

Diet-dependent fecundity of the spiders *Atypena formosana* and *Pardosa pseudoannulata*, predators in irrigated rice

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- Abstract**
- 1 The fecundity of the spiders *Atypena formosana* and *Pardosa pseudoannulata* was assessed on diets of brown planthopper *Nilaparvata lugens* (BPH), green leafhopper *Nephotettix virescens* (GLH), Collembola (Entomobryidae), *Drosophila melanogaster* and three prey mixtures; BPH–GLH, BPH–GLH–Collembola and a full mixed diet of BPH–GLH–Collembola–*D. melanogaster*.
 - 2 Egg production and hatching success was high in *A. formosana* except on the BPH, the GLH and the BPH–GLH diets. In *P. pseudoannulata* egg production and hatching success was lowest on diets of GLH and BPH–GLH, whereas this spider used BPH better.
 - 3 Differences between offspring sizes were small.
 - 4 Survival of *A. formosana* females was lowest on the GLH and BPH–GLH diets. In *P. pseudoannulata* survival did not differ significantly.
 - 5 Food conversion efficiency was highest on the Collembola and the *D. melanogaster* diets for both spiders.
 - 6 Overall, diets of Collembola and *D. melanogaster* had the highest quality for both spiders, the BPH–GLH–Collembola and the full mixed diets were intermediate in quality, the quality of the BPH diet was intermediate to low and quality of the GLH and BPH–GLH diets was low.
 - 7 There need not be a contradiction between low dietary value of hoppers and successful natural biological control provided that the nutritional needs of the spiders are met by sufficient alternative prey.
 - 8 The hopper-spider relationship is comparable to that of aphids and spiders in temperate cereals, suggesting that low dietary quality of Homoptera to spiders may be widespread.

Keywords *Atypena formosana*, biological control, Collembola, *Drosophila melanogaster*, fecundity, *Nephotettix virescens*, *Nilaparvata lugens*, *Pardosa pseudoannulata*, spider, prey.

Introduction

Spiders are an important part of the natural enemy complex that normally keeps insect pests in check in unsprayed, irrigated rice (Matteson, 2000). In the Philippines, the money spider *Atypena formosana* (Ooi) (Linyphiidae) and the wolf spider *Pardosa pseudoannulata* (Bosenberg & Strand) (Lycosidae) are the

dominant spiders in the first 35–40 days after transplanting. Together with *Tetragnatha* spp., they are the most abundant spiders across the rice-cropping season (Barrion & Litsinger, 1984; Heong *et al.*, 1992). *Atypena formosana* lives among the rice tillers at the base of rice hills. It hunts for nymphs of planthoppers and leafhoppers, Collembola and small dipterans. The web is a sheet web or an irregular web of about 8 cm in diameter, placed 0–20 cm above the ground. In the webs, 36% of the prey is Homoptera and 57% Collembola (Barrion, 1999). *Pardosa pseudoannulata* spins no web but hunts most commonly among the tillers at the base of the plants (Ooi & Shepard, 1994; Barrion, 1999).

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Pardosa pseudoannulata is recognized as a significant biological control agent of insect pests in irrigated rice. It can effectively regulate the pest population of leafhoppers and planthoppers, and is perhaps the single most important predator of brown planthopper (BPH) *Nilaparvata lugens* Stål (Hemiptera: Delphacidae) (Kiritani *et al.*, 1972; Kobayashi & Shibata, 1973; Kiritani & Kakiya, 1975; Kenmore *et al.*, 1984; Ooi & Shepard, 1994). Reports of the importance of *A. formosana* are more recent (Reddy & Heong, 1991; Barrion, 1999). High predation rates demonstrate that both spiders have the potential to control populations of BPH and *Nephotettix virescens* (Distant) (Hemiptera: Cicadellidae) (GLH) (Heong & Rubia, 1989; Heong *et al.*, 1991; Sigsgaard & Villareal, 1999).

A high density of spiders in the field early in the cropping season can probably contribute significantly to a reduction in the number of BPH and GLH (Kenmore *et al.*, 1984; Settle *et al.*, 1996). A community of alternative prey would help to support such a high density of spiders in the field (Wu *et al.*, 1994; Guo *et al.*, 1995; Settle *et al.*, 1996). In Japan, releases of *D. melanogaster* in dikes surrounding a rice field prior to transplanting significantly increased the control of two hoppers, *Nephotettix cincticeps* and *Laodelphax striatellus*, illustrating the importance of abundant prey in the fallow (Kobayashi, 1975).

Spiders are generalist predators and can potentially add to the control of a variety of insect pests (Riechert & Luczak, 1982; Riechert & Lockley, 1984; DeKeer & Malfait, 1988; Axelsen *et al.*, 1997; Sunderland *et al.*, 1997). However, spiders are affected by prey quality, which in turn may affect their effectiveness as natural enemies. Thus, the money spider *Erigone atra* has a limited ability to prey on the cereal aphid *Rhopalosiphum padi* (Toft, 1995), its offspring are smaller on pure aphid diets than on aphid-*D. melanogaster* diets (Bilde & Toft, 2001), and Alderweireldt (1994) observed that a large proportion of the aphids caught in the webs of money spiders were not consumed. We demonstrated that young *A. formosana* were unable to develop to maturity on diets of BPH or GLH, whereas Collembola were high-quality prey (Sigsgaard *et al.*, 2001). Thang *et al.* (1988) found faster development of *P. pseudoannulata* on a mixture of BPH nymphs and *D. melanogaster* larvae than on a pure diet of either. Suzuki & Kiritani (1974) showed that its fecundity was higher on mixed prey than on the leafhopper *N. cincticeps* alone. Finally, survival of spiderlings of *Pardosa amentata* was significantly poorer on diets of aphids than on diets of *D. melanogaster* or Collembola (Toft, 1995).

