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The springtail *Sinella curviseta*: the most suitable prey for rearing dwarf spiders

Коллембола *Sinella curviseta*: наиболее подходящая добыча для выращивания пауков-пигмеев

D. Vanacker[1*], K. Deroose[1], L. Van Nieuwenhuyse[1], V. Vandomme[1], J. Vanden Borre[1] & J.-P. Maelfait[1,2]

[1] Terrestrial Ecology Unit, Ghent University, Ledeganckstraat 35, 9000 Ghent, Belgium. email: Danny.Vanacker@UGent.be

[2] Institute of Nature Conservation, Kliniekstraat 25, 1070 Brussels, Belgium.

* = corresponding author

ABSTRACT. In order to evaluate its quality as food for spiders, the springtail *Sinella curviseta* was compared with three other commonly used prey species: the springtails *Isotoma viridis* and *Lepidocyrtus cyaneus* and the fruit fly *Drosophila melanogaster*. The dwarf spider *Oedothorax gibbosus* was used as a predator, and we also investigated its active prey choice. The longevity, fecundity (rate of cocoon production and number of eggs) and progeny developmental rate (hatching success and offspring size) were used as fitness parameters. In addition to single-species diets, the quality of a mixed-species diet consisting of *S. curviseta* and fruit flies was investigated. *S. curviseta, I. viridis* and *D. melanogaster* were high-quality prey, in contrast to the low quality of *L. cyaneus.* Spiders fed on *L. cyaneus* died during early juvenile instars. *S. curviseta* was superior to *I. viridis* because a significantly smaller consumption rate of *S. curviseta* yielded better performance for three of the five fitness parameters investigated. A mixed diet of the two high-quality prey species *S. curviseta* and *D. melanogaster* did not yield beneficial effects. Prey choice of *O. gibbosus* did not completely concur with prey quality; juveniles and adults preferred *I. viridis* to *S. curviseta* despite the better quality of the latter. *S. curviseta* is one of the best prey species for culturing dwarf spiders, and in combination with fruit flies, also certainly for other spiders.

РЕЗЮМЕ. Для того, чтобы оценить качество коллемболы *Sinella curviseta* как пищи пауков, ее сравнили с тремя другими обычными видами-жертвами: коллемболами *Isotoma viridis* и *Lepidocyrtus cyaneus*, и плодовой мушкой *Drosophila melanogaster*. Паук пигмей *Oedothorax gibbosus* был использован как хищник; оценивали также активный выбор добычи у этого паука. В качестве критериев пригодности использовали продолжительность жизненного цикла, плодовитость и скорость развития молоди. Кроме диеты, состоящей из одного вида, изучили качество смешанных диет, состоящих из *S. curviseta* и плодовой мушки. *S. curviseta, I. viridis* и *Drosophila melanogaster* составили высококачественную пищу, в противоположность низкокачесвенной из *L. cyaneus*. Пауки, которых кормили только *L. cyaneus*, умирали на ранних стадиях. *S. curviseta* были лучше *I. viridis* поскольку при существенно более низкой скорости потребеления *S. curviseta* три из пяти параметров пригодности были выше. Смешанная диета из двух высококачественных типов добычи *S. curviseta* и *D. melanogaster* не продемонстрировала преимуществ. Выбор добычи *O. gibbosus* не был в полном соответствии с качеством добычи; молодь, также как взрослые, предпочитали *I. viridis* вместо *S. curviseta*, несмотря на то, что последняя лучше. *S. curviseta* — самая лучшая пища для разведения пауков-пигмеев, а в комбинации с плодовыми мушками также для других пауков.

KEY WORDS: Araneae, *Oedothorax gibbosus*, *Sinella curviseta*, *Isotoma viridis*, *Lepidocyrtus cyaneus*, *Drosophila melanogaster,* prey quality, prey choice, spider fitness.
КЛЮЧЕВЫЕ СЛОВА: Araneae, *Oedothorax gibbosus*, *Sinella curviseta*, *Isotoma viridis*, *Lepidocyrtus cyaneus*, *Drosophila melanogaster,* качество добычи, выбор добычи, кондиция пауков.

