The value of Collembola from agricultural soils as food for a generalist predator

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Summary

1. The Collembola is one of the important prey groups for generalist arthropod predators in agro-ecosystems. Differences in the quality of available species may play a significant role in the build-up of a community of natural enemies. The value of some common epigeic and hemi-edaphic Collembola as prey for adults and larvae of the carabid beetle *Bembidion lampros* was assessed in laboratory experiments.

2. Consumption capacity, egg production and the efficiency of converting prey into eggs were used as quality criteria for beetle adults, kept on diets of the collembolans *Isotoma anglicana*, *Isotoma notabilis*, *Isotomurus prasinus*, *Folsomia fimetaria* and *Lepidocyrtus cyaneus*, with fruit flies *Drosophila melanogaster* used as a high quality comparison prey. Survival, developmental time and teneral adult weight were used as quality criteria for beetle larvae on diets of *Isotoma anglicana*, *Isotoma notabilis*, *F. fimetaria*, *D. melanogaster* and a starvation treatment.

3. Collembola were offered to adults in dead and live treatments to assess the cost of prey capture and handling in relation to prey quality.

4. *Bembidion lampros* ate more dead than live Collembola. Egg production declined over time on all collembolan diets, indicating a lower quality of all species compared with *D. melanogaster*, but there was considerable variation between species. The highest food conversion efficiency occurred on *F. fimetaria*, *L. cyaneus* and *D. melanogaster*, while *Isotoma notabilis* could not be utilized by *B. lampros* for egg production.

5. Larvae completed development with low mortality on *Isotoma anglicana* and *F. fimetaria*, although there were differences in developmental time. The two Collembola seemed to be of relatively higher quality for larvae than for adults. Significantly higher teneral weight occurred on a diet of *D. melanogaster* compared with the Collembola.

6. The effect of Collembola quality on the beetle fecundity and larval developmental time suggests that agricultural management for natural enemies, should aim to benefit the species composition of the prey population.

Key-words: fecundity, larvae development, polyphagous predator, prey quality.

Journal of Applied Ecology (2000) **37**, 672–683

Introduction

The importance of generalist arthropod predators as natural enemies of agricultural pests such as cereal aphids is generally accepted. Generalist predators affect aphid populations because they can initiate predation in the early establishment phase of the aphids (Edwards, Sunderland & George 1979; Chiverton 1986; Sunderland, Fraser & Dixon 1986; Winder 1990). The early spring breeders (Luff 1987; Wallin 1989; Riedel 1991; Fadl & Purvis 1998) may play a significant role in the build-up of a potent community of beneficial predators by reproducing

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before the pests arrive. In a simulation study of aphid predation, a high level of alternative prey increased aphid predation up to a certain stage due to the increased reproductive output of spring breeders (S. Toft & J.A. Axelsen, unpublished data). Sunderland, Fraser & Dixon (1986) found real predator population sizes to be a limiting factor for the natural control of aphids. The potential for suppression of aphid densities may thus be significantly improved if predator reproduction can be increased.

Availability and value (or quality) of prey are two major factors influencing reproductive outcome (Sunderland *et al.* 1996a). Natural populations of predators often experience a more or less continuous shortage of food (Baars & van Dijk 1984; Sota 1985; Juliano 1986; Bilde & Toft 1998), which limits their reproductive outcome. Under food shortage, the value of prey comes into focus, as high nutritional quality may partially counteract a shortage of prey. The quality of the prey strongly influences the number of eggs and young produced by the predators. Studies on prey quality assessed by means of predator fitness parameters such as egg production and growth rates, have revealed significant differences in quality of potential prey species (Diptera, Collembola and aphids) for generalist carabid beetles and spiders (Bilde & Toft 1994; Toft 1995; Sunderland *et al.* 1996b; van Dijk 1996; Marcussen, Axelsen & Toft 1999; Toft & Wise 1999). Based on these findings it is hypothesized that quality of the early season prey may have a strong influence on the reproductive output of the predators, and thus on later aphid populations.

Collembola in fields have long been recognized as an important prey group for generalist predators, and constitute a considerable proportion of their diets (Mitchell 1963; Sunderland 1975; Hengeveld 1980; Pollet & Desender 1987, 1989; Alderweireldt 1994). If differences in quality exist among species of Collembola as prey for predators, it may have consequences for the build-up of a community of natural enemies. The aim of this study was to determine the value of a range of common Collembola species from agricultural soils as prey for a generalist predator, the carabid beetle *Bembidion lampros* (Hbst.). It was expected that different species of Collembola would differ in value to *B. lampros*, as assessed by measuring prey consumption and egg production of the carabid when fed single-species diets of five species of Collembola. The question whether different Collembola have the same value for larvae as for adults of *B. lampros*, was addressed by measuring survival, developmental time and teneral adult weight when larvae were reared on single-species diets of Collembola. The value of two Collembola species, *Isotoma anglicana* (Lubbock) and *Folsomia fimetaria* (L.), as food for the linyphiid spider *Erigone atra* (Bl.) was assessed in a similar experiment, in which *Isotoma anglicana* turned out

to be of excellent value but *F. fimetaria* of low value to the spider (Marcussen, Axelsen & Toft 1999). These two Collembola were included in the experiments reported here in order to test whether a prey species is of similar value to different species of generalist predators.

