

Larval omnivory in *Amara aenea* (Coleoptera: Carabidae)

KAREL HŮRKA and VOJTĚCH JAROŠÍK

Department of Zoology, Charles University, Viničná 7, CZ-128 44 Praha 2, Czech Republic; e-mail: hurka@natur.cuni.cz

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Abstract. The duration of development, survivorship and adult size were compared for the larvae of *Amara aenea* reared in the first generation on pure diets of seeds (*Stellaria media*, *Capsella bursa-pastoris*, *Tussilago farfara*, *Plantago major*, *Urtica dioica*, or *Potentilla argentela*), or a pure diet of yellow mealworms (*Tenebrio molitor* larvae), and on a mixed diet of seeds and mealworm larvae (*T. molitor*, *S. media* and *C. bursa-pastoris*). To ascertain any long-term effects of pure diets, the beetles were reared on the same pure diet for several generations, or on different pure diets in different generations. The hypothesis that the larvae are primary omnivorous was tested. The evidence that the larvae of *A. aenea* are primary omnivorous was obtained by revealing that the larvae reared on the mixed diet of insects and seeds survived better, and developed faster in larger adults than those reared on the pure diets of seeds or insects. When the beetles were reared on the same pure diet for several generations, survivorship, and in most cases also the duration of development, did not change. However, when the beetles were reared on a different pure diet each generation, survivorship significantly decreased in successive generations.

INTRODUCTION

The adults of the genus *Amara* Bonelli (Coleoptera: Carabidae) are generally considered granivorous, since many have been observed feeding on flower heads or plant-seeds (Kleine, 1912, 1914; Burmeister, 1939; Lindroth, 1945; Burakowski, 1967; Forsythe, 1982; Hůrka, 1996; Luka et al., 1998). Although dissections (Hengeveld, 1980) and rearing experiments (Bílý, 1971; 1972; 1975; Hůrka & Ducháč, 1980a, b; Hůrka, 1998) revealed that the adults also eat animal food, the abundance of adults of several species is significantly higher in weedy than weedless fields (Jarošík & Hůrka 1986; Kokta, 1988; de Snoo et al., 1995; Honěk & Jarošík, 2000; Honěk et al., 2003) and the fecundity of females of *A. similata* (Gyllenhal) is highest when reared on a diet of a mixture of weed-seeds (Bracht Jørgensen & Toft, 1997). Therefore, seeds are the preferred food of adults of several *Amara* species and a potential food of their larvae.

For a long time the larvae of the genus *Amara* were regarded as insectivorous (e.g. Burakowski, 1967; Luff, 1993), only occasionally eating plant roots (Burmeister, 1939). Consequently, *Amara* larvae were usually fed an insect diet in the laboratory (Bílý, 1971, 1972, 1975; Hůrka & Ducháč, 1980a, b; Desender et al., 1986; Desender, 1988; Hůrka, 1998; Hůrka & Jarošík, 2001). The granivory of *Amara* larvae was first suggested by Thompson (1979) and Hůrka (1998) who successfully reared some species on a diet of oat flakes. The first convincing evidence that *Amara* larvae are granivorous was obtained by Bracht Jørgensen & Toft (1997) that recorded that the lowest mortality of larvae of *A. similata* occurred when they fed on seeds of *Capsella bursa-pastoris*. Morphological features (e.g. broad larval mandibles) also suggest a seed-feeding adaptation (Zetto Brandmayr et al., 1998).

Recently, an investigation of nine closely related *Amara* species suggested that their larvae can be divided into granivorous, omnivorous and insectivorous forms (Saska & Jarošík, 2001). In this study, larvae of *Amara aenea* (De Geer), one of the most common and important species, were reared on a range of diets. This species overwinters in the adult form and then develops as larvae in the spring and early summer (Hůrka, 1996). The hypothesis that the larvae are primary omnivorous (Saska & Jarošík, 2001) was tested. The duration of development, survivorship and adult size was compared for larvae reared in the first generation on either pure diets of seeds, or on a mixed diet of seeds and insect larvae. To ascertain any long-term effects of pure diets, the beetles were reared on the same pure diet for several generations, and on a different pure diet in different generations.

