a pure diet of fruit flies and a mixed diet of the collembolan *Folsomia candida* and fruit flies, the mixed diet caused a decrease in growth efficiency of the spiders (Toft & Wise, 1999b). If the effect of the aphid food is similar, adding *S. avenae* to *D. melanogaster* would prevent the spider

from making full use of the fruit fly food. Thus, potentially positive nutritional effects of the aphids in mixed diets may be counteracted by negative effects of their toxins.

The aphids used in the experiments were homogenized for size, which means that spiders were fed aphids of different age and stage. Toft, 2000) found that food value of *R. padi* to spiders decreased with aphid age, indicating that aphids increase their investment in chemical defence with age. Because the spiders were fed young *S. avenae* and adult *R. padi* the effect of aphid species would have been even more pronounced if aphids of same age-class had been used.

A main conclusion from the experiments reported here is that all three cereal aphid species were of low value as food for *E. atra*. Some differences in the value of the three aphid species was found, with a ranking of *M. dirhodum* > *R. padi* > *S. avenae*, as summarized by the index of diet quality in Table 1. Notice that although the single rankings do not agree in detail, none contradicts the overall result. No difference in ranking was found in the fecundity experiment of aphid-only diets, whereas a lower ranking of *S. avenae* than of the other two aphid species was found in the fecundity experiment of aphid-fruit fly diets. A ranking of *M. dirhodum* > *R. padi* > *S. avenae* was found in the experiment of juvenile development and survivorship, which means that there is accordance between the ranking of aphid species for the different fitness parameters measured. In both diet groups, *S. avenae* had the highest score (= lowest quality), whereas *M. dirhodum* obtained the overall lowest score and highest ranking. Indications from earlier studies that *M. dirhodum* is of the highest palatability or quality of the three aphid species for predators (Bilde & Toft, 1997b; Jørgensen & Toft, 1997; Toft, 1997; Hauge *et al.*, 1998) is thus supported by the study reported here.

### Implications for predation on cereal aphids

The poor value of aphids as prey for *E. atra* implies that large predation rates of cereal aphids in the field would not be expected. Generalist predators are characterized by utilizing a variety of prey types in mixed diets in the field. It is often assumed that dietary mixing improves the performance of predators by optimizing nutrient composition of diets (Wallin *et al.*, 1992; Uetz *et al.*, 1992; review in Sunderland *et al.*, 1996a). However, this might be a generalization, because evidence that mixed diets does not necessarily improve predator performance compared to a single-species diet of high nutritional quality is increasing (cf. results of the present study; Sunderland *et al.*, 1996b; Marcussen *et al.*, 1999; Toft & Wise, 1999a). An improved effect of dietary mixing seems to depend on the quality of alternative prey available for the predators. Mixing of species of cereal aphids has not so far proved beneficial for predator performance (cf. present study; Toft & Nielsen, 1997; Hauge *et al.*, 1998; Bilde & Toft, 1999), while mixing of aphids with fruit flies in some cases improves predator egg production, hatching success or offspring survival compared to single-species diets of both prey species (Bilde & Toft, 1994, 2000a; Toft, 1995). A consequence of improved

performance of dietary mixing could be that predators accepted more less-preferred prey such as aphids in order to optimize nutrient composition. As it is clear that *E. atra* as well as other species of arthropod generalist predators in the field include cereal aphids in their diet (Nyffeler, 1982; Nentwig, 1983; Chiverton, 1987; Sunderland *et al.*, 1987; Alderweireldt, 1994) despite their low prey value, it is likely that alternative prey is either scarce (Baars & van Dijk, 1984; Sota, 1985; Juliano, 1986; Bilde & Toft, 1999) or of low or intermediate quality (Marcussen *et al.*, 1999; Toft & Wise, 1999a; Bilde & Toft, 2000b). Further studies of the mechanism underlying the foraging behaviour of dietary mixing by determining the quality of each prey item in the natural diet separately, may provide further insight into why generalist predators include low quality prey in their diets.

## Acknowledgements

## References

Alderweireldt, M. (1994) Prey selection and prey capture strategies of linyphiid spiders in high-input agricultural fields. *Bulletin of the British Arachnological Society*, **9**, 300–308.

Baars, M.A. & van Dijk, T.S., (1984) Population dynamics of two carabid beetles at a Dutch heathland. II. Egg production and survival in relation to density. *Journal of Animal Ecology*, **53**, 389–400.

Bilde, T. & Toft, S. (1994) Prey preference and egg production of the carabid beetle *Agonum dorsale*. *Entomologia Experimentalis et Applicata*, **73**, 151–156.

Bilde, T. & Toft, S. (1997a) Limited predation capacity by generalist arthropod predators on the cereal aphid *Rhopalosiphum padi*. *Biological Agriculture and Horticulture*, **15**, 143–150.

Bilde, T. & Toft, S. (1997b) Consumption by carabid beetles of three cereal aphid species relative to other prey types. *Entomophaga*, **42**, 21–32.

