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Effects of prey quality on the outcome of dietary mixing in a generalist predator, the wolf spider *Pardosa prativaga* (L. Koch)

Søren Toft

ABSTRACT

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Groups of wolf spider hatchlings were raised on eight different single-species diets and five mixed diets. The prey species were selected to represent a variety of food qualities for the spider, from "high-quality" to "toxic". Six species were potential prey species from the spider's agricultural habitat; two were "laboratory" animals, included as comparison prey. The mixed diets included combinations of different quality prey. The experiments tested the possible benefits for survival, growth and development of mixed diets to a generalist predator, depending on the quality of the prey being mixed. In no case did a mixed diet result in better performance than with the best single species of the mixture, in most cases spider performance was intermediate between that of the respective single-species diets. The mixed diet of high-quality *Drosophila melanogaster* and the poor-quality aphid *Rhopalosiphum padi* was of high quality, whereas the mixed diet of *D. melanogaster* and the poor-quality collembolan *Folsomia candida* was of poor quality. The mixed diet of the two poor-quality prey species was also poor quality.

Key words: Araneae, Lycosidae, insectivore, mixed diet, prey quality, cereal aphids, collembola, Diptera

Introduction

Generalist (or polyphagous) predators are defined by their relatively broad prey spectrum. Though preference for certain prey types has been demonstrated, it is generally assumed that generalists will kill and consume most types of available prey that they can handle, considering the size, armour and particular defence mechanisms of the prey (e.g. Riechert & Lockley 1984). Ideas about the benefits of polyphagous feeding habits were mainly developed for herbivorous animals, but they have served as the basic hypotheses for predators as well. It is thus assumed that polyphagy has evolved because consumers benefit from the presumably more varied nutrient composition of a mixed diet. Two mechanisms may explain this effect: either a diverse diet is most likely to fulfil the animal's nutritional needs; or the generalist strategy allows them to select between available food types so as to obtain an optimal balance of nutrients (Westoby 1978, Waldbauer & Friedman 1991, Simpson & al. 2004, Mayntz & al. 2005). A second benefit of polyphagy may be that the animals avoid consuming large amounts of particular toxic chemicals that certain plants or prey may use as an anti-predatory defense mechanism (cf. Freeman & Janzen 1974). The role of these two main hypotheses is still debated as far as herbivores are concerned (Bernays & al. 1994, Bernays & Minkenberg 1997), and they are very poorly investigated with respect to predators. Several investigators have demonstrated a fitness benefit of dietary mixing in arthropod predators (Uetz & al. 1992, Toft 1999) and insectivorous birds (Borg & Toft 2000). However, Toft & Wise (1999a) found both positive and negative effects of mixed diets in a wolf spider, and proposed that the value of the mixed diet depended on the nutritional characteristics of the constituent prey species. In particular, they proposed that toxins in prey might interfere with the predator's utilization of good prey, so that the mixed diet could be no better than the toxic prey alone, even if it included high-quality prey. They defined toxic prey as prey that resulted in higher spider mortality than in starved control spiders. Modified for mixed diets, toxic prey can be defined as prey which reduces the predator's fitness if included, compared to the same diet without that prey. Marcussen & al. (1999) obtained such results with respect to fecundity of a linyphiid spider on diets including the collembolan *Folsomia fimetaria*. Bernays & Minkenberg (1997) also found no benefits of dietary mixing in two types of herbivores, lepidopteran caterpillars and heteropteran bugs.

Toft & Wise (1999a, b) admitted one shortcoming of their study, viz. that they combined predator and prey species that were not coexisting in nature as far as the exact species were concerned. The present paper reports on a similar experiment, selecting a predator and several prey species that occur together in Danish agricultural fields. It extends the earlier study by including a wider range of prey species and more combinations of mixed diets. This was done in order to be better able to answer the question: How does the value of a mixed diet depend on the food quality of the prey types being mixed? The generality of the conclusions is further widened by choosing a wolf spider species from a different genus (*Pardosa* vs. previously *Schizocosa*) which inhabits a different type of habitat (open vs. forest) and occurs on a different continent (Europe vs. North-America).

According to the "nutrient diversity hypothesis" a mixed diet of two palatable prey species should result in improved predator performance because the mixed diet is likely to contain a wider range of nutrients or the predators can obtain a better balance of available nutrients by optimal self-selection. According to the "toxin dilution hypothesis" we would expect a mixed diet of two prey types, that are low quality for the predator due to chemical defences, to result in improved performance compared to that on the single-species diets because more food can be ingested with the same toxic load. This assumes, though, that the toxins do not act synergistically. No clear predictions can be derived from the two hypotheses for the outcome of mixed diets consisting of nutritionally high-quality prey and low-quality toxic prey. In reality, nutrient composition and toxin content is likely to interact in complex ways (Simpson & Raubenheimer 2001, Singer & al. 2002). The mechanisms of this cannot be revealed by experiments using actual prey animals as in the present study, but require artificial diets and are therefore outside the scope of this paper.