MATERIAL AND METHODS

Laboratory experiments were performed in four seasons (1998–2001). Adults were collected in the field at several localities in the vicinity of Prague (50°N, 14°E). The beetles were individually picked from the ground or collected using unbaited pitfall traps at the onset of the breeding period in spring. Beetles were transported in plastic bottles (100–250 ml, filled with damp substrate and closed with a lid that allowed air circulation), and then placed into rearing vials.

The rearing of larvae followed Hůrka (1996). Breeding pairs were placed in glass vials (diameter 12 cm, height 7 cm) containing a 3–4 cm deep layer of a sieved garden soil and covered by gauze. A flat stone placed on the top of the substrate served as a natural shelter. Food was supplied *ad libitum* and placed in the centre of the vials, and changed twice a week to avoid the development of mould or the propagation of mites. Mouldy food or substrate was removed immediately. Humidity was kept high by moistening the substrate. Both adults and pre-imaginal stages were kept at 21 ± 1°C, under natural photoperiod (50°N).

The breeding pairs were initially examined twice a week or, following the discovery of the first egg or larva, daily. The eggs

were laid and the larvae sheltered in the substrate. Each day, larvae were removed from the substrate with a pair of forceps after spreading substrate on a photographic tray. Both eggs and larvae were transferred individually into petri dishes (diameter 6 cm, height 1.5 cm), containing a 0.5 cm layer of a garden soil. The development of eggs, larvae and pupae was checked daily, and the length and survival of each stage of each individual was recorded. Newly emerging, fully sclerotized adults were measured by ocular micrometer to the nearest 0.1 mm. The adults were fed by the experimental diet, and kept in the glass vials for four months. After a five-month hibernation (+2 – + 5°C at permanent dark), the adults were re-used in the rearing experiments.

Larvae and adults were reared on either a pure diet of seeds (*Stellaria media*, *Capsella bursa-pastoris*, *Tussilago farfara*, *Plantago major*, *Urtica dioica*, or *Potentilla argentata*), or on a pure diet of yellow mealworms (*Tenebrio molitor* larvae). The seeds of convenient size were taken from the most abundant plants growing in the habitats where the species lived, or those recorded in the literature as being a food resource (Kleine, 1912; Burmeister, 1939; Lindroth, 1945; Bracht Jørgensen & Toft, 1997; Saska & Jarošík, 2001).

The results obtained following the protocol above were compared with rearing on a mixed diet of the larvae of *T. molitor* and the seeds of *S. media* and *C. bursa-pastoris*. More generations were reared on several pure diets. Two generations were reared on *C. bursa-pastoris*, *T. farfara*, and *T. molitor*, and three generations on *S. media*. Beetles reared in the first generation on *C. bursa-pastoris* were transferred in the second generation either to *S. media* or *T. molitor*, and those transferred to *T. molitor* were put back to *C. bursa-pastoris* in the third generation.

Statistical analysis

Survivorship was based on a cohort of freshly hatched 1st instar larvae, with the mean time to death measured in terms of survival to the 1st, 2nd and 3rd larval instar, pupal and adult stages. The data were described by likelihood ratio tests in which survival was fitted by an exponential function (which is characterised by a constant death rate), and a Weibull function (which is characterised by a continuous increase or decrease in death rate; Appendix I), and tested by a χ^2 test. The appropriate likelihood test (exponential or Weibull) was then selected based on the comparisons of the residual deviance and the explanatory power of the models. The structure of the models was checked following Crawley (1993) by error-checking plots for exponential and Weibull data on age at death (see Aitkin et al., 1989). The models were simplified by deletion tests (see Crawley, 1993).

The duration of development was determined for the 1st, 2nd, 3rd larval instars, the pupae, and for the total pre-imaginal development (excluding eggs), with the mean developmental time measured in days. The appropriate transformation of the mean developmental times was chosen by the Box - Cox method (Box & Cox, 1964, 1982). The adequacy of the transformation was checked by comparing the raw and the transformed data by plotting standardised residuals of the models against fitted values and against explanatory variables, and the ordered residuals against expected order statistics (Crawley, 1993).

The data were analysed by fixed-effect analyses of variances (ANOVAs). Mean times to death, transformed developmental times, and size of emerging adults were the explanatory variables, while larval diet, generation (for larvae reared on pure diets several generations) and sex (for adult size) were factors. The *a priori* notion that individuals reared on the mixed diet survived better, developed faster and emerged larger than those

reared on the pure diets, was tested using orthogonal contrasts. Differences among generations on pure diets were compared by LSD tests. *A posteriori* notions about differences among pure diets were tested using the Scheffé method (Sokal & Rohlf, 1994).