Introduction

Sinella curviseta Brook, 1882 (Arthropleona: Entomobryidae) is a springtail species that is easy to rear in the laboratory. It is oval in shape, with few hairs and of a pale colour, with an average size of 1.4 mm. They jump less than other springtails like *Isotoma viridis* Bourlet, 1839 (Arthropleona: Isotomidae) and *Lepidocyrtus cyaneus* Tullberg, 1871 (Arthropleona: Entomobryidae) [Niijima, 1973]. The scientific literature consists of few publications relating to *S. curviseta* [Waldorf, 1974, 1976; Nakamura, 1984; Nakamura *et al.,* 1992], two of which describe the life history [Niijima, 1973; Gist *et al.*, 1974]. Despite being an easy species to rear, this springtail or more specifically its eggs have only been used twice as a food for rearing animals. Takahashi *et al.* [1993, 1995] used the fresh eggs of *S. curviseta* to feed larvae of the mite *Leptotrombidium akamushi* Brumpt, 1910 (Acari: Trombiculidae), which is the primary vector for scrub typhus. No study has mentioned *S. curviseta* as a food for rearing spiders. Could this be due to the food quality of this springtail being lower than the more commonly used spider prey, such as *I. viridis*, *L. cyaneus* or fruit flies? To determine whether this is the case, it is necessary to study the prey quality of *S. curviseta* in comparison with those of the other prey species. To complete the picture, it would also be interesting to study prey preferences of a spider and the value of a mixed diet with *S. curviseta.* This can be easily studied in the laboratory, where the effect of prey on several fitness parameters can be measured.

We chose *Oedothorax gibbosus* (Blackwall, 1841) (Araneae: Linyphiidae: Erigoninae) as a spider predator, a rare dwarf spider bound to the oligo- and mesotrophic alder carrs and one that had been rather difficult to rear in the laboratory [De Keer & Maelfait, 1989; Alderweireldt, 1992]. According to Alderweireldt [1994], springtails and aphids are the most important prey for *Oedothorax* spiders because of their high occurrence in the webs. Several publications [Toft, 1996; Toft & Nielsen, 1997; Marcussen *et al.,* 1999; Toft & Wise, 1999a] have demonstrated that the food quality of springtails can differ enormously: *Folsomia fimetaria* Folsom, 1927 and *F. candida* Willem, 1902, for example, are toxic species, whereas *Tomocerus bidentatus* Folsom, 1913 and *Isotoma anglicana* Lubbock, 1862 are high-quality species. Toft [1999] distinguished different quality categories: high-quality, intermediate-quality, low-quality, poor-quality and toxic prey. In addition to single-species diets with no possibility for selection, analyzing the effect of mixed-species diets is interesting as the effect of dietary mixing depends on the nutrient quality of the prey species being mixed [Toft, 1999; Toft & Wise, 1999a,b].

The prey choice of spiders, especially if young and inexperienced, can differ from the expected choice on the basis of prey quality [Toft & Wise, 1999b]. Active prey selection should serve to find the optimal compromise between maximum energy intake, nutrient balance of the spider body and minimum toxin intake [Toft, 1999].

In the current work we aim to investigate (1) the prey quality of *S. curviseta, I. viridis* and *L. cyaneus* springtails and of *Drosophila melanogaster* fruit flies (Diptera: Drosophilidae), and (2) to analyze the preference of *O. gibbosus* for the three springtail species. This was studied for each juvenile instar and for adult spiders. To evaluate the prey quality we used longevity, fecundity and offspring development time as fitness parameters.

Material and methods

Oedothorax gibbosus were caught in the nature reserve ‘Het Walenbos’ at Tielt-Winge (50°55′N, 4°51′E), *c.* 30 km north-east of Brussels in Belgium, one of the most important river associated woodlands of Flanders. In this nature reserve *O. gibbosus* occurs in the oligo- to mesotrophic alder marshes. All spiders were kept separately in small plastic vials (5 cm diameter and 2.5 cm tall) with a thin

Table 1.
The initial sample sizes of each diet treatment per instar in the prey consumption experiment.

Таблица 1.
Изначальные размеры образцов каждого варианта использования диеты на возраст в эксперименте по потреблению добычи.

	1st instar	2nd instar	3rd instar	4th instar	Adult	Adult (parents)
Mixed-*S. curviseta*	55	22	21	23	18	25
L. cyaneus	40	2	0	0	0	27
S. curviseta	36	12	9	9	10	25
I. viridis	45	13	11	14	13	25
Fruit fly	51	39	33	34	32	29
Mixed-fruit fly	55	22	21	23	18	25

bottom of plaster, in a climate chamber at a photoperiod L : D 16 : 8 and a temperature of 20°C. The vials were moistened regularly to maintain a relative humidity close to 100%.