Materials and methods

Bembidion lampros is an abundant predator in European cereal fields. It disperses into the fields early in the season (in Denmark in March/April) and immediately begins to reproduce (Wallin 1985; Fadl & Purvis 1998). The Collembola evaluated were *Isotoma anglicana*, *Isotoma notabilis* (Schäffer), *Isotomurus prasinus* (Reuter), *Lepidocyrtus cyaneus* (Tullberg) and *F. fimetaria*, which are among the most common epigeic and hemi-edaphic Collembola in agricultural fields (Lagerlöf & Andrén 1991; Krogh 1994). *Isotoma anglicana* belongs to the *Isotoma viridis* (Bourlet) species complex, but has been distinguished as a separate species (Fjellberg 1980; Simonsen *et al.* 1999; see Filser 1999 for the ecology of the two species). *Isotomurus prasinus* belongs to a species complex that until recently was considered to be one species, *Isotomurus palustris* (Reuter) (Deharveng & Lek 1993). Wild-type fruit flies *Drosophila melanogaster* (Meig.) were used as a standard comparison prey, as they are readily accepted by carabid beetles and are of relatively high quality (Bilde & Toft 1994, 1997).

Beetles were collected by ground search in late April/early May 1998. Females and males were kept together and fed fruit flies and ground dog food *ad libitum* for 3 days. Females were separated from males and starved for 3 days, then they were weighed and entered the first 24-h consumption experiment. The starvation period served to increase food demand and thus more clearly expose low relative consumption rates of prey with chemical defence. During the starvation and subsequent food consumption measurement, females were kept in 5-cm plastic Petri dishes with a bottom of moist plaster-of-Paris mixed with charcoal, to assure a high humidity. The pre-experimental standardization, as well as all subsequent experiments, was carried out at 20 °C and a 16L : 8D photoperiod.

Folsomia fimetaria was obtained from a laboratory culture maintained on baker's yeast; the other Collembola species were extracted from grass field turf. The fruit flies used in the experiments were reared on instant *Drosophila* medium (Formula 4-24 Plain; Carolina Biological Supply, Burlington, NC) mixed with crushed dog food (Techni-Cal maintenance®, Martin Pet Foods, P.O. Box 100 Elmira, Ontario, Canada N3B 2Z5) to assure a high nutritional quality of the flies (C. Kristensen and S. Toft, unpublished data).

CONSUMPTION RATE OF DIFFERENT PREY SPECIES

If energetic and nutritional requirements are fulfilled on a certain prey type, the daily amount consumed can be defined as the daily food demand of the predator (Bilde & Toft 1997). Freeze-killed *D. melanogaster* was used to determine the beetles' food demand. The consumption of the different Collembola relative to the food demand was determined in 24-h experiments. The 24-h food consumption by adult female *B. lampros* of five collembolan species was determined just prior to, and again 2 weeks into, the egg-laying experiment (see below). The five collembolan species were used as prey in both dead (freeze-killed) and live prey treatments, in order to account for effects of capture efficiency and handling on consumption capacity. A total of 10 collembolan treatments (five live and five dead) plus one *D. melanogaster* treatment (dead), with sample sizes of $n = 12$ female *B. lampros* in each treatment, was performed.

The large size differences between the different prey types meant that different numbers of prey were offered in order to approximate similar overall dry weights. The beetles were offered a weighed sample of 10 specimens of each of *Isotoma anglicana* and *Isotomurus prasinus*, which are large species of $c.5$ mm length, and of *D. melanogaster*. Other weighed samples of each of the two Collembola and the fruit flies were dried for determination of wet weight/dry weight coefficients. Dry weights were always measured after at least 2 days of drying at $60\,^{\circ}$C in a vacuum oven. After the 24-h feeding experiment, uneaten prey were dried and weighed. The 24-h dry weight consumption was determined by subtracting the dry weight of uneaten prey from the calculated dry weight of food offered. In experiments with the small Collembola, 50 *Isotoma notabilis*, 50 *L. cyaneus* and 30 *F. fimetaria* were offered to the beetles, and three samples with similar numbers of each species were dried for determination of average dry weights. After 24 h, uneaten Collembola were counted and consumption in dry weight was calculated.

Two-way ANOVA on log-transformed consumption rates (to obtain homogeneity of variance) was used to analyse for effects of collembolan prey species, prey state (dead or live) and their interaction. As beetles were expected to consume more dead than live prey because dead prey is easier to obtain, the effect of state was analysed as a one-tailed test of whether beetles consumed more dead than live prey (the probability of the ANOVA is two-tailed).

EGG PRODUCTION

The value of prey species was assessed from the egg production of females, continuing the experimental diets from the 24-h food consumption measurements. After the first measurement of 24-h consumption, the beetles were transferred to Petri dishes (5 cm in diameter), with fine, moist, sand ($< 150\,\mu$m) provided as medium for egg laying. The beetles were fed an excess of prey two times per week. Eggs were counted twice per week by washing the sand gently through a 150 μm sieve, leaving the eggs (packed with fine particles but easily recognizable) behind (Mols, van Dijk & Jongema 1981). Males were reintroduced to the females for a few hours once during the experiment, i.e. after approximately 1·5 weeks.