Calculations were made using general linear modelling in the commercial statistical package GLIM 4.0 (Francis et al., 1994).

RESULTS

First generation on pure and mixed diets

Larvae reared on the mixed diet of *Tenebrio molitor*, *Stellaria media* and *Capsella bursa-pastoris* survived better, and developed faster in larger adults than those reared on the pure diets of seeds of *S. media*, *C. bursa-pastoris*, *Tussilago farfara*, *Plantago major* and *Urtica dioica*, or the pure diet of *Tenebrio molitor* larvae (Table 1, Figure 1). The only exception was the rate of pupal development, which was significantly slower on the mixed than on the pure diets (orthogonal contrast of mixed vs. pure diet: $F = 23.38$; $df = 1, 100$; $P < 0.001$, Table 1). No eggs were laid on the seeds of *Potentilla argentata*.

Survivorship from the initial cohort of freshly hatched larvae, measured in terms of survival to individual developmental stages, was, in the 1st larval instar, 100% on the mixed diet, and 95.4–100% on the pure diets. The values for the 2nd, 3rd larval instar, pupa, and moulting to adults, respectively, were, on the mixed vs. the pure diets, respectively, 98.3 vs. 45.5–100%, 88.3 vs. 27.3–90.0%, 88.3 vs. 27.3–90.0%, and 81.7 vs. 27.3–62.5% (Fig. 1A). There were no significant differences in survivorship among the pure diets (ANOVA: $\chi^2 = 9.37$; $df = 5$; NS).

The mean developmental length for the 1st, 2nd, 3rd larval instar, pupa, and total (1st larval instar - adult) pre-imaginal development, respectively, were, on the mixed vs. pure diets, respectively, 4.22 vs. 5.00–7.25, 6.34 vs. 6.71–13.00, 15.58 vs. 14.40–26.00, 9.92 vs. 8.33–9.61, and 37.22 vs. 37.50–52.50 days (Table 2). The developmental rate thus appeared significantly (Table 1) higher on the mixed than on the pure diets, except for pupa with a significant (Table 1), reverse trend (Fig. 1B, Table 2). The mean developmental time in the 1st, 2nd larval instar and pupa, was on average about 20% of the total developmental time, and, in the 3rd larval instar, about 40% of the total time. On average, the 3rd instar lasted nearly 3 times longer than the 1st and 2nd instar (Table 2).

Developmental rates also differed among pure diets (Fig. 1B, Table 2). In the 1st instar, beetles developed significantly slower on the larvae of *T. molitor* than on the seeds of *S. media*, *C. bursa-pastoris*, *T. farfara*, *P. major* and *U. dioica* (Scheffé test: $C = -6.18 \pm 4.94$; $P < 0.05$). In the 2nd and 3rd larval instar, the beetles developed significantly slower on the seeds of *U. dioica* than on other pure diets, including *T. molitor* (2nd instar: $C = -27.07 \pm 8.38$; $P < 0.05$; 3rd instar: $C = -40.27 \pm 10.27$; $P < 0.05$). Consequently, the total pre-imaginal development also appeared significantly slower on the seeds of *U. dioica* than on other pure diets ($C = -59.43 \pm 14.05$; $P < 0.05$).

The average adult size on the mixed diet, 7.82 mm, was significantly (Table 1) larger than the average on the pure diets, 7.25 mm (Fig. 1C). The adults that emerged on the