The dietary value of an alternative prey determines its role in maintaining a high population of *A. formosana* and *P. pseudoannulata* early in the cropping season. Thus, we designed an experiment to assess the dietary quality of the most common prey in irrigated rice, represented by BPH for planthoppers, GLH for leafhoppers, *D. melanogaster* Meigen (Diptera: Drosophilidae) for flies and Collembola (Entomobryidae). *Drosophila melanogaster* is known as a valuable food source (Toft, 1995) and the importance of Collembola to money spiders seems to be general for cereal fields in temperate regions (Chiverton, 1986; Sunderland *et al.*, 1986; Nyffeler, 1999). Evidence suggests that this may also be true in Asian rice fields (Settle *et al.*, 1996; Barrion, 1999; Sigsgaard *et al.*, 2001). Collembola are important for immature *P. pseudoannulata*

(Gavarrá & Raros, 1975) and *P. pseudoannulata* prefer Collembola to *Sogatella furcifera* (Pang *et al.*, 1998). *Drosophila melanogaster* has been recognized as a high-quality diet for money spiders and wolf spiders, the quality to some extent dependent on the substrate offered to *D. melanogaster* (Mayntz & Toft, 2001). Food value depends on the energy and nutrient content of a prey, sometimes interacting with deterrents or toxins. It may be expressed by a fitness estimate for the predator combined with measurement of the feeding rate. Egg production, hatching success, size of offspring, food conversion efficiency (eggs produced per mg diet) and female survival were used as fitness parameters for evaluating the food quality of BPH, GLH, Collembola, *D. melanogaster* and mixed diets for *A. formosana* and *P. pseudoannulata*. We tested the hypothesis that, due to differences in food quality, these diets would differentially affect the reproduction of spiders. Prey quality may not affect initial acceptance because prey rejection is an acquired response (Toft, 1995; Toft & Wise, 1999a, b). However, prey quality will affect subsequent predation rates and spider fitness in terms of number of offspring (numerical response) and survival and development of spiderlings. Therefore, it is likely to affect the diet composition eaten by the spider over a longer time span.

Materials and methods

Spiders

To obtain adult female spiders of the same age for the experiment, late-instar *A. formosana* and *P. pseudoannulata* were field-collected in Laguna province, the Philippines, and reared on excess of a mixed diet of BPH, GLH, Collembola and *D. melanogaster* until they became adults. Spiders were collected over a month and adults developed over a period of 6–7 weeks. Spiders that became adults were assigned treatments in turn, so that the time spread in treatments was equal. There was no statistically significant difference in female initial weight among treatments.

Prey species

All cultures were established from arthropods collected in Laguna Province, the Philippines. Cultures of BPH and GLH were maintained in insect cages in the greenhouse following the procedure described in Heinrichs *et al.* (1985). Young second-instar nymphs of GLH and BPH were used as prey for *A. formosana* and fifth instars for *P. pseudoannulata*. A *D. melanogaster* culture was established by collecting adults from ripe banana. The culture was maintained on ripe banana in test tubes in the greenhouse. Ten adults were put in a test tube with ripe banana for 24 h for oviposition. Newly emerged adults were used for spider food. Collembola were field-collected. We used a mixture of Collembola from the family Entomobryidae, which was the predominant collembolan family in field collections.

Experimental conditions

One male and one female *A. formosana* were kept as a pair in test tube vials 180 mm long and 15 mm in diameter, closed with a

moist cotton plug in fine nylon mesh. Under these conditions, females readily produced egg sacs. After oviposition, the two adult spiders were moved to a new vial. The small space was meant to prevent escape of the prey and make sure that the spiders' food demand could be met at all times. Prey was fully replenished every second day, ensuring that there was prey in excess of demand. Egg sacs were left undisturbed in the test tubes. Water was provided daily on the cotton plug to maintain humidity in the test tubes.

To reduce the risk of cannibalism (Samu *et al.*, 1999), *P. pseudoannulata* females were mated in larger mating cages (diameter base: 7.5 cm, diameter top: 11 cm, height: 7 cm). A moistened filter paper covered the base of the cage, and slanting dry rice straw created a refuge for the spiders as well as a support while mating. The risk of cannibalism was further reduced by providing surplus diet. At the time of mating, females were 2 days old, so they were fully recovered after their final moult. To assure mating, *P. pseudoannulata* were kept in the mating cages for 4 days before being moved to the test tubes. After each oviposition and subsequent emergence of spiderlings, mating was repeated with a delay of 24 h to ensure that the female had regained strength. Experiments were performed in a climate chamber at day temperatures of 29 ± 1 °C and night temperatures of 21 ± 1 °C, with a photoperiod near LD 12 : 12 h and an RH of $70 \pm 20\%$.

Diets

Seven different diets were offered to 15 spiders in each treatment. Single-prey diets were: (a) BPH, 30 second instars for *A. formosana* and 60 fifth instars for *P. pseudoannulata*; (b) GLH, 30 second instars for *A. formosana* and 60 fifth instars for *P. pseudoannulata*; (c) Collembola (Entomobryidae), 15 for *A. formosana* and 60 for *P. pseudoannulata*, and (d) *D. melanogaster*, 15 for *A. formosana* and 60 for *P. pseudoannulata*.

Mixed diets were (e) BPH and GLH, 15 of each for *A. formosana* and 30 of each for *P. pseudoannulata*, (f) BPH, GLH and Collembola, 15 of each for *A. formosana* and 30 of each for *P. pseudoannulata*, and (g) a full mixed diet of BPH, GLH, Collembola and *D. melanogaster*, 15 of each for *A. formosana* and 25 of each for *P. pseudoannulata*.

Spiders were fed this excess diet every second day. In the mixed diets, the numbers used ensured that all prey was available in excess. If the male died, it was immediately replaced with another male. The production of egg sacs was recorded daily. In addition, the number of eggs, emergence date and the percent emergence from egg sacs were recorded.

Fecundity, hatching success and offspring size

The food value of a prey type can be assessed by the resulting female fecundity and offspring size (Bilde & Toft, 1994; Toft, 1995; Marcussen *et al.*, 1999). Adult fecundity and offspring viability were measured as egg production and number and size of newly emerged spiderlings.