Unexpectedly, egg production on all Collembola diets declined compared with the fruit fly control. The experiment was continued in order to determine whether egg production could be recovered after a shift to a high quality diet. Following the second 24-h prey consumption experiment, beetles on Collembola diets were fed a high quality diet of freeze-killed fruit flies and dog food for 1 week. Eggs were counted twice more over the next 7 days during which the high quality diet was continued.

Beetles that produced no eggs (1–2 females per treatment) were excluded from the analysis and from the second 24-h food consumption measurement. The number of eggs per female (log-transformed in order to improve sphericity; Mauchley's test) was analysed with a two-way repeated measures ANOVA, with Collembola species and state (dead/live) as independent factors.

CONVERSION EFFICIENCY OF DIFFERENT PREY TYPES

In order to combine data from the 24-h consumption measurements with the egg production experiment for assessing the quality of prey, the conversion efficiency of food into eggs was determined as the number of eggs produced per mg food consumed. The data presented were based on the second 24-h consumption measurement and the number of eggs produced in the preceding 24-h period (calculated as mean number of eggs per day from the egg numbers produced within a 3- or 4-day interval between counts), because the strongest diet effects were anticipated at this stage. Log-transformed data were analysed with a two-way ANOVA with diet and state (dead/live) as main effects.

LARVAL DEVELOPMENT

The effect of prey species on juvenile growth and development was tested. *Bembidion lampros* larvae of mothers fed a monotypic diet of *Isotoma anglicana* (dead) were used in order to exclude maternal diet effects on the performance of offspring. Eggs

were collected and placed individually in Petri dishes (5 cm in diameter) with moist plaster-of-Paris mixed with charcoal to ensure a high humidity. As larvae hatched, they were assigned randomly to one of five diet treatments: *Isotoma anglicana* ($n = 17$); *F. fimetaria* ($n = 17$); *Isotoma notabilis* ($n = 6$) (the low replication was due to a shortage of *Isotoma notabilis*); *D. melanogaster* ($n = 17$); and complete starvation ($n = 21$). The starvation group was included to control for detrimental effects of prey affecting survival of larvae (cf. Toft & Wise 1999). Freeze-killed prey were used to exclude effects of capture and handling from determination of prey value. The larvae were fed daily and uneaten prey were removed; when fed to first instar larvae, large prey (*Isotoma anglicana* and *D. melanogaster*) were cut into pieces, to make them more accessible. Larvae were kept at 20 °C in darkness due to photophobia (Boye Jensen 1990). Survival time, number of days spent in each instar and in the pupal stage were recorded, as well as teneral weight. Tenerals were freeze-killed and dried for 2 days at 60 °C to determine dry weights.

Developmental time in days (log-transformed to obtain sphericity) was analysed with repeated measures ANOVA with instars as repeated factor, and prey species as categorical factor. Total developmental time (log-transformed) and teneral dry weight (log ($\sqrt{(x)} + 1$) transformed) were analysed with ANOVA.

Results

CONSUMPTION RATE OF DIFFERENT PREY SPECIES

There was no relationship between 24-h prey consumption and the weight of beetles (regression analyses). Therefore, prey consumption was not expressed in weight-specific terms, but as absolute food consumption per individual per 24 h (Fig. 1). In both measurements differences in consumption revealed a significant diet effect of collembolan species (Table 1), as revealed by differences in consumption rates. More dead than live Collembola were consumed (effect of state; Table 1). The large effect of state in the second measurement was mainly due to a significantly larger consumption of dead than live *Isotomurus prasinus*. If *Isotomurus prasinus* was excluded from the analysis, the effect of state was still significant (one-tailed, $P < 0.05$). In the second measurement there was a significant interaction (diet × state).

EGG PRODUCTION

A significant decline in egg production occurred on all collembolan diets (Fig. 2). There was no difference in egg numbers between dead and live collembolan diets, while a main effect of diet was revealed (two-way repeated measures ANOVA; Table 2a). The diet × time interaction was significant, indicating
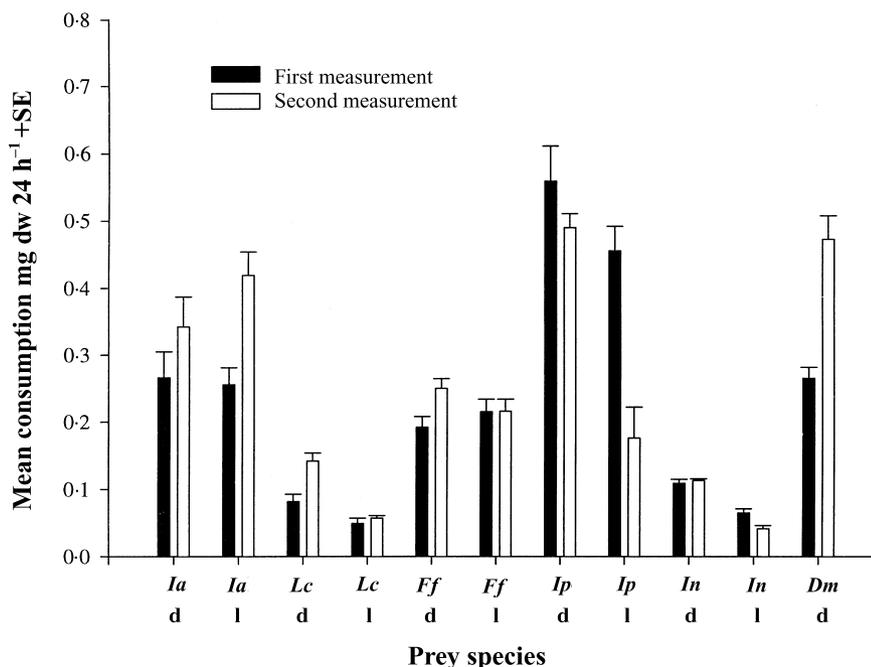