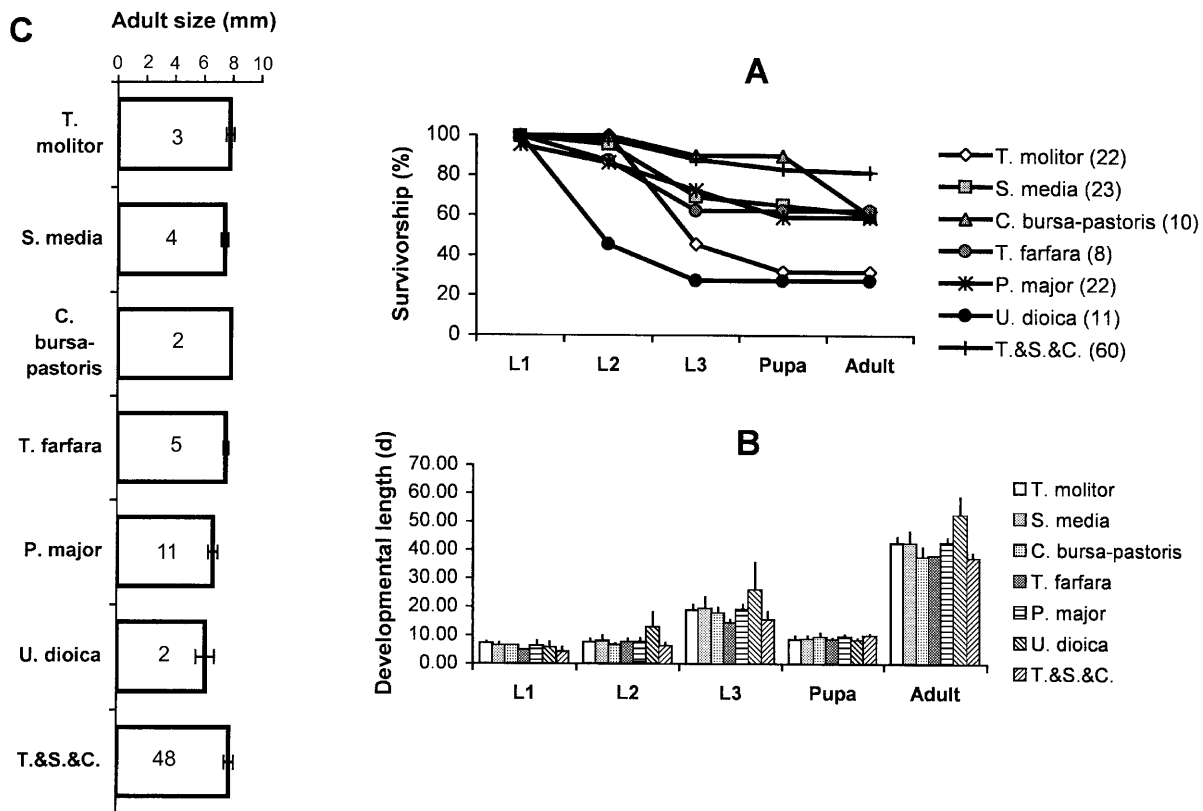


Fig. 1. (A) Mean percentage survivorship (%); (B) mean developmental length (days, d) for the 1st (L1), 2nd (L2), 3rd (L3) larval instar, pupa, and total (L1-adult) pre-imaginal development time (Adult); (C) mean size of emerging adults. Individuals of *Amara aenea* were reared in the first generation on pure (*Tenebrio molitor*, *Stellaria media*, *Capsella bursa-pastoris*, *Tussilago farfara*, *Plantago major*, *Urtica dioica*) and mixed (*Tenebrio* & *Stellaria* & *Capsella*) diets. The figures in legends (A) and bars (C) are sample sizes, cross lines (B, C) are standard deviations.

seeds of *U. dioica* were smaller than on the other pure diets, but, unlike the developmental rate, this difference was not significant ($C = 6.53 \pm 13.45$; NS), probably due to small sample size on *U. dioica* (Fig. 1C). The average adult size was not significantly affected by the sex of

emerging adults, nor by the interaction between sex and diet (Table 3).

More generations on pure diets

When reared on the same pure diet for further generations, survivorship, and in most cases also duration of

TABLE 1. The results of ANOVA tables of differences among diets, and orthogonal contrasts of differences between mixed vs. pure diets, for survival (mean survivorship, days), duration of development (developmental rate, day⁻¹) and adult size (mm). Individuals of *Amara aenea* reared in the first generation on pure (*Tenebrio molitor*, *Stellaria media*, *Capsella bursa-pastoris*, *Tussilago farfara*, *Plantago major*, *Urtica dioica*) and mixed (*Tenebrio* & *Stellaria* & *Capsella*) diets. ** = $P < 0.01$, *** = $P < 0.001$.