Although females fed some diets had longer reproductive periods, we limited the study to a period of 25 days in *A. formosana* and 55 days in *P. pseudoannulata*, starting from the

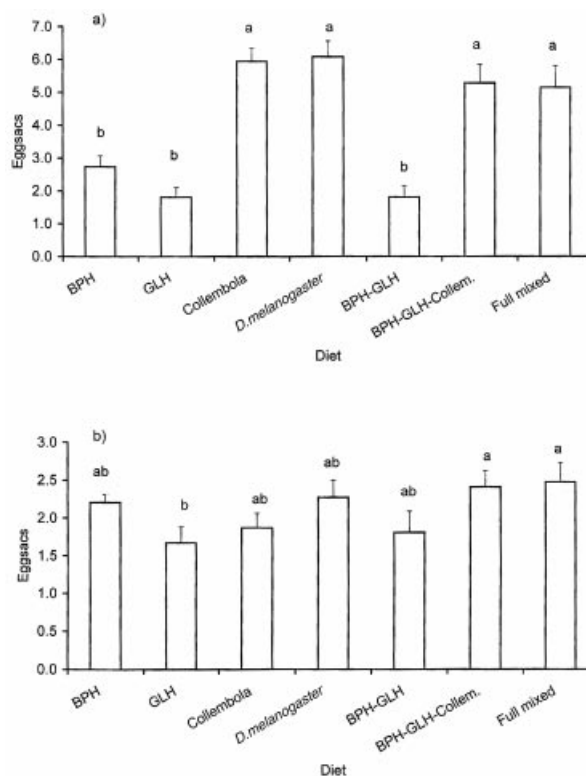


Figure 1 Mean number of egg sacs (+ SE) produced by (a) *A. formosana* and (b) *P. pseudoannulata* on different diets. Columns with different letters are significantly different (Student–Newman–Keul test, $P < 0.05$).

first oviposition, which was sufficient to observe clear differences between treatments.

To evaluate the quality of eggs and offspring, the number of eggs hatching was expressed as a percentage of the number of eggs laid. The number of hatched offspring and the number of unhatched eggs in every egg sac were counted. Unhatched eggs were examined under a binocular microscope and recorded as round, deflated or with embryo. As soon as they hatched from the egg sac, the offspring were preserved in alcohol. The size of the offspring was determined by measuring the length and width of their carapace, as well as their total body length, with an ocular micrometer under a binocular microscope. Ten randomly selected spiderlings were measured from each egg sac. If fewer than 10 emerged all were measured.

Food consumption

We estimated the daily food consumption by each female at 10 days intervals. For analysis we used the average food consumption based on the 10 and 20 days measurement after the spiders had become adults for *A. formosana* and the measurements after 10, 20, 30, 40 and 50 days for *P. pseudoannulata*. Females that produced an egg sac during the 24-h period were excluded from the analysis. Males were removed from the tube during this period. The dry weight of each prey type was estimated by drying 20 samples of 20 individuals of each prey

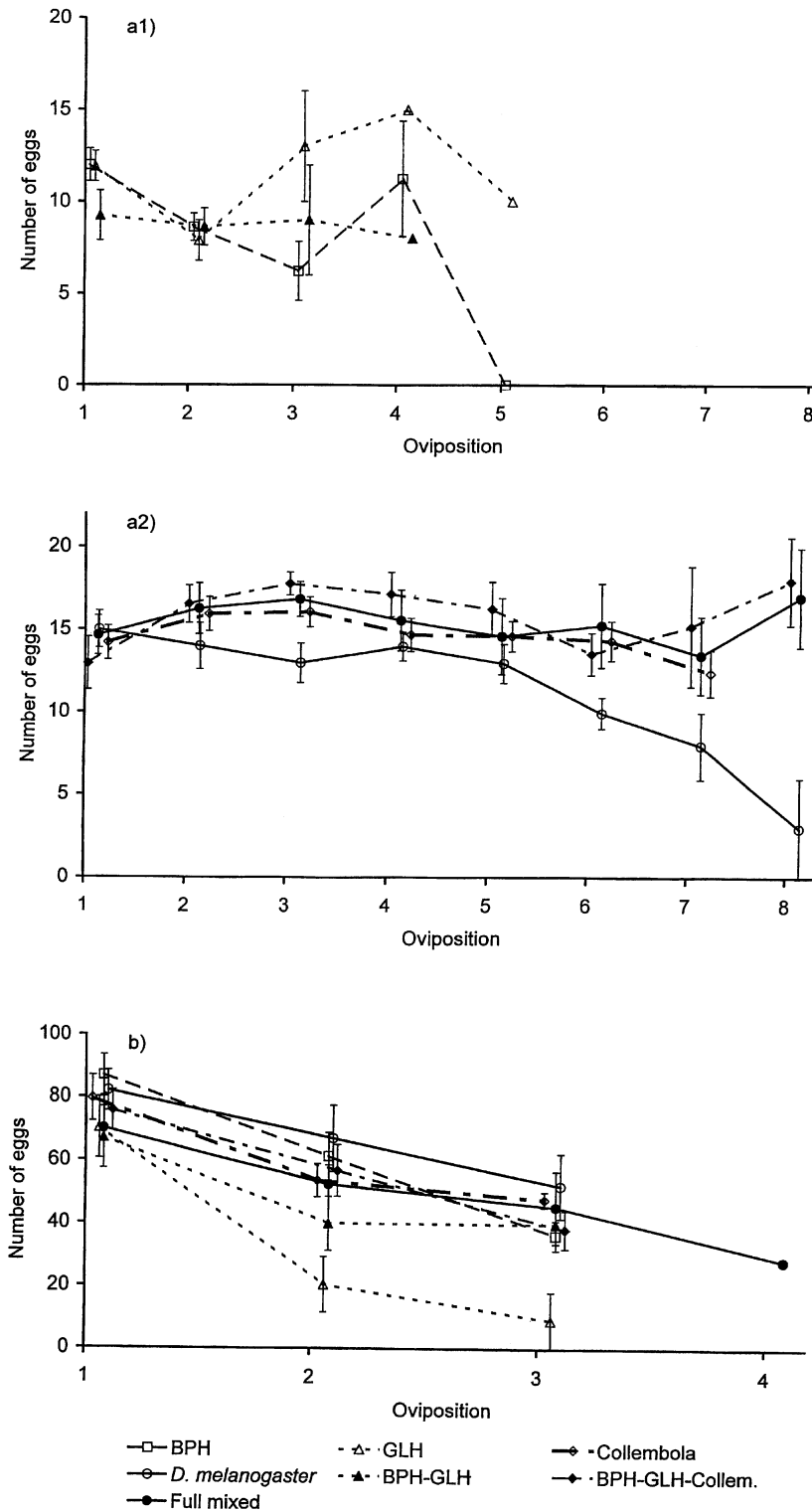


Figure 2 Mean number of eggs per egg sac (\pm SE) in subsequent egg sacs by (a) *A. formosana* and (b) *P. pseudoannulata* on different diets. Figure (a) is separated in a1 and a2 to improve readability.

