

Laboratory Study of Larval Food Requirements in Nine Species of *Amara* (Coleoptera: Carabidae)

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Abstract

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Food requirements of the larvae of nine closely related species of the genus *Amara* (Coleoptera: Carabidae) were studied in the laboratory. Mealworms, a mixed diet of mealworms and oat flakes, and seeds of *Capsella bursa-pastoris* and *Stellaria media* were offered as food. Survival and developmental rate were monitored daily from the 1st larval instar. *Amara aenea* is omnivorous while *A. similata* and *A. familiaris* are granivorous in the larval stage. Larvae of *A. familiaris* appeared to be specialist feeders of seeds of *Stellaria media*. The larvae of all three species are probably important predators of weed seeds. Food specialization of the other species remained uncertain. The origin of granivory in the genus *Amara* is discussed. It is considered to be an apomorphic character of some species.

Keywords: *Amara*; larvae; food requirements; weed-seeds; origin of granivory

Since the first study on food biology of carabid beetles (Coleoptera: Carabidae) more than a hundred years ago (FORBES 1883), their feeding biology has become an important subject of interest (reviewed by THIELE 1977; HENGVELD 1980a; LUFF 1987; LÖVEI & SUNDERLAND 1996). The knowledge of food requirements in field carabids is basically important for evaluating their potential as pest control agents, especially in sustainable farming systems (reviewed by KROMP 1999). Most carabids are considered carnivorous, both in the adult and larval stages. However, adults of many species often feed on plants, particularly those of the families *Poaceae*, *Brassicaceae* and *Apiaceae*. They belong mostly to the tribes Harpalini (e.g. BURMEISTER 1939; LINDROTH 1945; SCHREMMER 1960; JOHNSON & CAMERON 1969; BRANDMAYR & ZETTO BRANDMAYR 1974, 1991; ZETTO BRANDMAYR & BRANDMAYR 1975; ALLEN 1979; ZETTO BRANDMAYR 1990) and Zabritini (e.g. BURMEISTER 1939; LINDROTH 1945; JOHNSON & CAMERON 1969).

The adults of the genus *Amara* 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 (HENGVELD 1980b) 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 (KOKTA 1988; DE SNOO *et al.* 1995; HONĚK & JAROŠÍK 2000) and the fecundity of females of *A. similata* is highest when reared on a diet of a mixture of weed-seeds (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. Recently, JØRGENSEN and TOFT (1997) reared larvae of *A. similata* on a variety of diets. Surprisingly, the lowest mortality was recorded

when the larvae were fed seeds of *Capsella bursa-pastoris*. The larvae were unable to complete their pre-imaginal development on an insect diet. This was the first convincing evidence that *Amara* larvae are granivorous.

The aim of this study was to investigate whether the larvae of related species of the subgenus *Amara* differ in food requirements and how the different types of diet influence developmental time and survival.

MATERIAL AND METHODS

Collecting Material: Nine species of the nominotypic subgenus *Amara*, which overwinter as adults and develop as larvae in spring and early summer (HŮRKA 1996), were used in the feeding experiments: *A. aenea* (De Geer), *A. familiaris* (Duftschmid), *A. lunicollis* Schiödte, *A. montivaga* Sturm, *A. nitida* Sturm, *A. saphyrea* Dejean, *A. similata* (Gyllenhal), *A. spreta* Dejean and *A. tibialis* (Paykull). The adults were collected in the field at several localities of the Czech and Slovak Republics (Appendix I). The beetles were individually picked from the ground or collected by unbaited pitfall traps at the onset of their breeding period in the 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. Species and sex of the beetles were determined according to HŮRKA (1996).

Rearing: The method of rearing larvae was described by 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 substrate (garden soil: *A. aenea*, *A. familiaris*, *A. lunicollis*, *A. montivaga*, *A. nitida*, *A. saphyrea* and *A. similata*, or sand: *A. spreta* and *A. tibialis*) 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 propagation of mites. Mouldy food and substrate were removed immediately. Humidity was kept by moistening the substrate. Both adults and pre-imaginal stages were kept at $21 \pm 1^\circ\text{C}$, 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 larvae sheltered in the substrate. They were removed from the substrate after spreading it on a photographic tray and picking them up with a pair of forceps. Both eggs and larvae were transferred individually into petri dishes (diameter 6 cm, height 1.5 cm), containing a 0.5 cm layer of the same substrate as used for the rearing of adults. The development of eggs, larvae and pupae was checked daily, and the length and survival of each stage of each individual was recorded.