We investigated four different single-species diets with *I. viridis*, *L. cyaneus*, *S. curviseta* and *D. melanogaster*. *I. viridis* and *L. cyaneus* were collected in a grass-field by means of a small vacuum cleaner, *S. curviseta* and *D. melanogaster* originated from laboratory cultures.*Sinella curviseta* were raised in rectangular plastic vials (11 cm long, 9.5 cm wide and 6cm high) with a thin bottom of carbonic plaster (= plaster mixed with carbon) and fed regularly with dry yeast. After approximately one month they became adult. The fruit flies were reared in plastic vials (9 cm long, 7 cm wide and 9 cm high) with a medium consisting of three bananas, two cups of rolled oats, 3 g agar, 3 g Methylis parahydroxybenzoas (against Fungi) and 5 g Absinthii herba (Wormwood, against Acari). We also investigated the quality of a mixed-species diet consisting of *S. curviseta* and fruit flies.

Prey consumption

To assess the quality of each prey species, we calculated the prey consumption rate for each species. We investigated the offspring of two cocoons per diet; all cocoons were laid by different females. Table 1 shows the initial sample sizes of each treatment. Because the total amount of cocoons produced by all the females on the *L. cyaneus* diet was one, we used a second cocoon from a female on the *D. melanogaster* diet. Every two days the parents and the young of the first generation (F1) on a single-springtail diet were fed four springtails; those on a single-fruit fly diet were fed three fruit flies, and those on a mixed-diet were fed four *S. curviseta* springtails and three fruit flies. The occurrence of moults and the production of cocoons were recorded daily.

Prey choice

To investigate the prey choice we used young of the second generation (F2) from four cocoons. We investigated 82 first instars, 42 second instars, 39 third instars, 36 fourth instars and 30 adults. Every two days these spiders were fed two *I. viridis,* two *L. cyaneus* and two *S. curviseta* springtails. Each time we checked the number of each springtail species consumed from which we could determine the prey choice. We used two rather than one springtail for each prey species in order to avoid a shortage of the preferred prey. We recorded the occurrence of moults.

In order to account for the weight of the different prey animals, we measured the weight of 20 prey animals of each species five times and calculated the average weight (weight *I. viridis*: 0.20 ± 0.04 mg, *L. cyaneus*: 0.08 ± 0.01 mg, *S. curviseta*: 0.14 ± 0.03 mg, *D. melanogaster*: 1.92 ± 0.24 mg). We used these mean weights as conversion factors: for each prey species the prey numbers consumed were multiplied by the conversion factor to obtain the prey weight consumed. For each juvenile instar and the adults the consumption rate was calculated as the total weight of consumed prey during an instar divided by the duration (number of days) of the instar.

Table 2.
The sample sizes of each diet regime per fitness parameters.

Таблица 2.
Размеры пробных образцов для каждого режима диеты и параметра кондиции.

	Lifetime of offspring	Rate of cocoon production	Number of eggs in 1st cocoon	Number of eggs in 2nd cocoon	Hatching success	Offspring size
L. cyaneus	3	17	1	0	0	0
S. curviseta	13	15	11	7	8	8
I. viridis	16	17	9	4	6	6
fruit fly	44	20	18	9	16	16
mixed diet	27	12	11	17	11	11