species at 50 °C for 72 h and calculating mean weight for one individual. The average weight (\pm SD) of a Collembola was 0.6 ± 0.3 mg, a second-instar BPH and GLH weighed 0.5 ± 0.2 mg and 0.6 ± 0.3 mg, respectively, fifth-instar BPH and GLH weighed 8.8 ± 1.4 mg and 8.6 ± 2.2 mg,

respectively, and *D. melanogaster* 3.1 ± 0.5 mg. Food consumption in terms of number of prey consumed was calculated as the difference between the weight of prey introduced and the weight of prey recovered the following day (alive and dead without visible signs of feeding). Food conversion efficiency

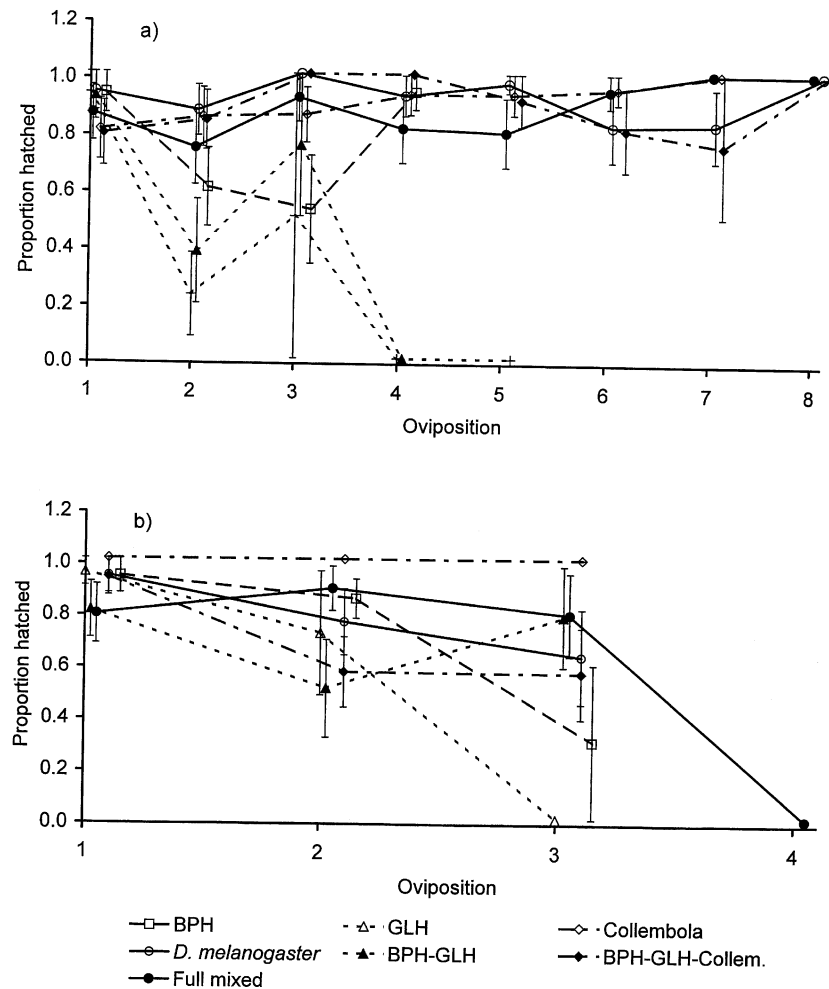


Figure 3 Hatching success in subsequent egg sacs (\pm SE) of (a) *A. formosana* and (b) *P. pseudoannulata* on different diets.

was calculated as mean number of eggs per 24 h, divided by mean food consumption in 24 h.

Data analysis

Data were analysed for normality and homogeneity of variances. If conditions for a parametric test could be met, if necessary by a transformation of the data, they were analysed by ANOVA (SAS Institute, 1990). In cases where data were transformed prior to analysis, this is indicated in the results section.

Fecundity of females, hatching success, size of offspring and food consumption and conversion efficiency on the different diets were compared by ANOVA, and the change between oviposition events was analysed using repeated measures analysis. Data were analysed for sphericity and when significant, *P*-values were epsilon-adjusted. The Student–Newman–Keuls multiple range test ($P < 0.05$) was used to compare all main effect means.

Survival of females was analysed with a nonparametric analysis for survival distributions, the LIFETEST procedure (SAS Institute, 1990), which yields survival distribution plots and product-limit survival estimates (Kaplan & Meier, 1958). Tests for homogeneity of survival curves over treatments include

the log-rank test, which is most sensitive to differences late in the survival curves, and the modified Wilcoxon test, which is most sensitive to differences early in the curves.

Results

Fecundity

The effect of diet on the mean number of egg sacs produced (Fig. 1) was significant for both *A. formosana* ($F_{6,98} = 17.7$, $P < 0.0001$) and *P. pseudoannulata* (log-transformed, $F_{6,92} = 2.6$, $P < 0.02$). The lowest number of egg sacs was produced on diets of GLH and GLH–BPH. For *A. formosana* the BPH diet was equally poor. *Pardosa pseudoannulata* fed BPH produced an intermediate number of egg sacs, not significantly different from the Collembola, *D. melanogaster*, the BPH–GLH–Collembola or the full mixed diets.

The statistical comparison of the number of eggs in successive egg sacs was restricted to the first two ovipositions for both species in order to include all diets. In *A. formosana* the number of eggs in successive egg sacs was subsequently compared for the first to fifth ovipositions for the better quality diets. For *A. formosana*, a few individuals on the hopper diets (the BPH, the

GLH and the BPH–GLH diets) produced more than two egg sacs (Fig. 2a). On these poor diets the number of eggs declined from first to second sac, but the picture is somewhat obscured in the later ovipositions, where the few remaining females produced a higher number of eggs per sac. After the fourth or fifth oviposition, the number of eggs produced on the *D. melanogaster* diet gradually decreased, whereas it remained high on the BPH–GLH–Collembola and the full-mixed diets. The average number of eggs per egg sac ranged between 9 and 15 in the first ovipositions, which was similar to the number of eggs per egg sac from field-collected *A. formosana* females of unknown age (Sigsgaard et al., 2001).