Materials and Methods

Spider

The spider species selected for the experiments, *Pardosa prativaga* (L.K.), is one of the most widespread wolf spiders (Lycosidae) of open habitats, i.e. agricultural fields, successional grassland, bogs etc. in Denmark. It has a mixed annual/biennial life-cycle with a long reproductive period in June – September. Egg sac carrying females were collected in the field at Stjær, eastern Jutland, Denmark. The hatchlings spend some days on the back of the mother before they disperse to live independently. Spiderlings were assigned a feeding treatment as they voluntarily left their mother. Care was taken that the young of each mother were spread evenly over the treatments and assigned randomly to them. Therefore, though replicates were not all started on the same date, this created no bias between treatments.

Diets

Prey animals included fruit flies, four species of Collembola and three species of cereal aphids. *Pardosa prativaga* is a predator of the soil surface and its natural prey most likely consist mainly of Collembola and small Diptera. The following prey animals were used (with abbreviations used in text and figures):

- *Drosophila melanogaster* (Meigen) – Diptera (*D. mel*). Fruit flies were included as a comparison prey because it has functioned in this role in many previous studies of spider feeding ecology. Besides, drosophilid and other flies of similar size do occur in most habitats and may be important prey of wolf spiders and several other generalist predators. The flies were raised on a 1:1 (by volume) mixture of Carolina fruit fly medium 4-28 (Carolina Biological Supply, USA) and crushed dog food (Maintenance Adult, Martin Group, Canada). Flies raised on this nutrient enriched medium are more nutritious, since spiders fed with these flies grow faster and survive better than spiders fed with flies raised on the plain medium (Mayntz & Toft 2001).
- *Isotoma anglicana* (Lubbock) – Collembola (*I. ang*). From earlier results (Toft & Nielsen 1997, Marcussen & al. 1999) this species was expected to be high-quality food for the spiders. Mature individuals were collected in agricultural fields and a culture was established in the laboratory. Here they were fed a mixture of baker's yeast and Carolina fruit fly medium. Unfortunately the culture expired after the second generation.
- *Hypogastrura* sp. – Collembola (*Hyp.* sp.). Preliminary (unpublished) observations indicated that this species is highly deterrent to the wolf spiders, indicating that it may be toxic. Offering these Collembola to the spiders could have two alternative results: if completely repellent, spider performance was expected not to differ from that of the starvation control; if accepted, they might have toxic effects. Animals were extracted from soil and a culture maintained on baker's yeast was established.
- *Folsomia candida* (Willem) – Collembola (*F. can*). In earlier experiments (Toft & Wise 1999a, b; Fisker & Toft 2004) this species was found to be toxic to wolf spiders. A laboratory culture was kept on baker's yeast. This species does not occur in the spider's natural habitat, but is included for comparison with the previous studies.
- *Folsomia fimetaria* (L.) – Collembola (*F. fim*). This species had a toxic effect on fecundity of the linyphiid spider *Erigone atra* (Marcussen & al. 1999). A laboratory culture was maintained on baker's yeast, established from animals extracted from soil.
- *Rhopalosiphum padi* (L.), *Sitobion avenae* (F.), *Metopolophium dirhodum* (Walker) – Aphidoidea (*R. pad, S. ave, M. dir,* respectively). All three aphid species were kept in laboratory cultures of wheat seedlings of mixed cultivars. Some of the results concerning these species have been reported

