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EVALUATION OF PREY FOR THE SPIDER *DICYMBIUM BREVISETOSUM* LOCKET (ARANEAE: LINYPHIIDAE) IN SINGLE-SPECIES AND MIXED-SPECIES DIETS

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Abstract

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The objective of this study was to asses effects of dietary mixing of prey of different quality for a generalist predator. Prey of three qualities were tested in single-species and mixed-species diets: the cereal aphid *Rhopalosiphum padi* as a low quality prey, and two qualities of fruit flies *Drosophila melanogaster* representing intermediate quality (Normal flies) and high quality (Enriched flies) prey. The two types of fruit flies were obtained by rearing the flies on different media. It was expected that aphids might contribute positively to the diet of intermediate quality flies, but contribute nothing or negatively to that of high quality flies. The value of prey was assessed by fitness parameters in an egg production experiment. Females of the linyphiid spider *Dicymbium brevisetosum* were assigned to one of 6 diet treatments: 1) Normal *D. melanogaster*, 2) Normal *D. melanogaster* + *R. padi*, 3) Enriched *D. melanogaster*, 4) Enriched *D. melanogaster* + *R. padi*, 5) *R. padi*, and 6) *R. padi* added to Normal *D. melanogaster* until the first eggsac appeared, then only *R. padi*. The following parameters were recorded: no. of egg sacs per female, no. of eggs/sac, and hatching success. Females on single-species diets of aphids produced fewer eggsacs containing fewer eggs than spiders on fruit fly diets. Normal flies supported a high egg laying rate but low hatching success compared to Enriched fruit flies. Mixing aphids with Normal fruit flies had no effect on the measured fitness parameters, whereas mixing aphids with Enriched flies resulted in a lower total production of spiderlings suggesting a toxic effect of aphids on spiders.
A survivorship experiment with hatchlings was conducted in order to investigate the effect of maternal diet on the offsprings´ ability to utilise a low quality prey (*R. padi*). Two hatchlings from each of the first eggsacs produced by females in the egg production experiment on diet treatments 1) Normal *D. melanogaster*, 2) Normal *D. melanogaster* + *R. padi*, 3) Enriched *D. melanogaster*, and 4) Enriched *D. melanogaster* + *R. padi,* were kept individually on a diet of *R. padi* and survival time was recorded. Maternal diet affected survival of those offspring feeding exclusively on *R. padi*. A lower survival was found on offspring from females reared on Normal fruit flies

compared to Enriched fruit flies, thus quality of offspring may vary with that of maternal diet. The results emphasise that effects of dietary mixing depend on the characteristics of the prey types composing the diet. Negative effects of adding aphids to Enriched flies was found by a lowered hatching success, while positive effects of adding aphids to Normal flies was found in the survival of offspring.

Introduction

Many spiders are polyphagous predators feeding on a varied range of prey types. It is often assumed that more than one prey type is needed to obtain a complete nutrient composition of the diet and polyphagy may be a feeding strategy for predators to optimise nutrient intake for successful growth, development and reproduction. Mixed diets frequently result in better growth rates and survival or in a higher fecundity than single-species diets, with several instances found in spiders (Miyashita, 1968; Suzuki, Kiritani 1974; Greenstone, 1979; Holmberg, Turnbull, 1982; Thang et al., 1990; Uetz et al., 1992; Toft, 1995; Toft, Wise, 1999). In some cases, however, mixed diets had no or even a negative effect on the measured fitness parameters compared to a pure diet of the best constituent (Sunderland et al., 1996; Marcussen et al., 1999; Toft, Wise, 1999; Bilde, Toft, submit.). Optimising nutrient composition of diet may not only be a question of prey mixing but of mixing the right types of prey or avoiding toxic prey (prey with defensive substances). The characteristics of prey which influence its quality as food was summarised by Toft (1996) as 1) energy gained per unit handling time (the traditional measure of prey quality (Stephen, Krebs, 1986)), 2) nutrient constituents, and 3) defensive substances. A prey with a high energy content may be deficient with respect to nutrients while defensive substances may reduce the quality of otherwise valuable prey.