There was a significant effect of oviposition number \times diet on the number of eggs produced by *A. formosana* in subsequent egg sacs when all diets were compared ($F_{6,76} = 3.1$, $P < 0.01$) (Fig. 2a). Multiple comparisons of means showed that in the first oviposition the high-quality diets were significantly better than the BPH–GLH diet. In the second oviposition they were also better than the BPH diet, whereas the GLH diet was not significantly different from any of the other diets. A comparison of the better quality diets only showed a significant effect of oviposition number ($F_{4,176} = 3.2$, $P < 0.02$), reflecting a gradual but slow decrease in the number of eggs per sac.

In *P. pseudoannulata* the average number of eggs in the first egg sacs ranged from 67 to 87 (Fig. 2b). There was no significant effect of diet on the number of eggs, but a significant effect of oviposition number ($F_{1,76} = 56.9$, $P < 0.0001$), reflecting a decrease in the number of eggs per sac over ovipositions, with the fastest decrease in the GLH and the BPH–GLH diets. The number of eggs produced by *P. pseudoannulata* females was significantly affected by diet in the second oviposition ($F_{6,76} = 3.2$, $P < 0.008$). Multiple comparisons showed that *P. pseudoannulata* fed pure GLH produced fewer eggs than females fed other diets, except the BPH–GLH diet, which was not significantly different from any of the other diets.

Hatching success

Hatching success was initially high on all diets (Fig. 3). In *A. formosana*, hatching success then began to decline on the hopper diets, while remaining high on the Collembola, the *D. melanogaster*, the BPH–GLH–Collembola and the full mixed diets. Repeated measures analysis of hatching success for all diets was restricted to the first two ovipositions. For *A. formosana*, there was a significant effect of position in the sequence of egg sacs \times diet on hatching success ($F_{6,75} = 3.3$, $P < 0.006$). The analysis for ovipositions 1–5 for the better quality diets showed no significant effects of diet, oviposition number or diet \times oviposition number.

Except for the Collembola diet, hatching success in *P. pseudoannulata* decreased with oviposition number on all diets, although to different extents. Repeated measures analysis showed a significant effect of oviposition number on hatching success ($F_{1,69} = 7.8$, $P < 0.007$), and a marginally significant effect of diet \times oviposition number ($F_{6,69} = 2.0$, $P = 0.08$).

The average number of offspring per female represents the reproductive success on a diet and was significantly different in both species (both log-transformed, *A. formosana*, $F_{6,91} = 17.8$, $P < 0.0001$, *P. pseudoannulata*, $F_{6,90} = 3.5$, $P < 0.05$; Fig. 4).

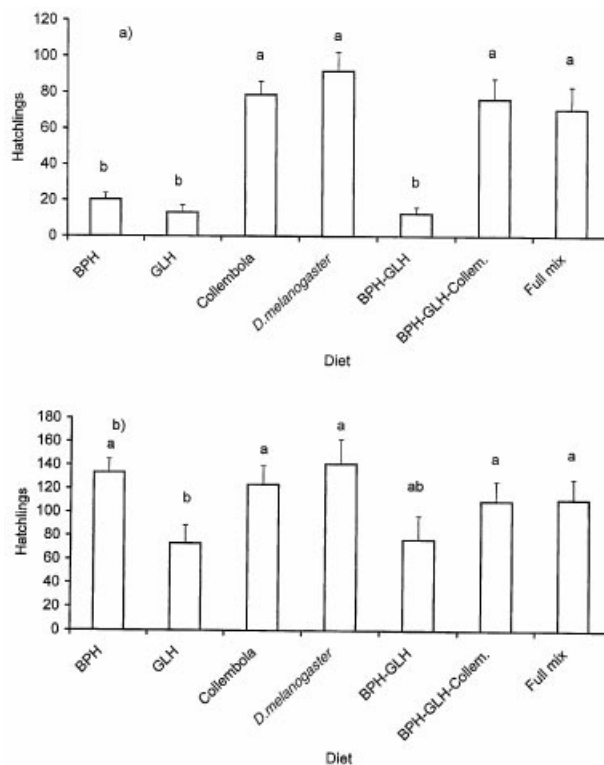


Figure 4 Mean number of hatchlings per female during the experimental period (+ SE). Columns with different letters are significantly different (Student–Newman–Keul test, $P < 0.05$).

The lowest number of *A. formosana* spiderlings was produced on the hopper diets. For *P. pseudoannulata* the lowest number was produced on the GLH diet, whereas the number of hatchlings produced on the BPH diet was high and not significantly different from the Collembola, the *D. melanogaster*, the BPH–GLH–Collembola and the full mixed diets. The BPH–GLH diet was not significantly different from any other diets.

Offspring size

Numerical differences between spiderling sizes in treatments were small. There were no consistent significant differences in the spiders when assessing carapace width and total body length. Repeated measures analysis of the effect of all diets on the carapace length of *A. formosana* spiderlings in successive ovipositions restricted to the first two ovipositions showed no significant main effect of diet or of the position in the sequence of egg sacs on carapace length. An analysis for ovipositions 1–5 for the better diets in *A. formosana* showed a significant effect of the position in the sequence of egg sacs \times diet ($F_{12,116} = 1.9$, $P < 0.04$) with shorter carapaces in later egg sacs.