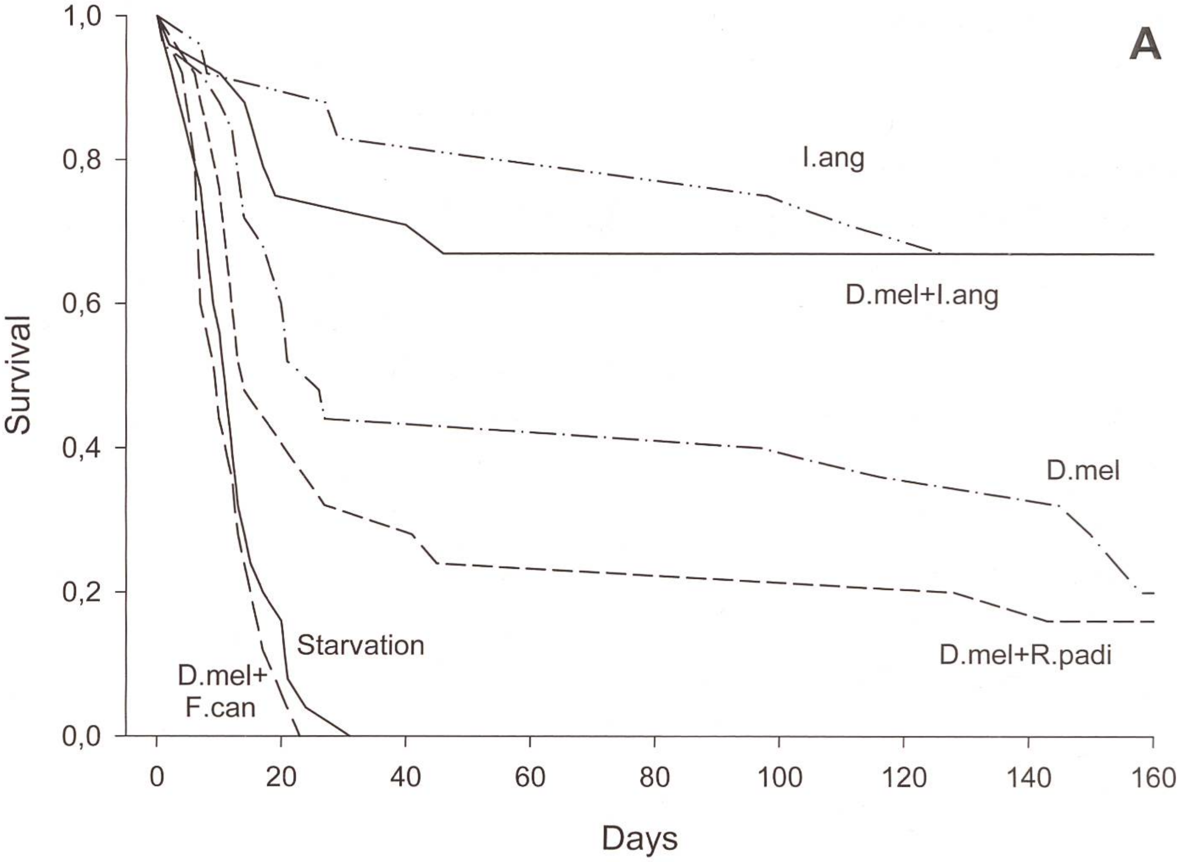
elsewhere (Toft 2000) and they are only summarily repeated here in order to allow comparisons with other types of prey.

All the above-mentioned species were used as single-species diets, i.e. the spiders were offered a monotypic diet of one of these species and nothing else. Some of the species were further included as constituents of mixed diets. Most of these were two-species mixed diets; however, a mixed diet of the three cereal aphid species was also included. They were chosen to represent various combinations of high-quality, low-quality and toxic prey:

- *D. melanogaster* + *I. anglicana* combined two supposedly high-quality prey species
- *D. melanogaster* + *R. padi* combined a high-quality and a low-quality prey species
- *D. melanogaster* + *F. candida* combined a high-quality and a toxic prey species
- *R. padi* + *S. avenae* + *M. dirhodum* combined three low-quality prey species (abbr.: aphmix),
- *R. padi* + *F. candida* combined a low-quality and a toxic prey species.

Procedure

The study consisted of a growth experiment in which the newly hatched juvenile wolf spiders were fed either a single-species diet or a mixed-species diet being a combination of two or three of the prey species mentioned. A starvation control treatment was also included. Every diet had 20 replicates at the beginning. The spiderlings were raised in plastic tubes (height 6 cm; Ø 2 cm) with a 1 cm bottom of plaster with charcoal to maintain high humidity. They were weighed initially and subsequently reweighed weekly. The spiders were kept in a constant-temperature cabinet at 20 ^{0}C and at a L16:D8 photoperiod. Food was added *ad libitum* 2–3 times per week. Food portions were not strictly controlled. For the mixed diets care was taken that all prey species were available in approximately the same amounts. At these inspections water was supplied as needed, and deaths or moults were recorded. Based on these observations, growth and survivorship curves could be established and the diets compared. Because of a shortage of *I. anglicana,* the two treatments with this species had to be ended after 15 weeks. For the remaining two treatments with suviving spiders the experiment was stopped after 21 weeks. No spider had yet reached adulthood at that time, but their growth rate had levelled off, presumably in expectation of hibernation.