Fitness component		Source of variation	Df	χ^2 or F-test
Survivorship		Among diets	6	20.23 **
		Mixed vs. pure diets	1	9.22 **
Developmental rate	Larva 1	Among diets	6, 99	3.53 **
		Mixed vs. pure diets	1, 104	21.54 ***
	Larva 2	Among diets	6, 132	8.11 ***
		Mixed vs. pure diets	1, 137	39.06 ***
	Larva 3	Among diets	6, 104	9.36 ***
		Mixed vs. pure diets	1, 109	33.58 ***
	Pupa	Among diets	6, 95	7.05 ***
		Mixed vs. pure diets	1, 100	23.38 ***
	Larva 1- adult	Among diets	6, 36	13.32 ***
		Mixed vs. pure diets	1, 41	31.69 ***
Adult size		Among diets	6, 68	25.75 ***
		Mixed vs. pure diets	1, 73	41.42 ***

TABLE 2. The mean developmental time (days), standard deviation (SD) and sample size (n) for the 1st (L1), 2nd (L2), 3rd (L3) instar larvae, pupae, and total (L1-adult) pre-imaginal development. Otherwise as in Table 1.

Diet		L1	L2	L3	Pupa	Total ¹
<i>Tenebrio molitor</i> larvae	Mean	7.25	7.57	18.90	8.57	42.50
	SD	0.50	1.29	1.97	1.27	2.12
	n	4	21	10	7	2
<i>Stellaria media</i>	Mean	6.45	8.14	19.40	8.87	42.38
	SD	0.93	1.88	4.22	1.06	4.27
	n	11	22	15	15	8
<i>Capsella bursa-pastoris</i>	Mean	6.50	6.71	17.78	9.56	37.50
	SD	0.02	0.49	2.11	1.33	3.54
	n	2	7	9	9	2
<i>Tussilago farfara</i>	Mean	5.00	7.67	14.40	8.60	38.00
	SE	0.00	1.21	1.14	0.55	0.00
	n	1	6	5	5	1
<i>Plantago major</i>	Mean	6.32	7.84	19.25	9.61	42.70
	SE	1.73	1.17	1.69	0.65	1.70
	n	19	19	16	13	11
<i>Urtica dioica</i>	Mean	5.80	13.00	26.00	8.33	52.50
	SE	1.87	5.20	9.64	0.58	6.36
	n	10	5	3	3	2
<i>Potentilla argentela</i>	Mean	–	–	–	–	–
	SE	–	–	–	–	–
	n	0	0	0	0	0
<i>T. molitor</i> & <i>S. media</i> & <i>C. bursa-pastoris</i>	Mean	4.22	6.34	15.58	9.92	37.22
	SE	1.65	1.08	2.82	0.70	1.83
	n	59	59	53	50	18

¹ Total mean developmental time does not correspond to the sum of L1-L3 and pupal stages, as only individuals surviving to the adult stage are included in the analysis.

development, did not change when the beetles were reared on the seeds of *C. bursa-pastoris* and *S. media*. Beetle survivorship and developmental rate remained the same on *C. bursa-pastoris* for two generations (Fig. 2), and for three generations on *S. media*. In the latter case, the exception was the developmental rate in the second generation, that was significantly faster than in the first and the third generation for the second larval instar and the total pre-imaginal development (Fig. 3). No eggs were laid on the same diet in the second generation by females that were reared in the first generation on *T. molitor* and *T. farfara*.

When beetles were reared for further generations, but switching to a different diet each generation, survivorship significantly decreased in successive generations. It was

so for beetles transferred from *C. bursa-pastoris* to *S. media* (Fig. 4), and for those transferred from *C. bursa-pastoris* to *T. molitor* (Fig. 5). Developmental rate remained the same for beetles transferred from *C. bursa-pastoris* to *T. molitor* (Fig. 5), and, in most cases, also for those transferred from *C. bursa-pastoris* to *S. media*. In the latter case, the exception was for the third larval instar and pupa, for which the developmental rate was significantly faster after the transfer to *S. media* (Fig. 4). When in the third generation beetles reared in the second generation on *T. molitor* were returned back to *C. bursa-pastoris*, only five 2nd instar larvae were recorded.

DISCUSSION

The probability of death always increased with increasing duration of development. This was indicated by the Weibull likelihood ratio test being a significantly better predictor of survivorship than the exponential model. The duration of development was best described by its reciprocal value, the developmental rate (days⁻¹). Models using developmental rates had the smallest residual deviance and the largest explanatory power. Their standardized residuals indicated constant variance, their deviates were normally distributed, and their standardized residuals did not show any systematic pattern.

TABLE 3. ANOVA table of differences among diets and sex in adult size (mm). NS = not significant. Otherwise as in Table 1.