In assessing the value of prey species Toft (1995) compared the cereal aphid *Rhopalosiphum padi* L. to fruit flies *Drosophila melanogaster* (Meig.) as food for the linyphiid spider *Erigone atra* (Blackwall) in single-species and mixed-species diets. In pure diets aphids were of extremely low quality and fruit flies of intermediate quality, measured by egg production rate and hatching success. The mixed diet of aphids and fruit flies improved the hatching success of eggs significantly, resulting in an overall much higher production of spiderlings than in the pure fruit fly groups (Toft, 1995). In a similar study three cereal aphid species (*R. padi*, *Sitobion avenae* (F.), *Metopolophium dirhodum* (Wlk.)) were assessed for *E. atra* in comparison with *D. melanogaster* (Bilde, Toft, submit.), but in contrast to the study of Toft (1995) the fruit flies were nutritionally improved by rearing them on an enriched medium. Mixing *R. padi* and *M. dirhodum* with fruit flies did not improve any of the measured fitness parameters relative to a pure diet of fruit flies, while *S. avenae* in combination with fruit flies reduced egg production of the spiders (Bilde, Toft, submit.). Apparently both positive, neutral and negative effects are possible outcomes of mixing aphids and fruit flies. The two studies suggest that the nutritional state of the fruit flies determined whether aphids contributed positively or negatively to spider fitness in a mixed diet. If the right prey type containing all necessary nutrients and a minimum of defensive substances is provided, no beneficial effects of mixing with other prey may be expected.

In the experiments reported here, three types of prey for a spider were evaluated: a low quality prey (the aphid *Rhopalosiphum padi*); an intermediate quality prey (Normal fruit flies *Drosophila melanogaster*, reared on plain medium); and a high quality prey (Enriched fruit flies, reared on nutritionally improved medium). Spiders were fed single-species diets and combinations of aphids and fruit flies in mixed diets to test the effect of mixing prey of different qualities. Diet quality was assessed by egg production and hatching success. The value of *R. padi* in mixed diets was expected to depend on the nutritional value of the fruit flies, i.e. positive effects of mixing aphids with Normal fruit flies, and no or negative effects of mixing with Enriched fruit flies. A survivorship experiment with hatchlings was performed to test the effect of maternal diet on offsprings´ ability to utilise a low quality prey (*R. padi*). It was hypothesised that offspring of females fed a nutritionally superior diet (Enriched fruit flies) would survive longer on a diet of aphids than offspring of females fed a deficient diet (Normal fruit flies).

Material and methods

The spider *Dicymbium brevisetosum* Locket, a small (c. 2-3 mm) sheet-web spider of the family Linyphiidae, was used in the experiments. Adult females and males were collected as aeronauts in the field on 1 April 1999. It is doubtful whether *D. brevisetosum* and *D. nigrum* (Blackwall) are separate species, and only males can be distinguished. All males collected (>100) had the *D. brevisetosum* characteristics. Spiders were kept at 5^0C until 17 April when the experiment was initiated. Throughout the experiment females and males were kept in pairs in cylindrical plastic tubes (h 6 cm, d 2 cm) with a base of plaster-of-Paris mixed with charcoal to maintain high humidity. The experiment was carried out at 20^0C and a photoperiod of 16L:8D.

The two qualities of fruit flies used in the experiments were reared on instant *Drosophila* medium (Formula 4-24 Plain, Carolina Biological Supply; Burlington, NC, USA): Normal flies were reared on plain medium and Enriched flies on medium mixed with crushed dog food (Techni-Cal maintenance®) to improve nutritional quality of the flies (Kristensen, Toft, unpubl.). The aphid species *R. padi* is one of the most abundant cereal aphids in Europe (Vickerman, Wratten, 1979). They were reared on wheat seedlings in laboratory cultures.