Fig. 1. Mean individual prey consumption (mg dry weight per 24 h + SE) by *Bembidion lampros* females of the five Collembola species *Isotoma anglicana* (*Ia*), *L. cyaneus* (*Lc*), *F. fimetaria* (*Ff*), *Isotomurus prasinus* (*Ip*) and *Isotoma notabilis* (*In*) in dead (d) and live (l) treatments, and of dead *D. melanogaster* (*Dm*) in two measurements (at the beginning and after 2 weeks of prey treatment).

Table 1. Two-way ANOVA of 24-h consumption by *Bembidion lampros* females of five species of Collembola (diet) presented dead or live (state) performed on log $(x+1)$ transformed data. Data presented in Fig. 1. P = two-tailed probability

Source	d.f.	F	P
First measurement			
Diet	4	79·55	< 0·0001
State	1	2·96	0·09*
Diet × state	4	1·18	0·32
Second measurement			
Diet	4	39·60	< 0·0001
State	1	20·73	< 0·0001
Diet × state	4	12·84	< 0·0001

*P < 0·05 when one-tailed.

that egg production did not decline at the same rate on all species. Egg production on *D. melanogaster* was higher than on Collembola (Table 2c). After the shift of diet from Collembola to *D. melanogaster* and dog food, egg production in all previous treatments except one increased to the *D. melanogaster* treatment level (Fig. 2). Although the *Isotoma anglicana* (dead) treatment seemed not to reach the level of egg production found in the fruit fly treatment, treatment differences were not significant after the shift of diet to *D. melanogaster* (Table 2b).

The number of eggs laid during the last week on the collembolan diet treatment (26 May−1 June), where treatment effects were expected to be most pronounced, was analysed by a two-way ANOVA
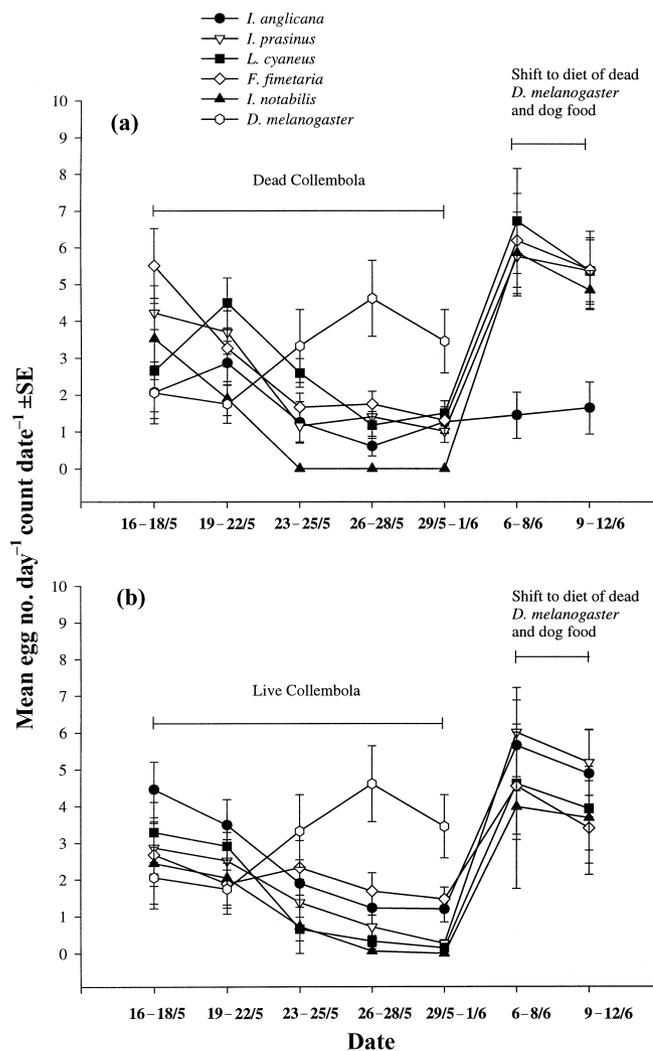

Fig. 2. Mean egg production ± SE of *Bembidion lampros* females on diets of five Collembola species in (a) dead and (b) live treatments and of *D. melanogaster* (dead) from 16 May to 1 June. Mean egg production after a shift of diet to *D. melanogaster* in all treatments from 6 June to 12 June.