Source	SS	Df	MS	F
Among diets	16.16	6	2.7666	25.52 ***
Sex	0.007519	1	0.007519	0.069 NS
(Sex) × (diet)	0.3832	5	0.0766	0.707 NS
Error	6.7219	62	0.1084	
Total	23.273	74		

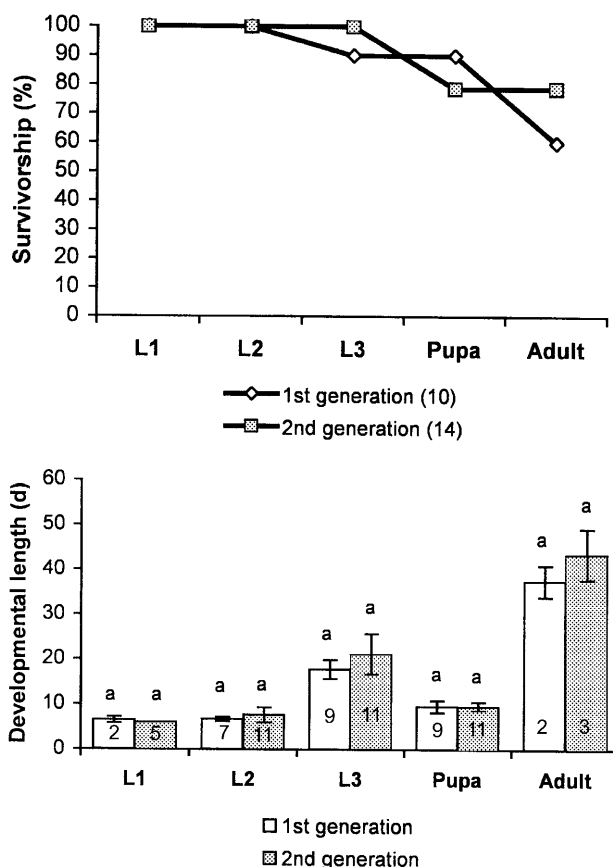


Fig. 2. Mean percentage survivorship (above) and mean developmental length (days, d) for the 1st (L1), 2nd (L2), 3rd (L3) larval instar, pupa, and total (L1-adult) pre-imaginal development time (Adult). Individuals of *Amara aenea* were reared on the seeds of *Capsella bursa-pastoris* in the first and the second generation. Cross lines are standard deviations and figures in bars sample sizes. Lines and bars with the same letter do not differ significantly in LSD tests ($p < 0.05$).

The duration of development, survivorship and adult size were used as characteristic of fitness of *Amara aenea*. Following the usual practice (e.g. Sibly & Calow, 1986), we assumed that fitness is equivalent to the value of the intrinsic rate of increase. The intrinsic rate of increase consists of the duration of development, survivorship and fecundity; the only component of fitness not directly measured was fecundity. Since female fecundity is directly proportional to body size (Honěk, 1993), the size of emerging adults served as a surrogate of fecundity. The hypothesis that the larvae are primary omnivorous (Saska & Jarošík, 2001) thus could be tested by assessment of all crucial components of fitness.

The evidence that the larvae of *A. aenea* are primary omnivorous was obtained by revealing that the larvae reared on the mixed diet of insects and seeds survived better, and developed faster to become larger adults than those reared on the pure diets of seeds or insects.

The average size of the adults on the mixed and the pure diets is consistent with the average size of 50 field collected adults, which was 7.5 mm (Hůrka, 1996). Thus, the average size of adults reared on the mixed diet, 7.82 mm, was larger than those collected in the field, while the