Eggsac production and number of offspring

Females were randomly assigned to one of 6 prey treatments: 1) Enriched *D. melanogaster*, 2) Enriched *D. melanogaster* + *R. padi*, 3) Normal *D. melanogaster*, 4) Normal *D. melanogaster* + *R. padi*, 5) *R. padi*, and 6) *R. padi* added to Normal *D. melanogaster* until the first eggsac appeared, then only *R. padi* (in the following termed “aphid + starter fly group”). Diets 1, 3, 5 and 6 are single-species diets, while diets 2 and 4 are mixed diets; diets 1-4 are termed the fruit fly diet groups and diets 5-6 the aphid-only diet groups. Replication was initially 20 females in each diet group, but due to some accidental deaths during the experiments and because females that never started egg laying were excluded from the analyses, sample sizes varied between 13-20 in the final analyses. The experiment was terminated when seven eggsacs had been laid by a female or after two months at most.

Spiders were watered and fed live prey in excess 2-3 times per week, so prey were always available. The tubes were checked daily for new eggsacs. When an eggsac appeared the female and male were transferred to a new plastic tube.

Eggsacs were kept under experimental conditions until hatching. Emergence date and number of hatchlings were recorded. Eggsacs were always dissected in order to record undeveloped eggs, embryos and larvae so that total egg number could be determined. Only eggs producing emerging spiderlings were considered as hatched.

Maternal effects on survival of offspring

Maternal diet effects were investigated in offspring which were all kept on a low quality diet of *R. padi*. Offspring from females of the egg production experiment under the diet treatments 1) Enriched *D. melanogaster*, 2) Enriched *D. melanogaster* + *R. padi*, 3) Normal *D. melanogaster*, and 4) Normal *D. melanogaster* + *R. padi* were used in the experiment. These treatments were selected to focus on differences between the two qualities of fruit flies. Two spiderlings from each of the 1st eggsacs laid were transferred individually to plastic tubes and fed nymphs of *R. padi*; aphids and water was supplied 2-3 times per week. Deaths were recorded by daily inspections. Replication was 18-25 hatchlings in each group.

Statistical analyses

The rate of eggsac production (log-transformed), number of eggs per eggsac, hatching success (arcsine transformed) and number of offspring produced per eggsac was analysed with Repeated Measures ANOVA. Sphericity was tested with Mauchley´s test and if necessary appropriate transformations applied; as the assumption of sphericity was fulfilled only univariate tests were performed. Too few eggsacs were produced in the aphid-only diet groups for these to be included in the Repeated Measures ANOVA. Survival data were analysed with Log-rank test (cf. Pyke, Thompson, 1986).

Results

Egg production experiment

Females in the aphid-only diet groups produced eggsacs at a lower rate and in much lower numbers than females of the fruit-fly diet groups (Fig. 1). The rate of eggsac production was higher in females provided Enriched flies and Enriched flies + aphids compared to the two Normal fly diet groups (Repeated Measures ANOVA of dates of laying eggsacs 1-5; time × treatment, $P<0.001$).

Females of the aphid-only diet groups produced much fewer eggs per eggsac than those of the fruit fly diet groups (Fig. 2). Egg numbers in the aphid + starter fly group were similar to the egg numbers found in the first eggsac of the fruit fly diet groups, but then declined steeply as soon as the spiders were provided with only aphids. There was a significant difference in egg numbers between the fruit fly diet treatments (Overall Repeated Measures ANOVA; $P<0.05$) with the highest egg number found for the single-species diet of Enriched flies and the lowest egg number found for the Normal flies + aphid diet. Egg numbers increased with eggsac number for the first c. three eggsacs and then decreased slightly again (Repeated Measures ANOVA, effect of eggsac number; $P<0.0001$).

Comparing the number of viable eggs with total eggs a different pattern emerged (Fig. 3). Hatching success in the Enriched fruit fly treatments remained high (from 80% decreasing to 60% with time) while steeply decreasing towards zero in the Normal fruit fly diet groups

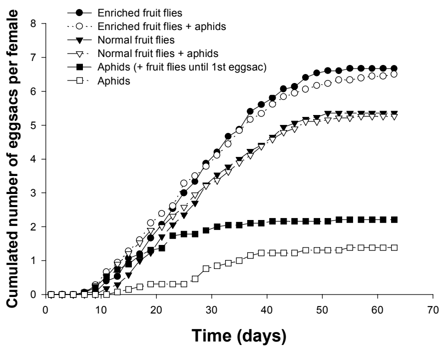

Fig. 1. Course of eggsac production by the average female *Dicymbium brevisetosum* on six diet treatments.