For *P. pseudoannulata* a very slight increase in carapace length from the first to second oviposition, except in *D. melanogaster*, where there was a similarly small decrease in size (from 1.678 ± 0.016 mm to 1.671 ± 0.068 mm), gave a significant effect of diet \times position in the sequence of egg sacs ($F_{6,46} = 3.7$, $P < 0.005$) on carapace length in repeated

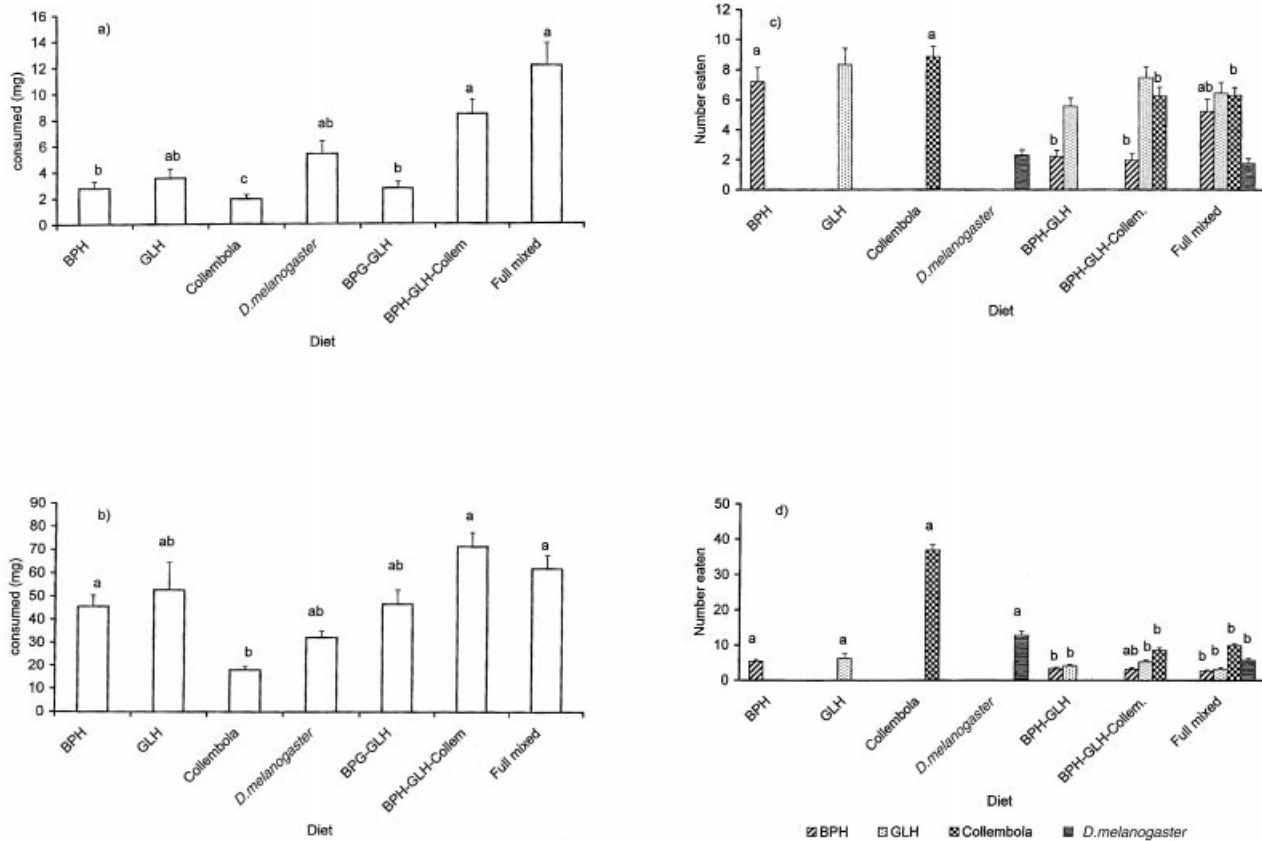


Figure 5 Biomass consumed during 24 h (+ SE) by (a) *A. formosana* and (b) *P. pseudoannulata* on different diets and average number of prey consumed in 24 h (+ SE) by female (c) *A. formosana* and (d) *P. pseudoannulata*. Columns of the same prey type with different letters are significantly different (SNK-test, $P < 0.05$). In (c) and (d) for prey types where no significant differences were found letters have been omitted for clarity.

measures analysis. Excluding the *D. melanogaster* diet from the analysis, only oviposition number was significant ($F_{1,38} = 8.1$, $P < 0.007$). There was no significant effect of including the female initial weight as a covariant for either of the spiders.

Food consumption

The effect of diet on biomass consumed during 24 h was significant for both *A. formosana* (log-transformed, $F_{6,98} = 8.4$, $P < 0.0001$) and *P. pseudoannulata* (log-transformed, $F_{6,98} = 3.9$, $P < 0.002$; Fig. 5a,b). For both *A. formosana* and *P. pseudoannulata*, the highest consumption was on the full mixed and the BPH-GLH-Collembola diets. For *A. formosana*, consumption was significantly lower in the BPH, the Collembola and the BPH-GLH diets, and not significantly different on the *D. melanogaster* and the GLH diets, whereas for *P. pseudoannulata*, only consumption of the Collembola diet was significantly less than of the BPH, the BPH-GLH-Collembola and the full mixed diets.

Consumption of a particular prey species was higher in the pure than in the mixed diets, although not always significantly so (Fig. 5c,d). In *A. formosana* consumption of BPH and Collembola but not of *D. melanogaster* and GLH was significantly affected by diet when comparing the treatments

in which the prey were included (BPH (log-transformed): $F_{3,47} = 13.6$, $P < 0.0001$, GLH: $F_{3,48} = 2.2$, $P = 0.2$, Collembola: $F_{2,37} = 6.1$, $P < 0.008$, *D. melanogaster*: $F_{1,24} = 1.2$, $P = 0.3$). Thus, whereas the number of BPH consumed was significantly less in the BPH-GLH diet than in the pure BPH diet, the number of GLH consumed was not significantly different in the GLH and the BPH-GLH diets. In *P. pseudoannulata*, consumption of individual prey species was significantly different depending on diet for all prey (BPH: $F_{3,58} = 8.3$, $P < 0.001$, GLH (log-transformed): $F_{3,53} = 6.1$, $P < 0.003$, Collembola: $F_{2,41} = 211.2$, $P < 0.0001$, and *D. melanogaster*: $F_{1,27} = 211.2$, $P < 0.001$).