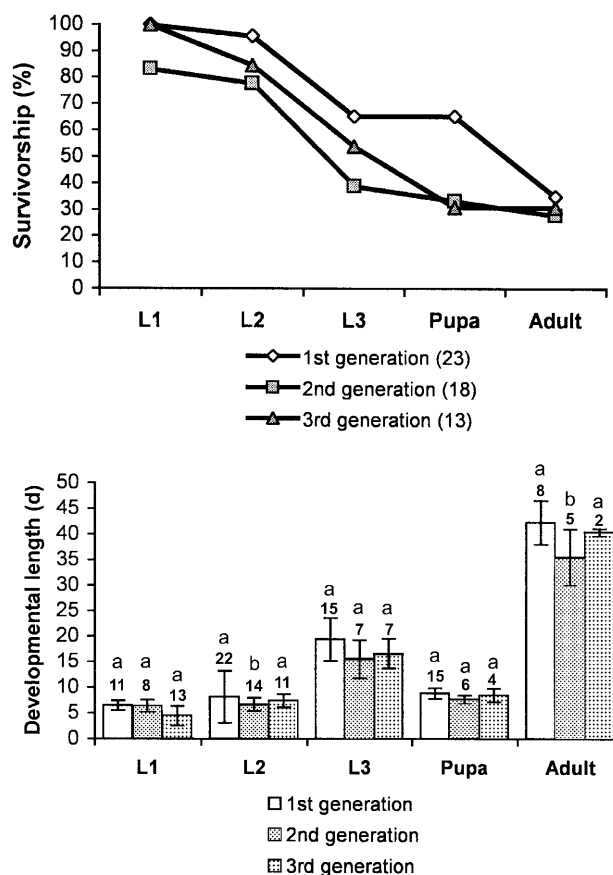


Fig. 3. Individuals of *Amara aenea* reared on the seeds of *Stellaria media* in the first, second and third generation. Otherwise as in Fig. 2.

average size of individuals reared on the pure diets, 7.25 mm, was smaller than in the field. The whole range of sizes recorded in the field, which is 6.1–8.4 mm. (Hůrka, 1996), suggests that the seeds of *Urtica dioica*, with the average size of adults 6.16 mm, are a very poor diet.

That the rate of pupal development was slower on the mixed diet than on the pure diets is not surprising, since the beetles do not feed in the pupal stage. The development in pupa thus can be long, because the emerging adults on the mixed diet are large, and may require a longer time for metamorphosis (cf. Sequeira & Mackauer, 1992).

The length of the third instar varied greatly, but it generally lasted nearly 3 times longer than the first and second instar, and formed about 40% of the total pre-imaginal development time. Similar results were previously obtained for other *Amara* species (Hůrka & Jarošík, 2001; Saska & Jarošík, 2001). The third instar is the largest, longest lasting and most voracious stage, and probably determines, in a great extent, the final size of the adult (Hůrka & Jarošík, 2001).

No egg production was recorded on the seeds of *Potentilla argentella*, and a slow larval development resulted when reared on the seeds of *Urtica dioica*. The first larval instar reared on the larvae of *T. molitor* developed slowly, but the following stages did not differ from larvae reared on the seeds. It suggests that the freshly hatched larvae could be better adapted to eating seeds than insects.

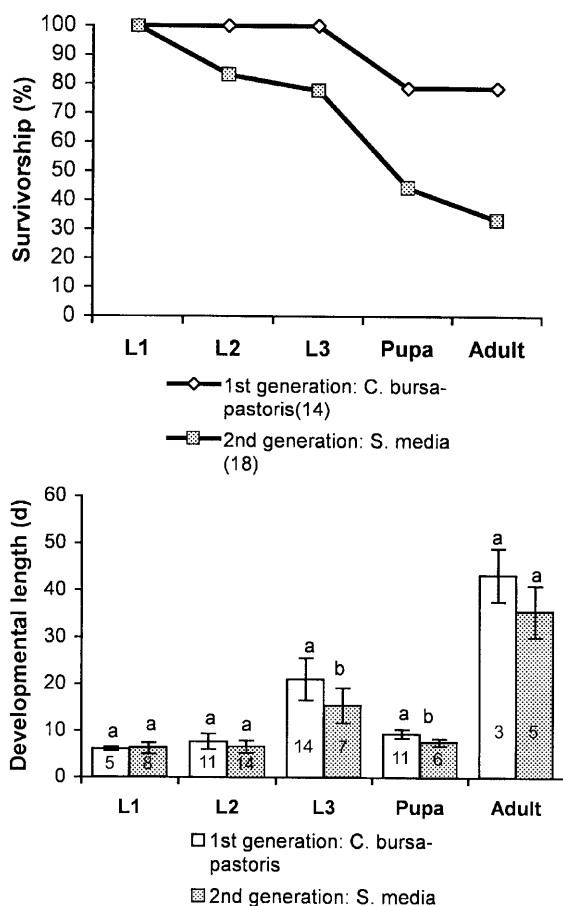


Fig. 4. Individuals of *Amara aenea* reared on the seeds of *Capsella bursa-pastoris* in the first, and on the seeds of *Stellaria media* in the second generation. Otherwise as in Fig. 2.