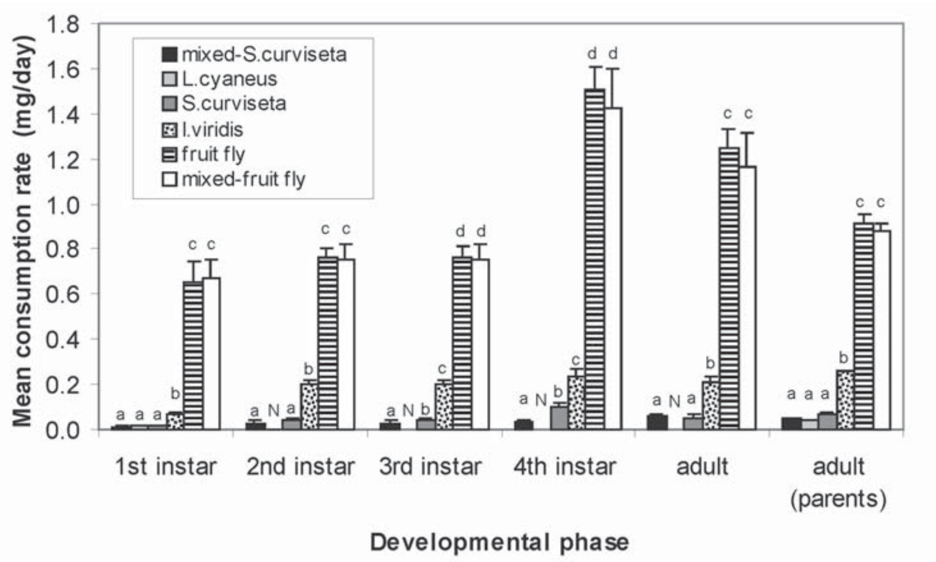

Fig. 1. Mean consumption rate (+SE) (in the different juvenile and adult instars of the first generation spiders and in the adult phase of the parents for the five different diets; the two prey species of the mixed diets were analyzed separately: mixed–*S. curviseta* and mixed–fruit fly). The consumption rate was calculated as the total consumed prey weight during an instar divided by the duration of the instar. The significance of the tests is indicated with a letter code (N = not observed).

Рис. 1. Средняя скорость потребления (+SE) (в различных ювенильных и взрослой стадиях пауков и во взрослой стадии родителей для первых пяти раличных диет; два вида добычи с смешанной диете были проанализированы отдельно: смешанная–*S. curviseta* и смешанная–плодовая мушка). Скорость потребления вычислялась как полный вес потребленной добычи в течении возраста поделенный на продолжительность возраста. Значимость тестов обозначена буквенным кодом (N = не наблюдался).

Fitness parameters

We measured offspring lifetime, rate of cocoon production, number of eggs per cocoon and hatching success. Table 2 shows the sample sizes of each diet regime. From each diet we put newly hatched juveniles that were not needed alive into 70% ethanol. These were used to determine the offspring size by measuring the circumference of their carapace using a digitalization table and computer program. We could not do this for spiders on the *L. cyaneus* diet because there were not young enough. To investigate the quality of each prey we compared the fitness parameters of spiders from each diet regime.

We used the Kolmogorov-Smirnov-test to analyze the assumptions of normality. If these were fulfilled we used ANOVA and the Scheffé post hoc test, but mostly we had to use the non-parametric Kruskal-Wallis ANOVA followed by pairwise Mann-Whitney *U*-tests. To determine the significance of each test we applied the Bonferroni correction. The Statistica software package was used for statistical analyses. To compare proportions we used the χ^2-test.

Results

Prey consumption

In all developmental phases the same trend in prey consumption rate was observed (Fig. 1), with the means ranking as follows: diet of *L. cyaneus* < mixed diet of *S. curviseta* (= *S. curviseta*) < diet of *I. viridis* < mixed diet of fruit flies (= fruit flies). It was not possible to demonstrate a significant difference between the instars in the consumption rate of *L. cyaneus* and *S. curviseta* when fed the mixed diet, nor in the consumption rate of *S. curviseta*. There was such a high mortality in the spider culture fed the *L. cyaneus* diet that only two out of forty first instar juveniles reached the second instar, and these two spiders died during the second instar. Because of this high mortality we could not demonstrate a significant difference between the consumption rate of *L. cyaneus* and *S. curviseta* diets. Only in the third and fourth instars was the amount of *S. curviseta* consumed per day significantly lower in the mixed *S. curviseta*–fruit fly diet than in the single *S. curviseta* diet; this is also the trend for the fruit flies though the differences were not significant.

The *S. curviseta* consumption rate in the single diet was significantly lower than the total consumption rate of *S. curviseta* and fruit flies in the mixed diet (Mann-Whitney *U*-test: N_{mixed} = 18, $N_{single\ S.\ curviseta}$ = 10, *U* = 19, P = 0.001). There was however, no significant difference between the fruit fly consumption rate in the single diet and the total consumption rate of *S. curviseta* and fruit flies in the mixed diet (Mann-Whitney *U*-test: N_{mixed} = 18, $N_{fruit\ fly}$ = 10, *U* = 279, P = 0.856). The same trend was also observed for the parental spiders.

Prey choice

In the prey choice experiment only three springtail species were used as prey. The observed trend in prey choice was again the same in the different developmental phases (Fig. 2); the prey ranking was: *L. cyaneus* < *S. curviseta* < *I. viridis*. Notwithstanding the obvious preference of *O. gibbosus* for *S. curviseta* over *L. cyaneus*, the differences between the consumption rates of these springtails were not significant in the second juvenile instar; in the other developmental phases the differences were significant. *O. gibbosus* preferred *I. viridis* above *S. curviseta*.