Bilde, T. & Toft, S. (1999) Prey consumption and fecundity of the carabid beetle *Calathus melanocephalus* on diets of three cereal aphids: high consumption of low-quality prey. *Pedobiologia*, **43**, 422–429.

Bilde, T. & Toft, S. (2000a) Evaluation of prey for the linyphiid spider *Dicymbium brevisetosum* in single-species and mixed-species diets. *Ekológia (Bratislava)*, **19** (Suppl. 3), 9–18.

Bilde, T. & Toft, S. (2000b) The value of Collembola from agricultural soils as food for a generalist predator. *Journal of Applied Ecology*, **37**, 672–683.

Chiverton, P.A. (1987) Predation of *Rhopalosiphum padi* (Homoptera: aphididae) by polyphagous predatory arthropods during the aphids' pre-peak period in spring barley. *Annals of Applied Biology*, **111**, 257–269.

De Keer, R. & Maelfait, J.-P. (1988a) Observations on the life cycle of *Erigone atra* (Araneae, Erigoninae) in a heavily grazed pasture. *Pedobiologia*, **32**, 201–212.

De Keer, R. & Maelfait, J.-P. (1988b) Laboratory observations on the development and reproduction of *Erigone atra* Blackwall, 1833 (Araneae, Linyphiidae). *Bulletin of the British Arachnological Society*, **7**, 237–242.

van Dijk, T.S. (1996) The influence of environmental factors and food on life cycle, ageing and survival of some carabid beetles. *Arthropod Natural Enemies in Arable Land II. Survival, Reproduction and Enhancement* (ed. by C. J. H. Booij and L. J. M. F. den Nijs). *Acta Jutlandica*, **71**, 11–24.

Edwards, C.A., Sunderland, K.D. & George, K.S. (1979) Studies on polyphagous predators of cereal aphids. *Journal of Applied Ecology*, **16**, 811–823.

Eisner, T. & Eisner, M. (1991) Unpalatability of the pyrrolizidine alkaloid-containing moth *Utetheisa ornatrix*, and its larvae, to wolf spiders. *Psyche*, **98**, 111–118.

Gilbert, N. (1984) Control of fecundity in *Pieris rapae* I. The problem. *Journal of Animal Ecology*, **53**, 581–588.

Gilbert, F. (1990) Size, phylogeny and life evolution of feeding specialization in insect predators. I*Insect Life Cycles, Genetics, Evolution and Co-ordination* (ed. by F. Gilbert), pp. 101–124. Springer, Berlin.

Griffiths, E., Wratten, S.D. & Vickerman, P. (1985) Foraging by the carabid *Agonum dorsale* in the field. *Ecological Entomology*, **10**, 181–189.

Hauge, M.S., Nielsen, F.H. & Toft, S. (1998) The influence of three cereal aphid species and mixed diet on larval survival, development and adult weight of *Coccinella septumpunctata* L. *Entomologia Experimentalis et Applicata*, **89**, 319–322.

Honek, A. (1993) Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos*, **66**, 483–492.

Janssens, J. & De Clercq, R. (1990) Observations on Carabidae, Staphylinidae and Araneae as predators of cereal aphids in winter wheat. *Mededelingen van de Faculteit Landbouwwetenschappen Rijksuniversiteit Gent*, **55**, 471–475.

Jørgensen, H.B. & Toft, S. (1997) Food preference, diet dependent fecundity and larval development in *Harpalus rufipes* (Coleoptera: Carabidae). *Pedobiologia*, **41**, 307–315.

Juliano, S.A. (1985) The effects of body size on mating and reproduction in *Brachinus lateralis* (Coleoptera: Carabidae). *Ecological Entomology*, **10**, 271–280.

Juliano, S.A. (1986) Food limitation of reproduction and survival for populations of *Brachinus* (Coleoptera, Carabidae). *Ecology*, **67**, 1036–1045.

Malcolm, S.B. (1989) Disruption of web structure and predatory behavior of a spider by plant-derived chemical defenses of an aposematic aphid. *Journal of Chemical Ecology*, **15**, 1699–1716.

Marcussen, B.M., Axelsen, J.A. & Toft, S. (1999) The value of two Collembola species as food for a cereal spider. *Entomologia Experimentalis et Applicata*, **92**, 29–36.

Nelemans, M.N.E. (1987) On the life history of the carabid beetle *Nebria brevicollis* (F.). *Netherlands Journal of Zoology*, **37**, 26–42.

Nentwig, W. (1983) The prey of web-building spiders compared with feeding experiments (Araneae; Araneidae, Linyphiidae, Pholcidae, Agelenidae). *Oecologia*, **56**, 132–139.

Nyffeler, M. (1982) *Field studies on the ecological role of the spiders as insect predators in agroecosystems (abandoned grassland, meadows and cereal fields)*. PhD Thesis, Swiss Federal Institute of Technology, Zürich.

Pyke, D.A. & Thompson, J.N. (1986) Statistical analysis of survival and removal rate experiments. *Ecology*, **67**, 240–245.

Rice, W.R. (1989) Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.