When the beetles were reared on the same pure diet for several generations, survivorship, and in most cases also duration of development, did not change. However, when the beetles were reared on different pure diets each generation, their survivorship significantly decreased in successive generations. It suggests that omnivorous larvae of *A. aenea* are able to adapt to a pure diet, similarly as aphidophagous larvae of ladybirds (Rana et al., 2002).

When subsequent generations are reared on different diets, increasing developmental rate, accompanied by decreasing survivorship, were observed for the third instar larvae and pupae in the second generation when reared on *S. media*. Increasing developmental rate, associated with increasing mortality, could be caused by the survival of the individuals with the fastest development rates, while the rest succumb the unsuitable food (Jarošík et al., 2002).

Carnivory is generally considered to be the plesiomorphic character state for the larvae of carabids (Hůrka, 1996). Larval carnivory is preserved at least in some species of the subgenus *Amara*, as with the larvae of *A. communis* aggregate (Hůrka & Jarošík, 2001), or, with a more closely related species to *A. aenea*, *Amara proxima* Putzeys (Hůrka, 1998). The evolution of granivory was probably gradual, with the omnivory of *A. aenea* possibly being a transient state from carnivory to granivory. The

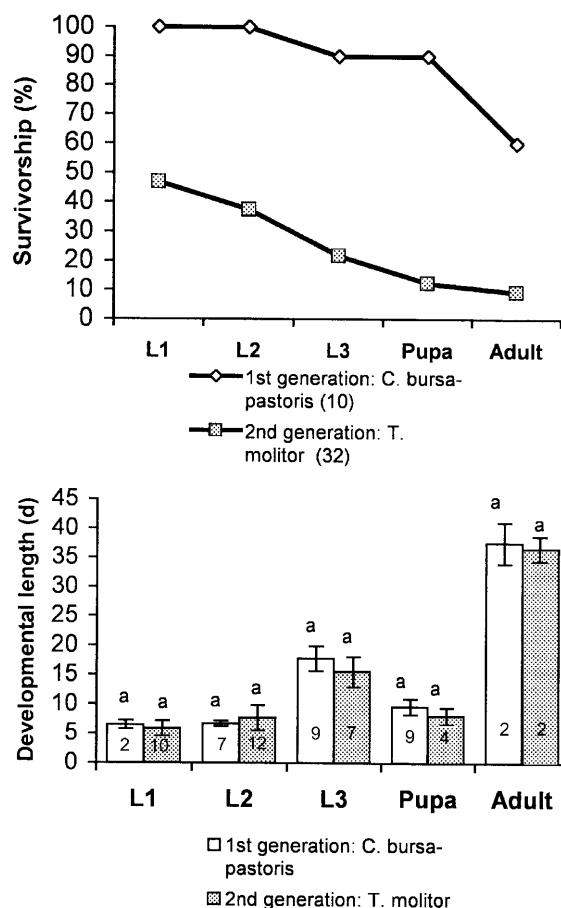


Fig. 5. Individuals of *Amara aenea* reared on the seeds of *Capsella bursa-pastoris* in the first, and on the larvae of *Tenebrio molitor* in the second generation. Otherwise as in Fig. 2.

evolution of granivory was associated with an increase in developmental time on insect diets, probably as a consequence of a decreasing ability of digestion (Allen & Hagley, 1982; Bracht Jørgensen & Toft, 1997). This may be the case with the increased developmental time associated with an insect diet observed with the first larval instar of *A. aenea*. Such an increase may lead to a gradual loss of the ability to complete post-embryonic development on an insect diet (Saska & Jarošík, 2001).

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APPENDIX I. Survival analysis

The differences in survivorship were fitted by a likelihood function described by two parameters, the mean time to death, μ , and a shape parameter, α . The mean time to death was the time to when 50% of the larvae have died. The shape parameter indicated the appearance of the mortality curve. The proportion P of larvae that have died as a function of time, t , was described as

$$P(t) = e^{-\lambda t^\alpha}$$

where $\lambda = \mu^\alpha$. The model indicates an exponential distribution of survivorship if α is equal to 1, and to Weibull distribution if α significantly differs from 1. With a Weibull distribution, $\alpha < 1$ indicates a decrease in death rate with increasing time, and $\alpha > 1$ an increase in death rate with time.

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