Fitness parameters

The following five fitness parameters were utilized: (1) longevity, (2) rate of cocoon production, (3) number of eggs, (4) hatching success and (5) offspring size.

The ranking of prey species with regard to offspring longevity (Fig. 3) was *L. cyaneus* < *I. viridis* = *S. curviseta* < fruit fly. *L. cyaneus* was evidently the poorest prey species because no juvenile spider was able to reach adulthood. There were no significant differences between the longevities of spiders fed on *I. viridis* and *S. curviseta*; spiders fed on fruit flies lived significantly longer. The longevity of spiders on the mixed diet was significantly lower than those fed on the single *D. melanogaster* diet.

Female spiders on the *L. cyaneus* diet had a significantly lower rate of cocoon production (Fig. 4). This rate was higher in *S. curviseta* than in *I. viridis* fed diets, but this difference was not significant. Spiders fed on fruit flies and the mixed diet had the highest rate of cocoon production, but there was only a significant difference between the two diets in the first cocoon produced. There were no significant differences in number of eggs in the first and the second cocoons of spiders fed on *S. curviseta* and *I. viridis*. The number of eggs in the first cocoon was significantly higher in spiders on the mixed diet than those on the other diets. The number of eggs in the second cocoon was also higher in spiders on the mixed diet than those on the other diets, but only the difference between the mixed diet and the diet consisting of *I. viridis* was significant (Fig. 5).

The hatching success was significantly higher in spiders on the *S. curviseta* diet according to a χ^2-test (P = 0.001); the ranking of prey species with respect to hatching success was: *I. viridis* (33%) < fruit fly (52%) < *S. curviseta* (100%). Spiders on the mixed diet (64%) had a significantly smaller hatching success than those on the *S. curviseta* diet (χ^2-test: P = 0.017); the difference between spiders on the mixed diet and the fruit fly diet was not significant.

Offspring of spiders on the *S. curviseta* diet were significantly smaller than those on the *I. viridis* diet (Fig. 6). The offspring size of spiders on the *D. melanogaster* diet was larger than those on the *I. viridis* diet, but this difference was not significant. The mixed diet again had a significantly lower result for this fitness parameter than did the *D. melanogaster* diet.

Discussion

According to our results the springtail *L. cyaneus* is a low-quality prey, i.e., a prey species only permitting a very slow growth and development or causing mortality during early juvenile instars [Toft & Wise, 1999a]. Only two spiders fed on *L. cyaneus* reached the second juvenile instar and female spiders on this diet laid few cocoons, of which many did not hatch. *S. curviseta* and *I. viridis* are a high-quality prey, permitting the complete development of

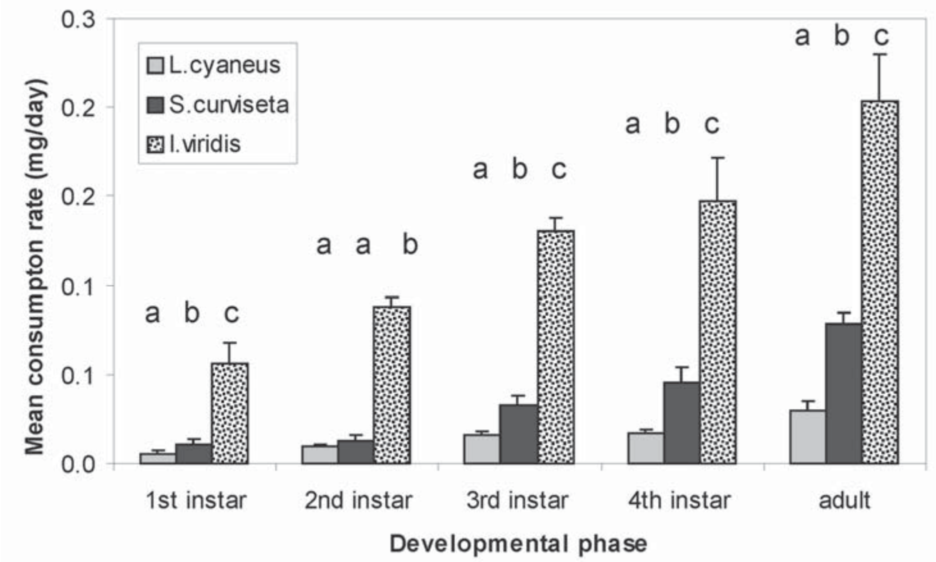

Fig. 2. Mean consumption rate (+SE) in the prey choice experiments for three springtail species in the different juvenile and adult instars.