Table 2. Repeated measures ANOVA (multivariate tests) of egg production rates (log (x + 1) transformed) of *Bembidion lampros* females maintained on five species of Collembola (diet) presented dead or live (state) and of *D. melanogaster* (dead). Data presented in Fig. 2

Source	Wilk's L	F	d.f.	P
(a) Collembola diets (diet × state × time) 16 May−1 June				
Diet	0·89	2·67	4	0·036
State	0·97	2·01	1	0·159
Diet × state	0·92	1·90	4	0·117
Time	0·36	36·93	4	< 0·0001
Diet × time	0·67	2·18	16	0·005
(b) Collembola diets (diet × state × time) 6 June−12 June				
Diet	0·90	2·12	4	0·085
State	0·99	0·21	1	0·640
Diet × state	0·88	2·74	4	0·033
Time	0·97	1·98	1	0·162
Diet × time	0·97	0·59	4	0·665
(c) All diets (diet × time) 16 May−1 June				
Diet	0·88	2·69	5	0·025
Time	0·56	19·11	4	< 0·0001
Diet × time	0·51	3·61	20	< 0·0001
Contrast: *D. melanogaster* vs. all Collembola				
Diet	0·95	5·33	1	0·022

(main effects = diet and state; Fig. 3). There were significant effects of both diet ($P < 0·001$) and state ($P < 0·05$), with more eggs laid on dead than live Collembola; no significant interaction was found ($P = 0·15$).

CONVERSION EFFICIENCY OF DIFFERENT PREY TYPES

Differences in conversion efficiency between collembolan species were significant (two-way ANOVA, diet, $P < 0·001$). Overall no difference between live and dead treatments was found (state, $P = 0·18$), but the interaction diet × state was significant ($P < 0·05$), mainly due to *L. cyaneus* (Fig. 4).

LARVAL DEVELOPMENT

Developmental time in the three larval instars and the pupal stage is shown in Fig. 5. An effect of diet on instar duration was revealed (repeated measures ANOVA, univariate test, sphericity test: Mauchley's criterion, $P = 0·39$; Table 3). Duration of instars differed, especially the third instar, which lasted longer than the other instars (Fig. 5). A significant diet × instar interaction was also found (Table 3), caused
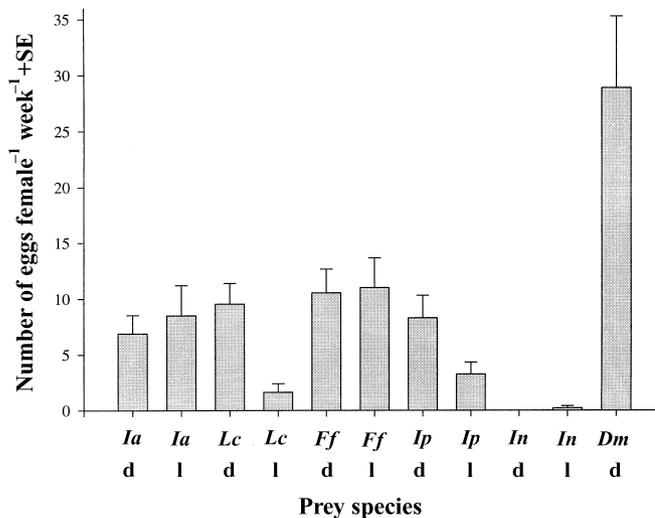
Fig. 3. Summed number of eggs +SE produced by *Bembidion lampros* on diets of five Collembola species in dead and live treatments during the last week of diet treatments (26 May to 1 June). For abbreviations, see Fig. 1.
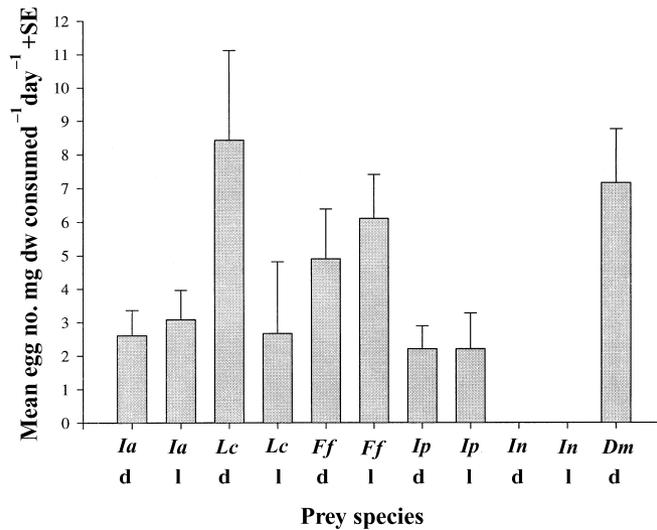
Fig. 4. Food conversion efficiency of *Bembidion lampros* (mean egg number per mg dry weight consumed per 24 h + SE) on diets of five Collembola species in dead and live treatments, and of dead *D. melanogaster*. For abbreviations, see Fig. 1.

by the prolonged third and fourth instar in the *F. fimetaria* treatment relative to the two other diets. The *Isotoma notabilis* treatment was excluded from all analyses because of low replicate number (four of the six replicates were killed in the third instar in a laboratory accident). Total developmental time was significantly longer for *F. fimetaria*-reared larvae than for *Isotoma anglicana*- and *D. melanogaster*-reared larvae (Table 4; $F = 16.27$, d.f. $= 2$, $P < 0.0001$; contrast, *F. fimetaria* vs. *Isotoma anglicana* and *D. melanogaster*, $F = 29.85$, d.f. $= 1$, $P < 0.0001$). There were significant differences between all diet treatments in the dry weights of newly hatched adults (Table 4; $F = 141.22$, d.f. $= 2$, $P < 0.0001$, Tukey–Cramer HSD for all comparisons). No difference in numbers completing development

between diet treatments was found (likelihood ratio χ^2-test, $P = 0.10$; Table 4). The starved larvae survived for 8.47 ± 0.24 days ($n = 21$). No toxic effect of prey was found that might have cause increased mortality of the larvae in comparison with the starvation group. The larvae remained extremely active, apparently searching for food during the starvation period.