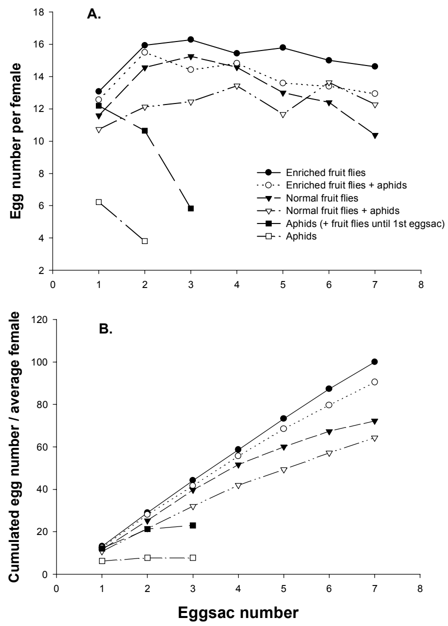

Fig. 2. A. Average number of eggs laid in successive eggsacs by *Dicymbium brevisetosum* on six diet treatments. B. Cumulative number of eggs laid by an average *Dicymbium brevisetosum* female on six diet treatments.

(Repeated Measures ANOVA of hatching success of eggsacs 1-5; P<0.0001). In the pure aphid diet treatment hatching success was high for the first eggsac but dropped to zero in the second eggsac; in the aphid + starter fly group hatching success resembled that of the Normal fruit fly diet groups (cf. Fig. 3). No significant effect of mixing aphid and fruit flies on viability of eggs was detected. As a result of higher hatching percentage total reproductive success of the Enriched fruit fly diets was far better than of any of the other diets tested (Fig. 4, Repeated Measures ANOVA of spiderlings hatched from eggsac 1-5; P<0.0001). The combined effect of slightly lower egg production and hatching success of the mixed Enriched fly + aphid diet group compared to the pure diet of Enriched flies (cf. Fig. 2 and 3) meant that significantly fewer spiderlings hatched in total from the mixed group (Fig. 4B, contrast analysis, Enriched flies + aphids vs. Enriched flies, P<0.05). No difference in number of offspring was found between the Normal fruit fly diet and the mixed diet of Normal flies + aphids.

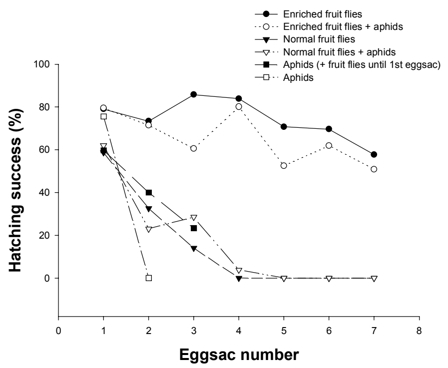

Fig. 3. Average hatching success (%) of successive eggsacs laid by *Dicymbium brevisetosum* on six diet treatments.

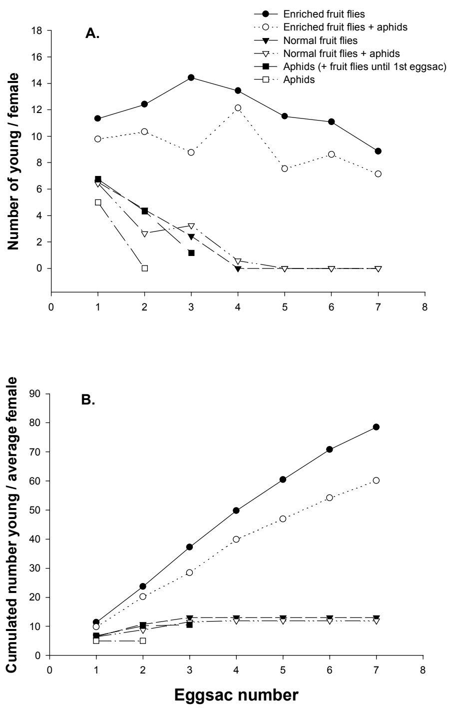

Fig. 4. A. Average number of spiderlings hatched from successive eggsacs laid by *Dicymbium brevisetosum* on six diet treatments. B. Cumulative number of spiderlings hatched per average *Dicymbium brevisetosum* female on six diet treatments.