Рис. 2. Средняя скорость потребления (+SE) в экспериментах по выбору добычи из трех видов коллембол для различных ювенильных и взрослой стадий пауков.

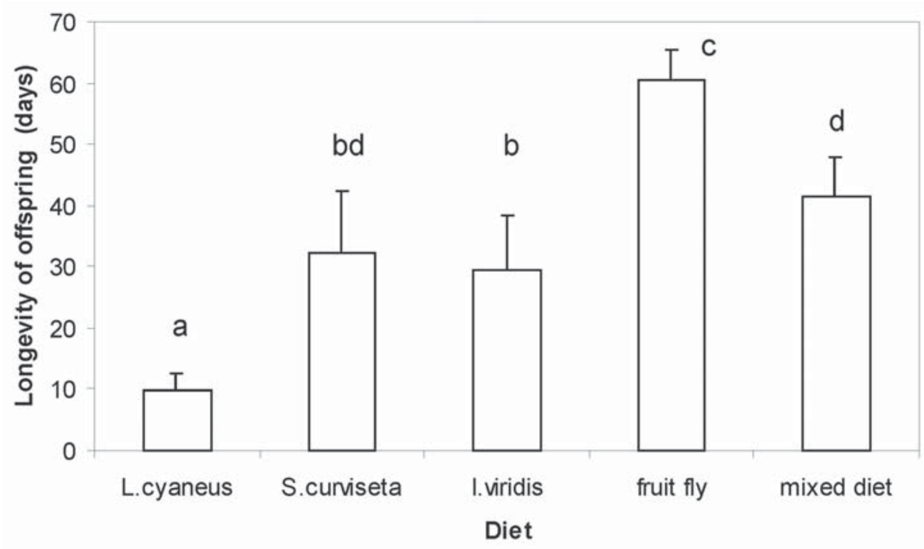

Fig. 3. Mean lifetime of the offspring (days) (+SE) for the five different diets. The significance of the tests is indicated with a letter code.

Рис. 3. Средняя продолжительность жизни потомства (дни) (+SE) для пяти разных диет. Значимость тестов обозначена буквенным кодом.

the predator [Toft & Wise, 1999a]. This is in agreement with the high quality of the springtail *Isotoma anglicana*, the sister species of *I. viridis* [Marcussen *et al*., 1999]. However, not all springtails of the genus *Isotoma* are high-quality prey species, e.g., *I. trispinata* MacGillivray, 1896 is a toxic prey [Toft & Wise, 1999a]. The quality of *S. curviseta* is apparently superior to that of *I. viridis*; in spite of the significantly smaller consumption rate of *S. curviseta,* spi-

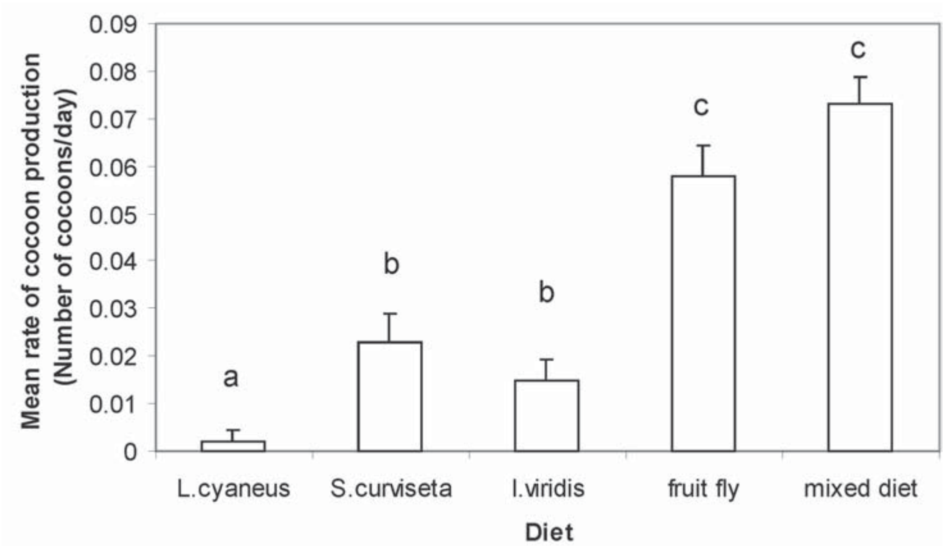

Fig. 4. Mean rate of cocoon production (number of cocoons/duration of adult phase) (+SE) for the five different diets. The significance of the tests is indicated with a letter code.