Discussion

PREY CONSUMPTION AND EGG PRODUCTION

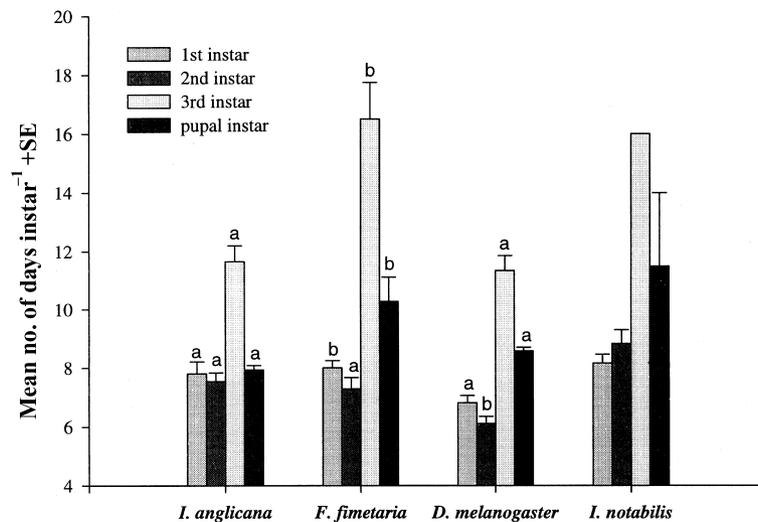The 24-h food consumption experiments revealed a larger prey intake of dead than of live Collembola,

Fig. 5. Mean number of days + SE spent in three larval instars and in the pupa by *Bembidion lampros* when raised on three collembolan diets or on *D. melanogaster*. Different letters indicate significant differences in instar duration between diet treatments. *Isotoma notabilis* was not analysed statistically.

Table 3. Repeated measures ANOVA (univariate test) of developmental time (log-transformed) in larval and pupal instars of *Bembidion lampros* kept on single-species diets of *Isotoma anglicana*, *F. fimetaria* and *D. melanogaster*. Data presented in Fig. 5

Source	MS	d.f.	F	P
Diet	0·12	2	15·65	< 0·0001
Instar	0·64	3	124·08	< 0·0001
Diet × instar	0·02	6	4·81	0·0002
Contrast *F. fimetaria* vs. *Isotoma anglicana* and *D. melanogaster*				< 0·0001

indicating that freeze-killing did not change the prey palatability and that *B. lampros* had a lower capture efficiency of live than of dead Collembola. It was observed that *B. lampros* had to attack several times to capture *Isotoma anglicana*, *Isotomurus prasinus* and *L. cyaneus*. This cost of handling live prey was reflected in the second week of the egg production experiment, where fewer eggs were laid when on a diet of live than of dead Collembola. The highest prey consumption was found on *Isotomurus prasinus* but apparently this did not result in a correspondingly high rate of egg production. The high consumption rate of *Isotomurus prasinus* indicates no chemical deterrence or toxicity of this Collembola while the low efficiency of converting food into eggs indicates nutrient deficiency (cf. Toft 1996). Consumption of *Isotoma notabilis* was low, indicating low predator tolerance to this species, which could be caused by feeding deterrents (Bilde & Toft 1997). The carabid apparently gained nothing from *Isotoma notabilis*, as egg production on an *Isotoma notabilis* diet practically ceased. Consumption of *L. cyaneus* was also low; this species is covered by scales, which might serve as a mechanical defence against predators (Bauer & Pfeiffer 1991). It is not known whether the higher food conversion efficiency on dead than live *L. cyaneus* found during the second week of the egg production experiment was caused by changes in nutrient composition from freezing. A significantly higher consumption of dead than live *L. cyaneus* found in the second food con-

sumption measurement may reflect a cost of capture and handling of live *L. cyaneus*. The highest food conversion efficiency occurred on diets of *L. cyaneus* (dead), *F. fimetaria* and *D. melanogaster*. The decline in egg production (Fig. 2) found on *L. cyaneus* and *F. fimetaria*, in spite of high conversion efficiency, could be partly due to energy deficiency caused by low consumption rates. This situation could occur if the prey contained chemical defence substances that had deterrent or toxic effects on the predator and thus limited its consumption capacity for that prey (Bilde & Toft 1994; Toft 1995, 1996). Possible chemical defences have been reported for some families of Collembola (Dettner *et al.* 1996; Hopkin 1997). Messer & Dettner (1997) found phenol derivatives that were shown to act as deterrents against a predatory mite, and Stenberg (1990) found indications for the presence of a deterrent substance in *Hypogastrura denticulata* (Bagnall) in feeding experiments with carabid beetles.