Food conversion efficiency

For both species diet significantly affected food conversion efficiency (*A. formosana* (log-transformed): $F_{6,85} = 27.9$, $P < 0.0001$, *P. pseudoannulata* (log-transformed): $F_{6,90} = 11.1$, $P < 0.0001$). Multiple comparisons revealed that food conversion efficiency was highest on the Collembola diet, followed by the *D. melanogaster* diet (Fig. 6). For *A. formosana* the remaining diets were equally poor when assessed by this parameter. For *P. pseudoannulata* food conversion efficiency was intermediate on the BPH diet and not significantly different

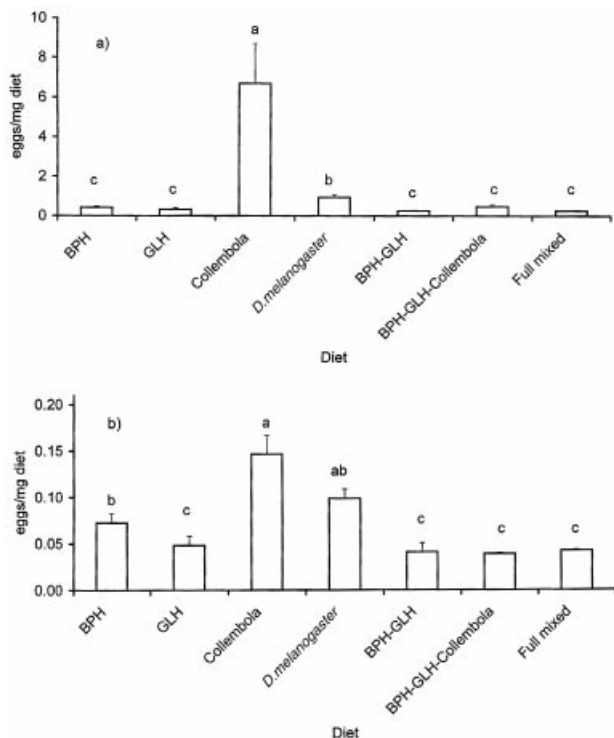


Figure 6 Food conversion efficiency (+ SE) of (a) *A. formosana* and (b) *P. pseudoannulata*

from the *D. melanogaster* diet, whereas it was low on the GLH, the BPH-GLH, the BPH-GLH-Collembola and the full mixed diets.

Female survival

In *A. formosana*, female survival differed significantly among diets (LIFETEST, Wilcoxon, $\chi^2 = 21.3$, d.f. = 6, $P < 0.0016$, Log-Rank, $\chi^2 = 23.7$, d.f. = 6, $P < 0.0006$; Fig. 7). Mortality was high on the GLH and BPH-GLH diets, where only four and six females, respectively, of the initial 15 females survived the experimental period of 25 days. On the other diets 11–14 females survived. In *P. pseudoannulata* female survival did not differ significantly on the different diets (LIFETEST, Wilcoxon, $\chi^2 = 9.4$, d.f. = 6, $P = 0.14$, Log-Rank, $\chi^2 = 9.7$, d.f. = 6, $P = 0.15$), although there was a tendency for higher mortality on the GLH diet and the BPH-GLH diet and a late increase in mortality on the full mixed diet (Fig. 7).

Discussion

Across most fitness parameters the dietary value of the three hopper diets was low for *A. formosana* and high on the diets of Collembola, *D. melanogaster*, BPH-GLH-Collembola and the full mixed diet. On the BPH-GLH-Collembola and the full mixed diets prey consumption was highest. Food conversion efficiency was highest on the Collembola diet, followed by the *D. melanogaster* diet. Both had higher food conversion efficiency than the BPH-GLH-Collembola and the full mixed

diets. More females survived on the BPH diet than on the GLH and the BPH-GLH diets. Based on the fitness parameters tested, the values of the diets for *A. formosana* can be ranked: Collembola diet \geq *D. melanogaster* diet \geq full mixed and BPH-GLH-Collembola diets $>>$ BPH diet $>$ GLH and BPH-GLH diets.

We found significantly higher survival and shorter development time of *A. formosana* spiderlings on BPH than on GLH, although both were poor diets (Sigsgaard *et al.*, 2001). This supports the tendency observed in this study of the BPH diet being better than the GLH diet for *A. formosana*. Shorter handling time of GLH nymphs than of BPH nymphs (Sigsgaard & Villareal, 1999) may partly explain why fewer BPH were eaten in the BPH-GLH diet than in the BPH diet, whereas the number of GLH eaten was not significantly reduced by diet mixing.

Pardosa pseudoannulata produced the highest numbers of egg sacs, eggs in successive egg sacs and hatchlings on the full mixed, the BPH-GLH-Collembola, the *D. melanogaster*, the Collembola and the BPH diets. The lowest numbers were found on the GLH and BPH-GLH diets. In contrast to *A. formosana*, *P. pseudoannulata*'s consumption of the BPH and the GLH diets was high and equal to consumption on the BPH-GLH-Collembola and the full mixed diets. Least was consumed on the Collembola and *D. melanogaster* diets. On these two diets food conversion efficiency was highest. The *D. melanogaster* diet was not significantly better than the BPH diet. Lowest food conversion capacity was found on the GLH diet and the three mixed diets. Across quality parameters tested the values of the diets for *P. pseudoannulata* can be ranked: Collembola diet \geq *D. melanogaster* diet $>$ BPH diet \geq full mixed and BPH-GLH-Collembola diet $>$ BPH-GLH diet \geq GLH diet.

Although BPH seems to be of relatively high quality to *P. pseudoannulata* by sustaining a high fecundity at the same level as on a Collembola diet, it is interesting to note that the BPH-GLH diet was no better than GLH alone, whereas the BPH-GLH-Collembola diet was significantly better (Fig. 4b). Thus, in the mixed diets Collembola make the positive contribution by alleviating the toxic effect of GLH, whereas BPH does not. This may indicate an overall higher value of Collembola than hopper food also to *P. pseudoannulata*. Probably Collembola is most important for young *P. pseudoannulata*. The low consumption of Collembola by adult *P. pseudoannulata* in the prey mixtures may be an effect of the small size of this prey in relation to the predator. Earlier studies of immature *P. pseudoannulata* show higher survival and better development when more than one prey was included in the diet (Suzuki & Kiritani, 1974; Thang *et al.*, 1988; Kumar & Velusamy, 1995). However, in this study a positive effect of dietary mixing was not consistent. Both species' food conversion efficiency was higher on the Collembola and *D. melanogaster* diets than on any of the mixed diets. Based on earlier results (Uetz *et al.*, 1992; Toft, 1995; Toft & Wise, 1999a), Toft (1999) hypothesized that the positive effect of dietary mixing depends on the quality of the prey species being mixed, such that (a) mixing of higher-quality prey may be beneficial, (b) mixing of high-quality prey with prey of inferior quality may be beneficial as long as toxic prey is not included, and (c) mixed diets including toxic prey may also be toxic even if higher-quality prey is included. The intermediary