Рис. 4. Средняя скорость продукции кокона (количество коконов/продолжительность взрослой фазы) (+SE) для пяти различных диет. Значимость тестов обозначена буквенным кодом.

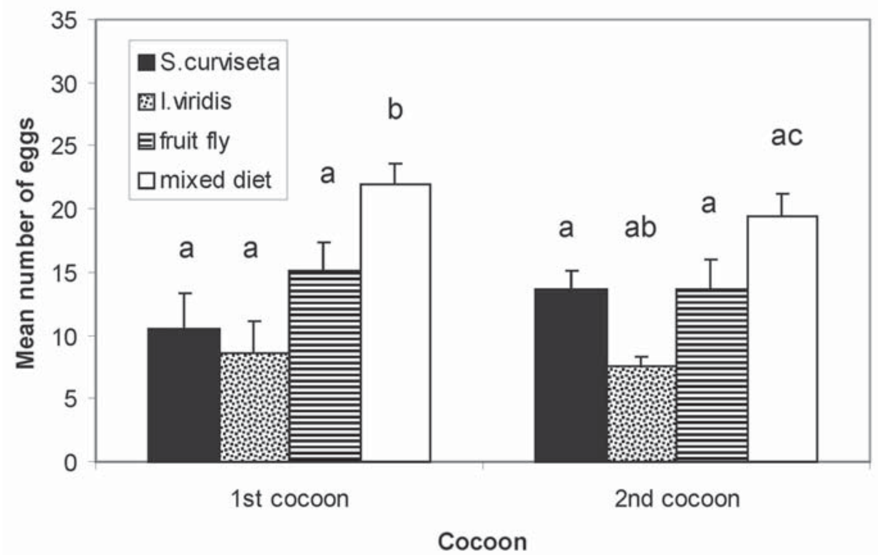

Fig. 5. Mean number of eggs in 1st and 2nd cocoon for four different diets (+SE). The significance of the tests is indicated with a letter code. We used an ANOVA and Scheffé-test for the number of eggs in the 2nd cocoon.

Рис. 5. Среднее количество яиц в 1-м и 2-м коконах для четырех типов диет (+SE). Мы использовали ANOVA и Scheffé-тест для количества яиц во 2-м коконе.

ders fed with a *S. curviseta* diet performed equally well or significantly better for three of the five studied fitness parameters, namely longevity of offspring, rate of cocoon production and hatching success. The quality of *D. melanogaster* is also very high, in four of the five fitness parameters spiders on this diet did better in comparison with a springtail diet; only for the number of eggs per cocoon was there no significant difference. Fruit flies were consumed at the highest rates and in most cases produced the highest fitness measures. Nevertheless, *D. me-*

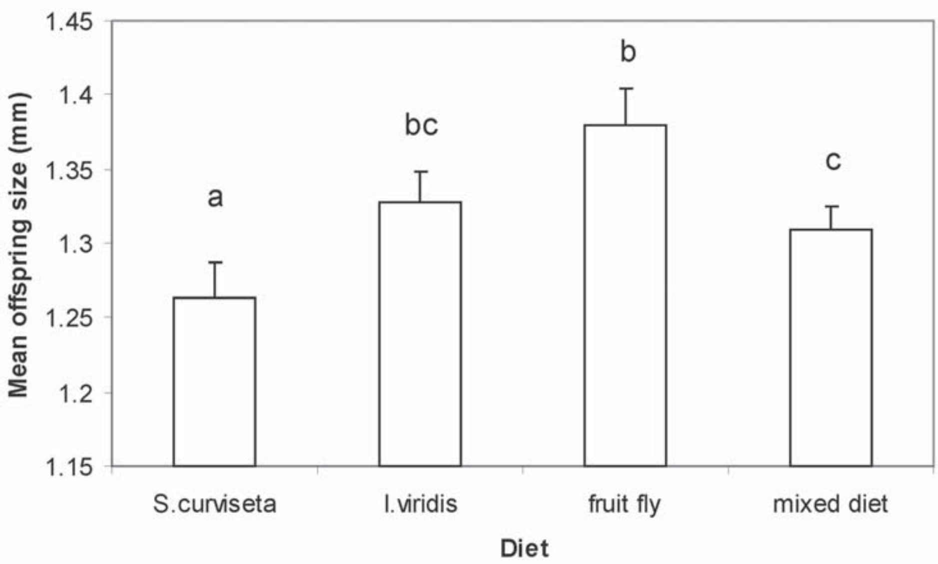

Fig. 6. Mean offspring size (+SE) for four different diets determined as the prosoma perimeter (mm). The significance of the tests is indicated with a letter code.