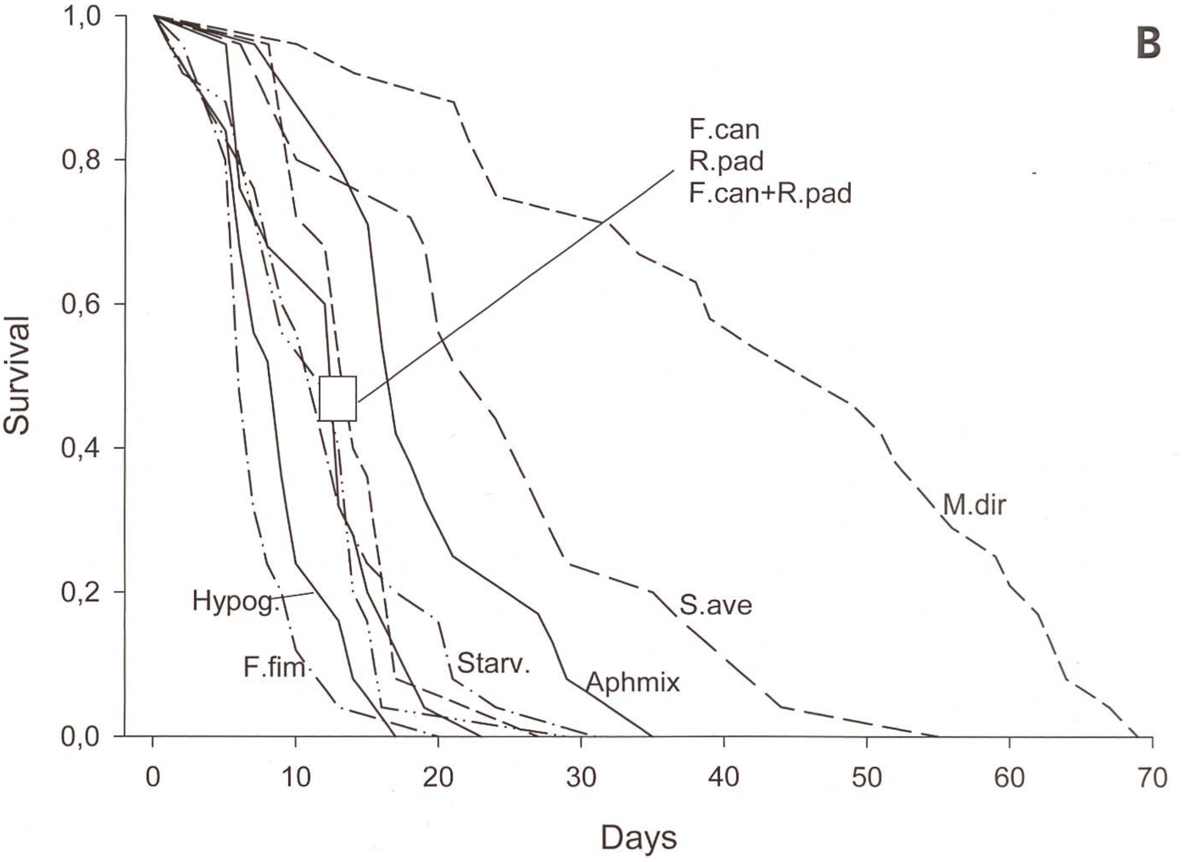


Fig. 1. Survivorship curves for groups of *Pardosa prativaga* spiderlings held on different single- or mixed-species diets. Notice different scale of the x-axis in A and B.

Statistical analyses

Differences in survival were tested with the Log-Rank test and the Wilcoxon test (Pyke & Thompson 1986). In no case did the two tests give conflicting results. Growth was analysed with Repeated Measures ANOVA. If Mauchly's sphericity criterion was fullfilled, univariate tests were used, if not, multivariate tests were applied. "Time spent in instar I" and "Weight at week 15" were compared with a one-way ANOVA using inverse transformations to homogenise the variances (Bartlett's test, $p>0.05$). Subsequent multiple comparisons used the Tukey-Kramer HSD ($p<0.05$). Development was compared with a Kruskal-Wallis ANOVA because instar is an ordinal variable. For pairwise comparisons of treatments the multiple comparisons procedure of Siegel & Castellan (1988) was used.