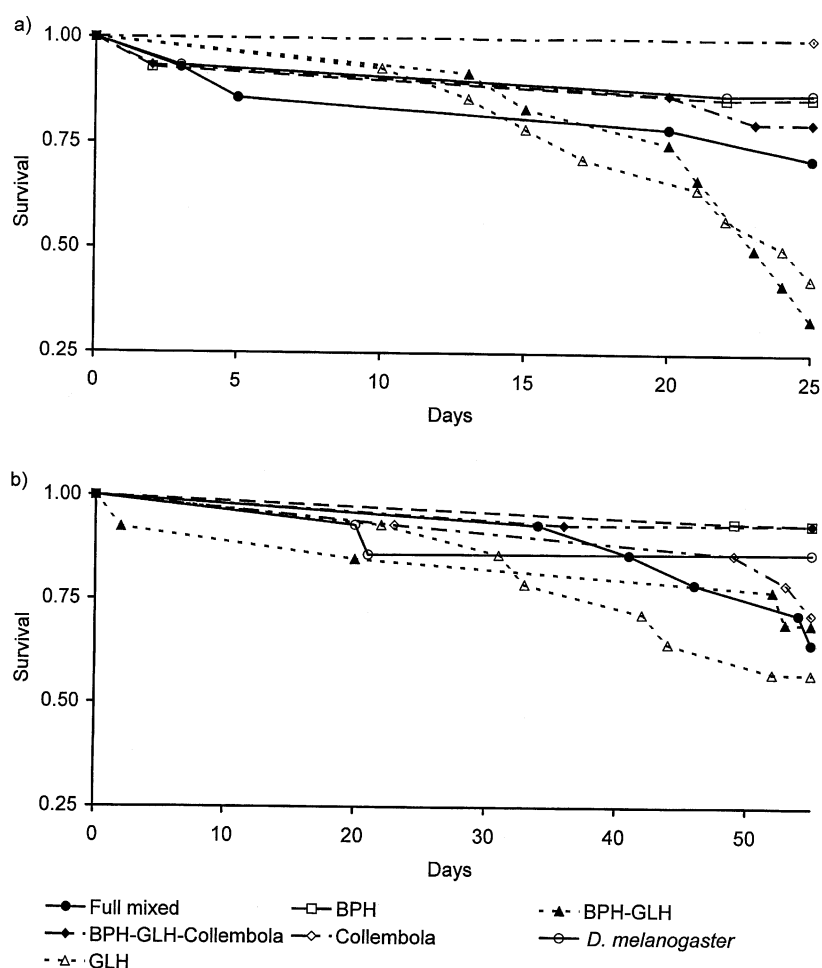


Figure 7 Survival of female (a) *A. formosana* and (b) *P. pseudoannulata* on different diets.

overall quality of the BPH–GLH–Collembola and the full mixed diets suggests that (b) or (c) applies. Furthermore, the lower quality of the BPH–GLH diet compared to the pure BPH diet, suggests that GLH may have a toxic component. The two hoppers react in distinctly different ways to predators. BPH is more active walking or jumping away in the event of a disturbance than GLH (Sigsgaard & Villareal, 1999). This behavioural difference between the two hoppers suggests that GLH might rely more on passive defence such as low dietary quality or a toxic component.

Both wolf spiders and money spiders can develop aversion against prey, as demonstrated in feeding experiments. These studies have revealed large differences in food quality between various types of prey (Toft, 1995; Toft & Wise, 1999a). Toft & Wise (1999b) found that a wolf spider *Schizocosa* sp. developed aversions against all low-quality, poor-quality and toxic prey species, but this spider lost its aversion faster than expected from an optimal diet perspective. The fact that aversions may develop against low-quality prey such as BPH and GLH does not reduce the number of prey types that are initially killed. However, the long-term predation rate on the hoppers will be low and the numerical response may be less when fitness of the spiders is reduced in the absence of sufficient alternative prey. This may

have important effects on spider populations and thus predation in the field. In contrast, if prey quality during fallow and early in the cropping season is high, the predator populations established in the rice field will have a high initial fitness. Under such conditions spiders can be expected to contribute significantly to the control of the hoppers early in the cropping season. Sustained good performance will depend on continued availability and quality of alternative prey. Possibly, however, genetic variation in the tolerance to hoppers can help the spider population to compensate for low availability of alternative prey. Thus, Beck & Toft (2000) found clear effects of selection on the tolerance to aphids in the money spider *Lepthyphantes tenuis* after only one generation.

Studies have indicated that an important role of Collembola and other alternative prey is to let sufficient beneficials survive the fallow period for timely and sufficient pest control (Wu *et al.*, 1994; Settle *et al.*, 1996). Settle *et al.* (1996) were able to significantly increase the number of detritus feeders, and subsequently spiders in field plots, after experimentally adding rice straw. When they experimentally reduced the number of alternative prey, Wu *et al.* (1994) found a negative impact on spiders. Evidence from decomposition food webs suggests that Collembola and other detritus feeders may

significantly influence spider populations, and vice versa (Wise *et al.*, 1999).

Our study shows that alternative prey in addition to providing an alternative food source when the number of insect pests are low, also provide spiders with a high quality dietary input necessary for them to realize their full predatory potential. The management of agricultural fields will determine not only the number but also the composition of alternative prey. The latter may be important because the quality of alternative prey may vary considerably, as shown for Collembola (Toft & Wise, 1999a; Bilde *et al.*, 2000). Several studies have documented that cereal aphids in the temperate areas are a poor quality prey to generalist predators including wolf spiders, money spiders and carabids (Bilde & Toft, 1994; Toft, 1995; Jørgensen & Toft, 1997; Bilde *et al.*, 2000). In the tropics planthoppers and leafhoppers fill equivalent niches. The finding that they are of equally low quality to generalist predators suggests that a low prey quality of Homopterans can be expected across cereal agroecosystems or perhaps a wider range of agroecosystems.

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