The lack of correspondence between consumption and food conversion efficiency of a prey means that consumption capacity does not reflect the relative quality of prey species (Toft 1995, 1996). This was confirmed in a study by Marcussen, Axelsen & Toft (1999), who found that smaller amounts of a high than of an intermediate quality prey was consumed in order to maintain a high rate of egg production in a spider. Bilde & Toft (1999) found a carabid beetle to consume high quantities of aphid prey but to produce very few eggs on aphid diets. Only *D. mela-*

Table 4. Effects of four diets on life-history characters of *Bembidion lampros*: survival (% completing development), total developmental time of larval and pupal stages (mean number of days ± SE) and weight of teneral adults (mean mg ± SE). Different letters in a column indicate significant differences between diet treatments (ANOVA, Tukey–Cramer HSD). The *Isotoma notabilis* treatment was not analysed statistically due to low replication (*n*)

Diet	*n*	% survival	Developmental time (days)	Teneral adult mass	
dry weight mg	fresh weight mg				
Isotoma anglicana	17	88	34·93 ± 0·80 a	0·244 ± 0·009 a	1·422 ± 0·004
F. fimetaria	17	82	41·15 ± 1·78 b	0·199 ± 0·011 b	1·346 ± 0·007
D. melanogaster	17	100	32·88 ± 0·72 a	0·601 ± 0·032 c	2·290 ± 0·011
Isotoma notabilis	2	–	46·0 ± 2·0	0·305 ± 0·015	1·565 ± 0·235

nogaster supported relatively high rates of consumption and egg production, indicating no toxic effects and high nutritive value of this species (cf. Toft 1996). *Drosophila melanogaster* has previously been reported as a high quality prey for arthropod predators (Bilde & Toft 1994; Toft 1995; Marcussen, Axelsen & Toft 1999), although long-term experiments may reveal nutrient deficiencies (Toft & Wise 1999). That none of the collembolan species tested were of a comparable quality to *D. melanogaster* was an unexpected result. *Isotoma anglicana* was of excellent value to the linyphiid spider *E. atra*, as revealed by continuous production of viable eggs through many egg sacs, whereas the spider ceased egg production after a few egg sacs when fed *F. fimetaria* (Marcussen, Axelsen & Toft 1999). As *B. lampros* and *E. atra* co-occur in time and space and have a considerable overlap in prey consumption (Sunderland 1975; Janssens & De Clercq 1990), *Isotoma anglicana* was expected to be of high value to *B. lampros* as well. *Folsomia fimetaria*, on the other hand, was expected to be of low quality; this was only partly confirmed in the egg production experiment. However, considering food conversion efficiency, the carabid performed better on a diet of *F. fimetaria* than on *Isotoma anglicana*.

The Collembola used in this study were extracted from soil except for *F. fimetaria*, which was reared on yeast. It can be questioned whether *F. fimetaria* would be of different value to the predator depending on whether it was derived from a laboratory culture or from a natural population, because of differences in its own diet. As the effect of *F. fimetaria* did not differ dramatically from that of the other Collembola, the diet of *F. fimetaria* is not likely to have a major influence on beetle fitness parameters. In this study, the beetles were offered prey in different densities due to the large size differences of the Collembola. This could lead to differences in predation rates caused by increased cost of handling small Collembola compared with larger ones. The highest consumption rates were actually found on the two largest Collembola species. Although more dead than live prey was consumed, consumption of dead and live prey was of a similar order of magnitude. It can be argued that these amounts reflect the beetles' actual consumption capacities of the prey. The differences in prey consumption between dead and live Collembola are likely to be even more pronounced under natural conditions, as the live Collembola were more vulnerable to capture in the small arenas with plain surfaces than under natural conditions.

After the shift of diet from Collembola to fruit flies and dog food in the egg production experiment, the beetles responded by increasing egg production rates significantly within 1 week. Apparently, carabids have the ability to respond very quickly to changes in food availability and quality (van Dijk

1982). As the beetles may have been starving on the Collembola diets, the response to the shift of diet could be caused by accumulation of 'mature' eggs in the ovaries, which only needed energy reserves before being laid. This may also explain the slightly higher egg number found in the first relative to the second egg count after the shift of diet to *D. melanogaster* (Fig. 2).

Apparently, no single species of the Collembola tested here can support a high fecundity in *B. lampros*. The fact that *D. melanogaster* is of high quality even as a single-species diet suggests that some Diptera may constitute valuable food sources for generalist predators. Diptera are reported as a major food for *B. lampros* in several studies (Mitchell 1963; Sunderland 1975; Hengeveld 1980; Pollet & Desender 1987, 1989). Diptera larvae, which are numerous in the soil in winter and spring (Carter, Lagerlöf & Steen 1985; Nielsen *et al.* 1994), might also constitute an important food source for mature as well as immature life stages of generalist predators.