Results

Survival

Four diets allowed some of the spiders to survive all through the experimental period (Fig. 1A). They were the two supposedly high-quality single-species diets (*D. mel* and *I. ang*), the mixed diet of these two, and a mixed diet of high-quality and low-quality prey (*D. mel + R. padi*). The difference between these four diets lies in the early mortality. After 3–4 weeks there is hardly any mortality at all, except at the end of the period when the *D. mel* treatment shows some mortality again. Part of the high early mortality in the *D. mel* and the *D. mel + R. padi* diets is due to difficulties for the young spiderlings of catching live flies, rather than a matter of nutritional quality. Mortality in the mixed *D. mel + R. padi* diet group is not different from that of the pure *D. mel* group. However, the mixed diet of *D. mel + F. can* was no better than starvation.

Though all spiders of the remaining diet groups died prematurely, it is nevertheless possible to distinguish three levels of performance (Fig. 1B). Spiders of three treatments (*M. dir*, *S. ave*, *Aphmix*) survived significantly better than those of the starvation control. Spiderlings on two single-species diets (*F. fim*, *Hyp.* sp.) survived significantly shorter than starved spiderlings. This indicates that these prey species are not so deterrent as to completely prevent the spiders from attacking and eating some of them. Apart from the *D. mel + F. can* diet, three diet groups were no better and no worse than starvation (*F. can*, *R. padi*, *R. padi + F. can*).

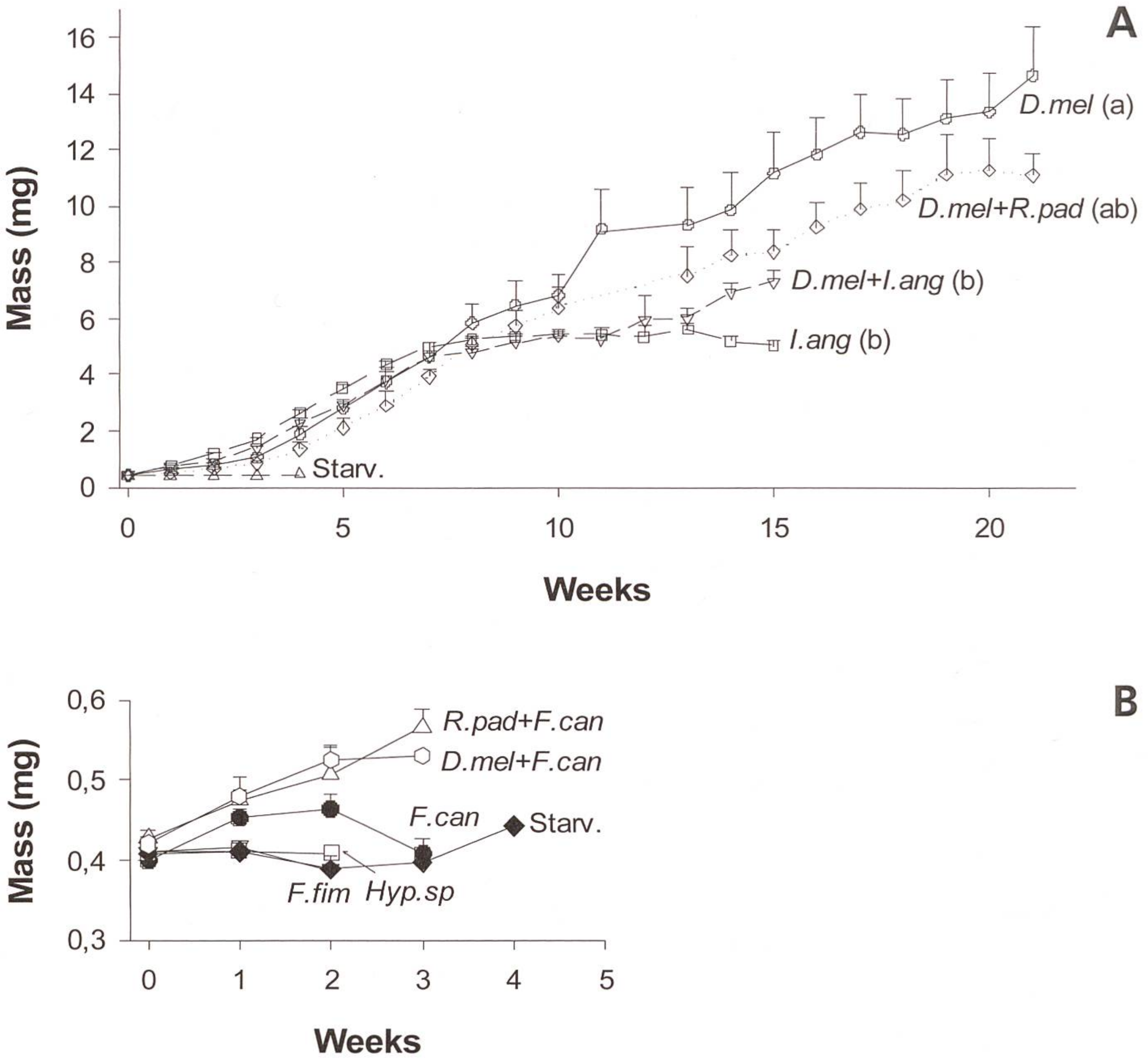


Fig. 2. Growth curves for groups of *Pardosa prativaga* spiderlings held on different single- or mixed-species diets. Notice different scales of both axis in A and B.