Solbreck, C., Olsson, R., Anderson, D.B. & Förare, J. (1989) Size, life history and responses to food shortage of two geographical strains of a seed bug *Lygaeus equestris*. *Oikos*, **55**, 387–396.

Sopp, P. & Chiverton, P. (1987) Autumn predation of cereal aphids by polyphagous predators in Southern England: a 'first look' using ELISA. *Bulletin SROP/WPRS*, **1987**, 103–108.

Sopp, P., Sunderland, K.D. & Coombes, D.S. (1987) Observations on the number of cereal aphids on the soil in relation to aphid density in winter wheat. *Annals of Applied Biology*, **111**, 53–57.

Sota, T. (1985) Limitation of reproduction by feeding condition in a carabid beetle *Carabus yaconicus. Researches on Population Ecology*, **27**, 171–184.

Stephen, D.W. & Krebs, J.R. (1986) *Foraging Theory*. Princeton University Press, Princeton, New Jersey.

Stewart, L.A., Hemptinne, J.-L. & Dixon, A.F.G. (1991) Reproductive tactics of ladybird beetles: relationships between egg size, ovariole number and developmental time. *Functional Ecology*, **5**, 380–385.

Sunderland, K.D., Bilde, T., Den Nijs, L.J.M.F., Dinter, A., Heimbach, U., Lys, J.A. *et al.* (1996a) Reproduction of beneficial predators and parasitoids in agroecosystems in relation to habitat quality and food availability. *Arthropod Natural Enemies in Arable Land II. Survival, Reproduction and Enhancement* (ed. by C. J. H. Booij and L. J. M. F. den Nijs). *Acta Jutlandica*, **71**, 117–153.

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.

Sunderland, K.D., Fraser, A.M. & Dixon, A.F.G. (1986a) Field and laboratory studies on money spiders (Linyphiidae) as predators of cereal aphids. *Journal of Applied Ecology*, **23**, 433–447.

Sunderland, K.D., Fraser, A.M. & Dixon, A.F.G. (1986b) Distribution of linyphiid spiders in relation to capture of prey in cereal fields. *Pedobiologia*, **29**, 367–375.

Sunderland, K.D., Topping, C.J., Ellis, S., Long, S., Van de Laak, S. & Else, M. (1996b) Reproduction and survival of linyphiid spiders, with special reference to *Lepthyphantes tenuis* (Blackwell). *Arthropod Natural Enemies in Arable Land II. Survival, Reproduction and Enhancement* (ed. by C. J. H. Booij and L. J. M. F. den Nijs). *Acta Jutlandica*, **71**, 81–95.

Tanaka, K. (1995) Variation in offspring size within a population of the web-building spider. *Agelena Limbata. Research in Population Ecology*, **37**, 197–202.

Toft, S. (1995) Value of the aphid *Rhopalosiphum padi* as food for cereal spiders. *Journal of Applied Ecology*, **32**, 552–560.

Toft, S. (1996) Indicators of prey quality for arthropod predators. *Arthropod Natural Enemies in Arable Land II. Survival, Reproduction and Enhancement* (ed. by C. J. H. Booij and L. J. M. F. den Nijs). *Acta Jutlandica*, **71**, 107–116.

Toft, S. (1997) Acquired food aversions of a wolf spider to three cereal aphids: intra- and interspecific effects. *Entomophaga*, **42**, 63–69.

Toft, S. (2000) Species and age effects in the value of cereal aphids as food for a spider. *Ekológia (Bratislava)*, **19** (Suppl. 3), 273–278.

Toft, S. & Nielsen, S.A. (1997) Influence of diet quality on the respiratory metabolism of a Wolf spider *Pardosa prativaga. Proceedings of the 16th European Colloquium of Arachnology*, 301–307. Siedlce, Poland.

Toft, S. & Wise, D.H. (1999a) Growth, development and survival of a generalist predator fed single- and mixed-species diets of different quality. *Oecologia*, **119**, 191–197.

Toft, S. & Wise, D.H. (1999b) Behavioral and ecophysiological responses of a generalist predator to single- and mixed-species diets of different quality. *Oecologia*, **119**, 198–207.

Uetz, G.W., Bischoff, J. & Raver, J. (1992) Survivorship of Wolf spiders (Lycosidae) reared on different diets. *Journal of Arachnology*, **20**, 207–211.

Van Praet, H. & Kindt, C. (1979) Influence de la température sur le développement embryonnaire d'*Erigone atra* (Blackwall) et d'*Oedothorax fuscus* (Blackwall) (Araneida: Linyphiidae). *Biologisch Jaarboek*, **47**, 107–116.

Vickerman, G.P. & Wratten, S.D. (1979) The biology and pest status of cereal aphids (Hemiptera: Aphididae) in Europe: a Review. *Bulletin of Entomological Research*, **69**, 1–32.

Wallin, H., Chiverton, P.A., Ekbom, B.S. & Borg, A. (1992) Diet, fecundity and egg size in some polyphagous predatory carabid beetles. *Entomologia Experimentalis et Applicata*, **65**, 129–140.