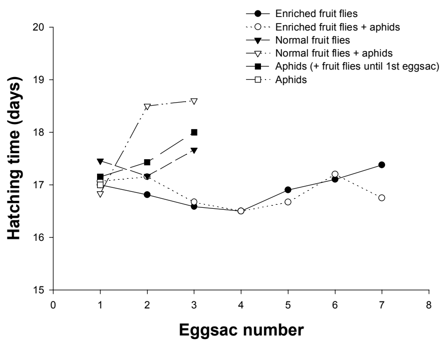

Fig. 5. Average hatching time (days) of successive eggsacs laid by *Dicymbium brevisetosum* on six diet treatments.

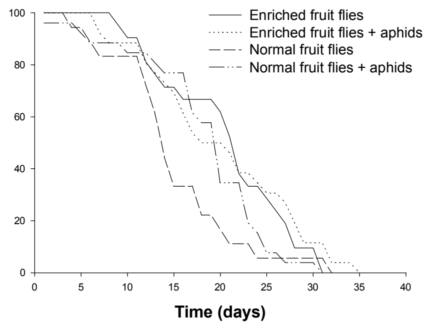

Fig. 6. Survivorship curves for hatchlings of *Dicymbium brevisetosum* from females on four diet treatments. All spiderlings were fed *R. padi*.

Hatching time of eggsacs (Fig. 5) was c. 17 days for the first eggsac of all diet treatments. This was persistent for all eggsacs produced on the Enriched fruit fly diets, while hatching time increased marginally to c. 18 days from first to third eggsac in the Normal fly diet treatment (Repeated Measures ANOVA of hatching time, $P=0.075$).

Survival of offspring

Survivorship curves for first instar spiderlings from females reared on four different diets are shown in Fig. 6. An overall effect of maternal diet on survival of offspring was revealed (Log-rank test, $P<0.05$). A lower survival (median 14 days) was found in hatchlings from females reared on Normal flies compared to spiderlings from females reared on the three other diets, (Normal flies + aphids: median 20 days, Enriched flies + aphids: median 19.5 days, Enriched flies: median 22 days).

Discussion

Egg production experiment

In single-species diets distinct differences in quality between the three tested prey types were found. Enriched fruit flies supported a continuously high egg production rate and a high hatching percentage of eggsacs whereas hatching success rapidly decreased when Normal fruit flies were offered, although a relatively high rate of egg production was upheld. This result indicates that Enriched flies contain energy as well as a sufficient nutrient composition for production of viable eggs, while Normal flies, although containing energy for egg production, do not contribute sufficient nutrients for the eggs to hatch properly. If spiders fed Normal flies use nutrients from their own body reserves to increase the quality of eggs in the first one or two eggsacs, the low hatching success of the following eggsacs may result from depletion of body reserves. Enriched flies also supported a substantially higher egg production and hatching success than Normal flies in similar experiments with *E. atra* (Toft, 1995; Bilde, Toft, submit.). The aphid *R. padi* is clearly of very low value to *D. brevisetosum* resulting in low egg numbers and a declining hatching success from first to second eggsac. Only approximately half the number of spiders tested initiated egg production on the pure aphid diet, suggesting that alternative prey in combination with aphid prey is needed to obtain sufficient energy or nutrients for egg laying. Indeed, in the treatment where Normal flies were added until the first eggsac was produced, almost all spiders initiated egg production, while egg numbers immediately declined after the first eggsac when only aphids were provided. As females not initiating egg laying were excluded from the analyses the real difference between these two groups is larger than appears from the figures.