Growth and development

The highest growth rate over the full experimental period was revealed by the group fed the pure *D. mel* diet, followed by the mixed *D. mel + R. padi* diet (Fig. 2). The weight after week 15 of the pure *I. ang* diet and the mixed *D. mel + I. ang* diet were both significantly lower than the *D. melanogaster* group.

Some growth, though very little, took place in three aphid treatments (*M. dir*, *S. ave*, *mixaph*, Fig. 2B). A small proportion of individuals in these groups moulted a single time, but then died off (details in Toft 2000). Not a single individual moulted in any of the remaining treatment groups, and the weight curves rise only slightly over the starvation curve. Increase in these curves, however, is not necessarily an indication of growth, but may merely reflect that small spiderlings die earlier than larger spiderlings (cf. increase in the starved group). The *F. fim* and *Hyp.* sp. groups follow the starvation curve closely, and show no sign of increase in weight.

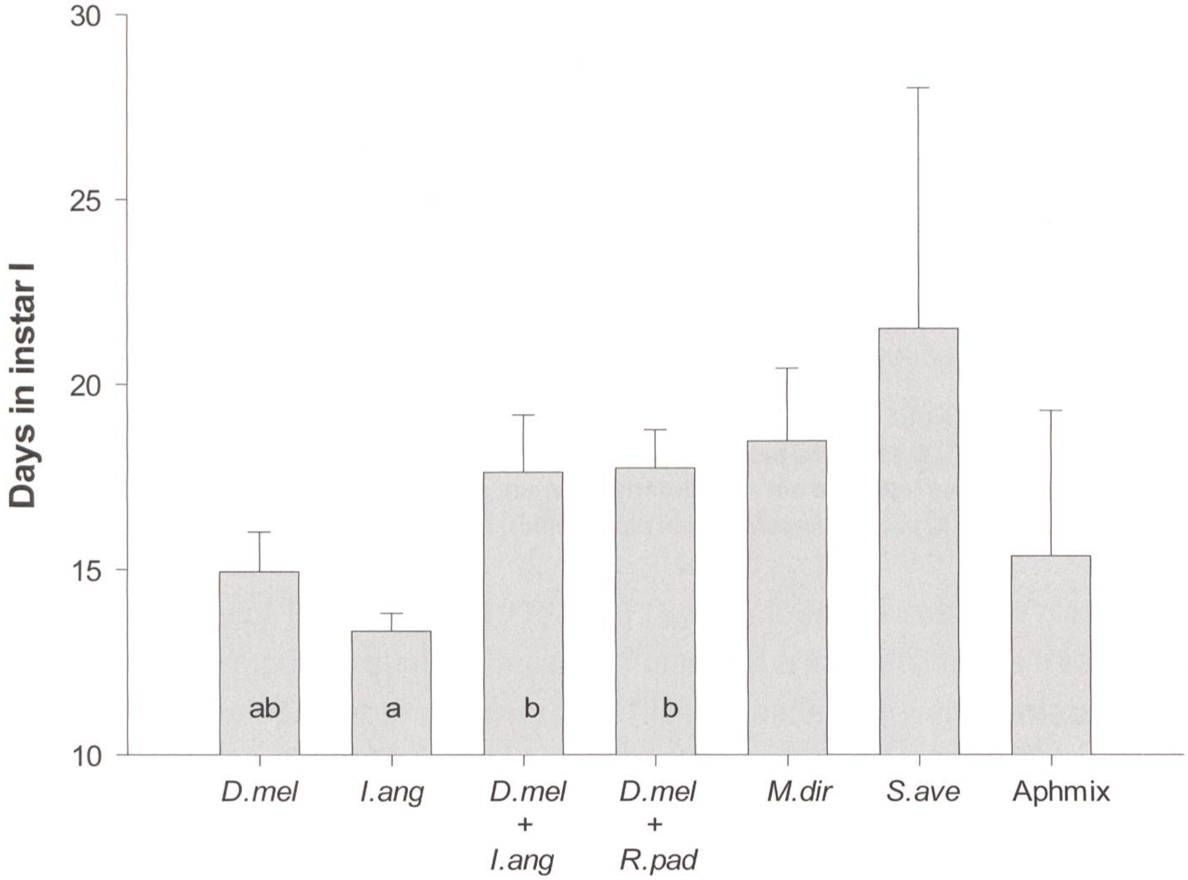


Fig. 3. Duration of instar I (or inverse speed of development) (avg. ± SE) for the first instar *Pardosa prativaga* spiderlings fed on different single- or mixed-species diets. Diets with the same letter are not significantly different. If no letter, diets were not included due to low sample sizes.