LARVAL DEVELOPMENT

Comparison of the results from the egg laying experiment and the larval growth experiment revealed differences between adults and larvae in the ability to utilize the same Collembola species as prey. Larvae completed development with high survival on single-species diets of *Isotoma anglicana*, *F. fimetaria* (and *Isotoma notabilis*), whereas egg production of females rapidly declined on these diets. However, *D. melanogaster* proved to be of highest value for the larvae, as for the adults. Although there were no differences in larval developmental time between *D. melanogaster* and *Isotoma anglicana* treatments, teneral beetles reared on *D. melanogaster* weighed more than twice as much as beetles fed *Isotoma anglicana*. In the first two instars, *D. melanogaster*-fed larvae had a slightly shorter developmental time than Collembola-fed larvae. The third instar and pupal duration were significantly longer in larvae fed *F. fimetaria* than in larvae fed *D. melanogaster* or *Isotoma anglicana*. This could be due either to nutrient deficiencies that accumulate because of the monotonous diet, or to effects of toxic substances. The starvation treatment served to control for toxic effects of prey affecting mortality (cf. Toft & Wise 1999). Such effects were not found, as even the *Isotoma notabilis*-reared larvae completed development, although egg production completely ceased on this diet.

The developmental times for larvae on diets of *D. melanogaster* or *Isotoma anglicana* resemble those found by Boye Jensen (1990) at a temperature of 19 °C. It should be noted that he kept larvae on a mixed diet consisting of butterfly eggs, housefly eggs, water fleas, worms and enchytraeids, probably

a sufficiently varied diet to avoid nutrient deficiencies. Unfortunately, he does not give the weight of the beetles at emergence. Apparently, a diet of *Isotoma anglicana* fulfils the nutrient and energetic requirements for minimizing larval developmental time, but not the requirements for maximal growth rate. The lower adult weight of beetles reared on Collembola diets compared with those reared on *D. melanogaster* may result in a lower reproductive potential, as fecundity is usually positively correlated with body size (Honek 1993; but see Leather 1988).

Theiss & Heimbach (1993) reared *B. lampros* larvae on the Collembola *Folsomia candida* (Willem) and on a diet of mealworms plus fly pupae. On a *F. candida* diet, developmental time (37 days) and adult beetle weight (1·4 mg fresh weight) were very similar to our findings on Collembola diets, whereas their mortality was higher (56%). On the mealworm/pupae diet, adult beetle weight (2·2 mg fresh weight) was similar to our findings on the *D. melanogaster* diet, whereas developmental time was longer (41 days). Two other carabid larvae showed a mortality of 93% (*Bembidion tetracolum* Say) and 100% (*Pterostichus cupreus* L.) on a diet of *F. candida* (Theiss & Heimbach 1993). Toft & Wise (1999) found *F. candida* to be toxic to a lycosid spider, and Sunderland *et al.* (1996b) also found this species to be of low quality for two of three species of linyphiid spiders. *Bembidion lampros* larvae seem better able to cope with *F. candida* than several other predators; they also seem better able to cope with *F. fimetaria* than the spider *E. atra* (cf. Marcussen, Axelsen & Toft 1999) (see above). Overall the Collembola tested were acceptable and of relatively high quality as food for *B. lampros* larvae; the low weight of Collembola-reared tenerals may reveal that single-prey diets are suboptimal although sufficient for development of carabid larvae (Theiss & Heimbach 1993; Sunderland *et al.* 1996a).

PERSPECTIVES AND MANAGEMENT RELEVANCE

The experiment reported here suggests that variation in value of alternative prey for predators may be of significance for the population build-up of natural enemies, although the question of whether a mixing of the different Collembola will improve the overall diet of generalist predators still remains to be answered. The species composition of alternative prey may provide a reason for the variable impact of predators on pest population growth (Holland, Thomas & Hewitt 1996). The community of alternative prey depends on the management of agricultural fields. Large numbers of *Isotoma notabilis* and *F. fimetaria* were found in fields with a high input of green manure (Axelsen & Thorup-Kristensen, in press). *Isotoma notabilis* may not support the build-

up of a predator population, as *B. lampros* could not reproduce on a diet of *Isotoma notabilis*, but it could be a food source for the hemi-edaphic larvae, as it occurs to a depth of 5 cm (Marinissen & Bok 1988). *Folsomia fimetaria*, which is also a hemi-edaphic species (Lagerlöf & Andrén 1991), was of relatively high value for both imagines and larvae. The population of *F. fimetaria* has also been found to be favoured by amending the soil with dried fodder rape (Lootsma & Scholte 1998). The other three collembolan species tested are surface active (Alvarez, Frampton & Goulson 1997; Mebes & Filser 1997), and may be available for predominantly imagines. Of these *Isotoma anglicana* was found to respond with a significant population increase to crops of winter rye and fodder radish (Axelsen & Thorup-Kristensen, in press). *Isotoma anglicana* was of relatively high quality for *B. lampros* and has proved to be of extremely high value for the linyphiid spider *E. atra* (Marcussen, Axelsen & Toft 1999), which is an abundant predator in arable land. The importance of generalist predators in suppression of pest species may thus vary with the community of alternative prey species.

The quantity of alternative prey (Collembola) has been found to play a role for the predator population size or for later predation effects on pests. Potts & Vickerman (1974) found a positive correlation between the quantity of Collembola of the family Isotomidae and numbers of carabid beetles, and Gravesen & Toft (1987) found a negative correlation between numbers of Collembola in spring and aphid density later in the season. It could be hypothesized that improving the availability of (high quality) alternative prey during the build-up of the predator population, and then removing it as the pest population increases so that predators are forced to switch to the pest prey, would maximize the impact on the pest. Such a system operates naturally in Asian rice (Settle *et al.* 1996).

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