Рис. 6. Средний размер потомства (+SE) для четырех различных диет, определнный как периметр просомы (мм). Значимость тестов обозначена буквенным кодом.

lanogaster is often considered as being an intermediate-quality prey [Bilde & Toft, 1994, 1999, 2000; Toft & Wise, 1999a]. According to Bilde *et al.* [2000] however, the egg production of the carabid beetle *Bembidion lampros* (Herbst, 1784) declined over time when fed on the springtail species *I. anglicana*, *I. notabilis* (Schäffer, 1896), *Isotomurus prasinus* (Reuter, 1891), *F. fimetaria* and *L. cyaneus*, indicating a lower quality of all species compared with *D. melanogaster*. There was considerable variation between species, and *Bembidion lampros* ate more dead than living springtails. The quality of the nutritional medium on which fruit flies are raised is apparently also very important; Toft [1999] and Mayntz & Toft [2001] demonstrated better performance of spiders fed on fruit flies raised on an enriched nutritional medium than of those raised on a plain medium. The nutritional medium we used for the fruit flies was consequently of good quality.

The multiple-species diet was composed of two high-quality prey species, but the effect of the mixed diet was not better than the effect of each single-species diet. Only the number of eggs per cocoon and the hatching success of spiders on the mixed diet were better than those on both single-species diets, but none of the differences were significant. According to Toft [1999], the mixing of higher-quality prey may or may not be beneficial; in our case the mixing is thus not beneficial. Mixing of higher-quality prey with prey of inferior quality may be beneficial as long as a toxic prey is excluded [Toft, 1999]. A mixed diet of the low-quality *L. cyaneus* with the high-quality *I. viridis* or *S. curviseta* or *D. melanogaster* might be beneficial.

Spiders are selective if they choose differentially between prey species offered. Active and passive selection can be distinguished if a prey is presented with or without possibilities to escape [Toft, 1999]. In the current work we investigated the active selection of *O. gibbosus* on three different springtail species. *O. gibbosus* preferred the low-quality prey *L. cyaneus* the least; however, they preferred *I. viridis* to *S. curviseta*, notwithstanding the better quality of *S. curviseta*. Jorgensen & Toft [1997] and Toft [1999] demonstrated that the preferences of the spiders are not always simply related to the nutritional value of the prey. Sometimes there are other criteria than food quality that affect prey choice; it is possible that *I. viridis* springtails are more attractive to *O. gibbosus* than *S.*

curviseta springtails because of their better smell and/or taste. It has been observed that first instar juveniles of *O. gibbosus* more easily catch *I. viridis* than *S. curviseta* [Vanacker, unpubl. data].

In all developmental phases there was the same trend in prey consumption rate and in prey choice. This facilitates the rearing of dwarf spiders, as it permits the use of a single diet for all juvenile and adult instars of this dwarf spider species. This is in contrast to the results of Bilde *et al.* [2000]: the two springtail species *I. anglicana* and *F. fimetaria* seemed to be of relatively higher quality for larvae than for adults of the carabid beetle *Bembidion lampros*. In cultures of the more common dwarf spider species like *O. fuscus*, *O. apicatus* and *O. retusus* fed on a diet of *S. curviseta* or fruit flies, the mortality is even lower than in cultures of the rarer *O. gibbosus* [Vanacker, unpubl. data].

Thus, *S. curviseta* is not only a very good prey for dwarf spiders, but it seems to be even better than the more commonly used spider prey species *I. viridis* and *L. cyaneus*. The culture of *S. curviseta* is easier than *I. viridis* and *L. cyaneus*. *S. curviseta* are also easier to handle because they use their furcula less. *S. curviseta* is not only the optimal candidate as dwarf spider food, but also as a spider food in general. For larger spider species it is good food for the first instars, the larger instars could then be fed on fruit flies. This is a suitable food regime for wolf spiders [Hendrickx *et al.*, 2001].

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