The time spent in an instar before moulting to the next instar is a measure of the speed of development. Only treatments that allowed the spiders to complete at least the first instar provided data for this analysis, and only the first instar had sample sizes that allowed meaningful comparisons (Fig. 3). Fastest development was in the *I. ang* group, which was significantly faster than the mixed *D. mel + I. ang* group, with the *D. mel* group intermediate. From Fig. 2A can be seen that the *I. ang* group also had the highest growth rate during the first seven weeks.

Differences in growth rate were also reflected in the developmental stage reached at week 15 (Tab. 1). The *D. mel* and the *D. mel + R. pad* groups were about one moult ahead in development compared to the *I. ang* group, with the *D. mel + I. ang* group being intermediate.

Diet	n	Instar IV	 V	 VI	Mult. comp.
D. mel	8	0	5	3	a
D. mel + R. padi	6	0	2	4	a
D. mel + I. ang	14	3	11	0	ab
I. ang	17	9	8	0	b

Tab. 1. Instar distribution of spiders surviving to week 15. The data were tested with a Kruskal-Wallis ANOVA (p = 0.0002), followed by pairwise multiple comparisons (cf. Siegel & Castellan 1988): diets followed by the same letter are not significantly different. Abbreviations: *D. mel = Drosophila melanogaster* (fruit fly); *R. padi = Rhopalosiphum padi* (aphid); *I. ang = Isotoma anglicana* (springtail).

Discussion

Food quality of single prey species

The results confirm earlier findings that potential prey insects are of widely different food value even to a generalist insectivorous predator. The range of prey values for *P. prativaga* was not lower among the prey species from the natural habitat than among the "laboratory" prey species used in this and earlier studies. This suggests that the prey available in the natural habitat have a great variability in food value. It is also noticed that most of the tested prey species were of low food quality or even toxic; only one of the natural prey species (*I. anglicana*) was partly of high food quality. As the prey species used in the present study were not drawn completely randomly from the total pool of available prey, it remains to be established whether a majority of spider prey species in nature are of low food quality as the data suggest.

With respect to survival *I. anglicana* proved to be of the highest quality, whereas *D. melanogaster* was the best with respect to growth. It was argued that the inferiority of *D. melanogaster* with respect to survival might not be due to nutritional inferiority but to difficulties of the small hatchlings with catching these flies alive. The fact that the early growth rate was also lower for the *D. mel* than for the *I. ang* diet might strengthen this argument. However, if this was the case we would expect the mixed diet of *D. mel + I. ang* not to be inferior to the pure *D. mel* diet. The fact that it is, indicates that survival and development require partly different nutrients.

Toft & Wise (1999a) described a five-step classification of prey value based on performance experiments similar to the ones presented here. The selection of prey used in the present paper can be approximately fitted into these categories: 1) "high-quality prey" allows spiders to complete their full development with low mortality (here the nutrient-enriched *D. melanogaster* probably belongs); 2) "intermediate quality prey" allows partial development and a good survival (*I. anglicana*); 3) "low-quality prey" allows only very little growth and development but prolongs survival considerably compared to the starvation control (*S. avenae*, *M. dirhodum*); 4) "poor prey" contributes nothing to growth and development, and survival is no better than in starving animals (*F. candida*, *R. padi*); and 5) "toxic prey" gives a survival rate lower than in the starved controls (*F. fimetaria*, *Hypogastrura* sp.).

In the study of Toft & Wise (1999 a, b) *D. melanogaster* could be classified only as of intermediate quality, because none of the animals in this treatment completed development to maturity. The flies of that study were raised on the plain Carolina medium. The present experiment was terminated before development was completed, but other experiments have demonstrated that *P. prativaga* can complete development on a monotypic diet of the nutrient enriched fruit flies (Jespersen & Toft 2003). The good survival and high early growth and developmental rate on the *I. anglicana* diet indicates that this prey is palatable and (at least initially) of very high nutritional value, but that the spiders after some time run short of certain nutrients. It remains to be established whether the spiders can reach maturity on this prey alone, perhaps after a prolonged developmental period. Toft & Wise (1999 a) also found a collembolan (*Tomocerus bidentata*) which allowed full development.