Slightly lower egg-laying rates and hatching success resulting in a lower total production of offspring were found in the mixed diet of Enriched fruit flies + aphids compared to the pure diet of Enriched flies. The lower reproductive outcome as a consequence of dietary mixing indicates toxic effects of the aphids on the spider. Prey is defined as toxic if inclusion of the prey in the diet lowers the measured fitness parameter significantly. A similar toxic effect of adding the cereal aphid *S. avenae* to Enriched fruit flies was found in an experiment with *E. atra* (Bilde, Toft, submit.). Negative effects on spider fitness parameters have also been demonstrated when low quality Collembola were added to fruit flies in mixed diets (Marcussen et al., 1999; Toft, Wise, 1999). No indication of improvement of diet was found when aphids were added to Normal flies compared to the single-species diet of Normal flies. This was an unexpected result, as Toft (1995) found a significant improvement of spider fitness (*E. atra*) when adding *R. padi* to a diet of Normal flies. It would seem as if the Normal flies are of lower quality to *D. brevisetosum* than to *E. atra*, as *E. atra* produced more viable eggsacs on a diet of Normal flies contrary to *D. brevisetosum* (Toft 1995). Adding aphids to Normal flies, both of which are low quality prey species to *D. brevisetosum* (cf. Fig. 4) is apparently not enough to improve overall dietary composition. When providing a mixed diet of cereal aphid species (*R. padi*, *S. avenae* and *M. dirhodum*) to other species of generalist predators no beneficial effect on predator fitness was found and in those studies all three aphid species were low quality prey in pure diets (Bilde, Toft, 1999, submit.; Toft, 2000). It might thus be hypothesised that cereal aphids can contribute positively to predator fitness in a mixed diet together with an intermediate quality prey, for example by adding nutrients to an energy-rich but nutrient deficient prey (Wallin et al., 1992; Bilde, Toft, 1994; Toft, 1995). If only low quality prey is available, e.g. due to defensive substances in the prey (aphids), energy sources may be lacking to utilise the nutrients of the prey. In conclusion, dietary mixing cannot unequivocally be regarded as beneficial to predators. If a high quality prey is available either no or even negative effects of mixing may be the result. Improvement of nutritional quality of diet by prey mixing depends on the characteristics of the individual prey types composing the diet.

Effects of maternal age were found in an experiment with *E. atra* where hatching time of eggsacs increased with eggsac number independent of diet treatment (Bilde, Toft, submit.). Such effects were not found in *D. brevisetosum* where hatching time of eggsacs was relatively constant on the two diets of Enriched fruit flies throughout the seven eggsacs recorded. The increasing developmental time of eggs seen on the Normal fruit fly diets could be an effect of lower quality eggs produced on nutritionally inferior diets, resulting from increasing nutrient depletion. Nutrient depletion could explain both a lowered hatching success and increasing developmental time of eggs seen of the Normal fly diet treatments.

Maternal effects on survival of offspring

Maternal diet had an effect on the survival of offspring with the lowest survival found in spiderlings from females reared on Normal fruit flies. This was the predicted result as a single-species diet of Normal fruit flies was expected to be of relatively low nutritional quality and subsequently producing the lowest quality eggs of the four diets tested. The mixed Normal fly + aphid diet did not improve any fitness parameters in the egg production experiment compared to the pure diet of Normal flies, nevertheless an improvement of survival of spiderlings was found comparing the two diet treatments. This result suggests that effects of diet cannot be completely evaluated from the fitness of the affected animals alone, but that subsequent generations may be affected through maternal effects. As a consequence, survival of spiderlings in an unfavourable environment (in this case with abundance of low quality prey) may be dependent on the quality of the maternal diet. This might have some importance in cereal fields, where spring breeding spiders reproduce on various prey types, i.e. Collembola, prior to the arrival of cereal aphids in the fields. With availability of high quality prey in the reproductive period, the juvenile spiders may be better able to cope with cereal aphids and thus be more effective in the limitation of these pests. Maternal diet effect on offspring size was not measured in the study presented here, but such phenotypic effects which may influence survival (WALLIN et al., 1992; TANAKA, 1995) have been demonstrated in spiders; i.e. TOFT (1995) found offspring size to depend on the quality of maternal diet. This result seems consistent with the effects of maternal diet on offspring quality (survival) found here.

Summarising over both experiments, the prediction that the value of *R. padi* in mixed diets depend on the nutritional value of the fruit flies was confirmed: negative effects of adding aphids to Enriched flies was found by a lowered hatching success, while positive effects of adding aphids to Normal flies was found in the survival of offspring.

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