Some poor-quality prey species resulted in survivorship times significantly longer than in the starvation control. This implies that acceptance of such prey may be beneficial when no other prey is available. Though the spiders do not grow or develop further on such prey, they increase their chances of surviving until the food situation improves. When this happens, the spiders should reject the poor-quality prey, but there is so far little evidence that they do so (Toft 1999). The same is true for the toxic prey no matter if better food is available or not.

Dietary mixing

For none of the response variables tested here did a mixed diet result in a better spider performance than with the best of the prey species in the mixture. As a matter of fact, for first instar developmental rate a single-species diet (*I.*

ang) was significantly better than the best mixed diet. Some single-species diets were also top ranking for survival and growth. At the same time, both the present and the earlier study (Toft & Wise 1999a) found several cases of mixed diets that gave reduced performance compared to the best of single species of the mixed diets. The mixture of two relatively high-quality prey species (*D. mel + I. ang*) was of the same quality as the best (*I. ang*) with respect to survival; it was slightly inferior to the best (*D. mel*) with respect to overall growth and significantly inferior to the best (*I. ang*) with respect to early developmental rate. Overall, fitness was somewhat reduced by the mixing.

The mixed diet of the high-quality *D. melanogaster* and the poor-quality aphid *R. padi* was only slightly inferior to *D. melanogaster* in all response variables, but never significantly so. This is in contrast to the mixed diet of *D. melanogaster* and *F. candida*. In no respect did this diet result in spider performance above that of the starved control. A pure diet of *F. candida* was also no better than the starved control and the same applied to all mixed diets including this collembolan, irrespective of the quality of other prey in the mixture.

These results confirm that it is not dietary mixing per se but the composition of the mixed diet that determines the spiders' performance. Our finding that fruit flies can become a high-quality prey by adding nutrients to the fly medium shows that nutritional composition of the prey is important, but if all essential nutrients are available in one prey type, mixing with other prey can as well reduce the value of the mixture. Bilde & Toft (2000) confirmed this experimentally. They found that a diet of normal (non-enriched) fruit flies could be improved by adding *R. padi*, whereas enriched fruit flies could not. Thus, to the extent that dietary mixing gives a benefit it may be because few natural prey are complete and balanced nutrient packages for their predators.

The mixed diets of fruit flies and two poor-quality prey species (*D. mel + R. pad* and *D. mel + F. can*) gave strikingly different results. Whereas the aphid gave only non-significant negative effects, the mixed diet of *D. melanogaster* and *F. candida* was no better than starvation (and than *F. candida* alone). This result repeats the earlier finding that ingestion of *F. candida* interferes with the utilization of better food (Toft & Wise 1999b, Fisker & Toft 2004). This was revealed by an increased consumption of fruit fly mass with nearly zero utilization efficiency (Fisker & Toft 2004). In the early study *F. candida* was mixed with intermediate-quality ("non-enriched") fruit flies, whereas in Fisker & Toft (2004) and in the present study with high-quality ("enriched") flies. It therefore appears that whatever in *F. candida* is responsible for the physiological interference in the spider, the mechanism is independent of the nutritional value of the food.

The difference in the effect of mixing *R. padi* and *F. candida* with *D. melanogaster* probably has the same underlying cause as the behavioural and physiological differences noted by Mayntz & Toft (2000). They found that *P. prativaga* juveniles developed an aversion against *R. padi* but not against *F. candida*. The aphid is sufficiently deterrent to preserve the spider from a toxic overload that would result from a large consumption. In contrast, a deterrency factor seems absent in *F. candida* and the spiders eat themselves to death when this species is available (Fisker & Toft 2004, Jespersen & Toft 2003).

In conclusion, neither the nutrient diversity hypothesis nor the toxin dilution hypothesis are supported by these results since both predict improved predator performance on mixed diets. The results call into question the generality of the notion that generalist predators benefit from the higher availability of food accruing from their polyphagous feeding habit, at least under certain circumstances. However, even in the absence of mixed diet benefits, spiders may benefit from being unspecialised predators, because high-quality prey from widely different insect taxa (i.e. insects of widely different morphology, behaviour, etc.) can be exploited. If high-quality Diptera are not available, maybe high-quality Collembola are. However, spiders may also suffer from being polyphagous because they run the risk of accepting low-quality or even toxic prey that may devalue partly or completely the nutritional benefit of the ingested food, even when high-quality prey forms most of it.

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