The rearing experiments were performed in 1997–1999. A step-wise design of testing the food requirements was used. In 1997, adults and larvae of all species were fed

bits of yellow mealworms (*Tenebrio molitor* larvae). In the next year, the species whose females did not lay eggs and where larvae did not develop on the insect diet were fed either seeds (*Capsella bursa-pastoris*, *Stellaria media*) or a mixed diet of mealworms and oat flakes. 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 (KLEINE 1912; BURMEISTER 1939; LINDROTH 1945; JØRGENSEN & TOFT 1997). The diets and numbers of larvae of each species reared on these diets are given in Table 1.

Statistical Analysis: Survival was based on cohorts of freshly hatched 1st instar larvae of each species, with the mean time to death measured in days, or in terms of survival to the 1st, 2nd and 3rd larval instar, pupal and adult stages. The individuals used for taxonomic studies (SASKA unpubl.) were censored to avoid underestimation of their life spans (COX & OAKES 1984; PYKE & THOMPSON 1986; HONĚK *et al.* 1998). The data were described by likelihood ratio tests in which the survival was fitted by exponential function (which is characterised by a constant death rate), and by Weibull function (which is characterised by a continuous increase or decrease in death rate; Appendix II). The appropriate likelihood test (exponential or Weibull), and the appropriate measurement of the mean time to death (days or developmental stages) were selected based on the comparisons of residual deviance and explanatory power of the models. The structure of the models was checked following CRAWLEY (1993) by error-checking plots for censored exponential and Weibull data on age at death (AITKIN *et al.* 1989).

Duration of development of each species were determined for the 1st and 2nd larval instars based on specimens moulted to the next instar, 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, the ordered residuals against expected order statistics (CRAWLEY 1993), and by testing the raw and the transformed data for skewness (SOKAL & ROHLF 1981).

The data were analysed by two-way analysis of variance (ANOVA) with interactions, using species and larval diet as factors, and the mean times to death and the transformed developmental times as explanatory variables. The differences in survival and developmental times were tested by LSD tests (SOKAL & ROHLF 1981) and by deletion tests. In the deletion tests, all parameters significantly ($P < 0.05$) different from zero and one from the other were obtained. This was achieved by a step-wise process of model simplification, beginning with the maximal model (containing both factors, i.e. species and diet, and their interaction), then proceeding by the elimination of non-

Table 1. Mortality of *Amara* species on different diets

Species	Larval diet	L1		L2		L3		P		A	
		N	D	N	D	N	D	N	D	N	D
<i>Amara aenea</i>	YM	10	2	7	–	5	–	–	–	–	–
	CP	11	–	11	–	7	–	2	–	–	–
<i>Amara familiaris</i>	YM	49	28	19	15	–	–	–	–	–	–
	CP	10	10	–	–	–	–	–	–	–	–
	SM	10	1	9	–	7	–	–	–	–	–
<i>Amara lunicollis</i>	YM	19	4	14	5	7	–	–	–	–	–
<i>Amara montivaga</i>	YM	4	–	3	3	–	–	–	–	–	–
	OM	22	12	10	5	2	–	–	–	–	–
	CP	9	9	–	–	–	–	–	–	–	–
<i>Amara nitida</i>	CP	5	–	4	–	3	–	–	–	–	–
<i>Amara saphyrea</i>	OM	29	21	8	6	1	–	–	–	–	–
<i>Amara similata</i>	YM	8	5	3	3	–	–	–	–	–	–
	CP	32	1	31	–	22	–	2	–	2	1
<i>Amara spreta</i>	YM	29	5	23	5	14	–	6	1	5	–
<i>Amara tibialis</i>	YM	25	12	13	1	6	–	1	–	1	–

YM – yellow mealworms (*Tenebrio molitor*); OM – oat flakes plus yellow mealworms; CP – seeds of *Capsella bursa-pastoris*; SM – seeds of *Stellaria media*; L1, L2 and L3 – larvae of 1st, 2nd and 3rd instar; P – pupae; A – adults; N – number of individuals entering the instar; D – number of individuals dead in the instar

The disproportion between $(N-D)_{\text{previous instar}}$ and $N_{\text{successive instar}}$ was a consequence of killing some larvae and using them for taxonomic studies, thus, the numbers entering successive instars are smaller than that of larvae completing the previous instar

significant terms (using deletion tests from the maximal model), and retention of significant terms (CRAWLEY 1993). Calculations were made using general linear modelling in the commercial statistical package GLIM 4.0 (FRANCIS *et al.* 1994).

RESULTS

The diet significantly influenced developmental rates ($F = 18.68$; $df = 1, 145$; $P = 2.86E-05$), and mean times to death measured in instars ($\chi^2 = 55.27$; $df = 3$; $P = 6.01E-12$) of particular species. The developmental times of the 1st and 2nd larval instars was on average 4–6 d on an optimal diet, those of the 3rd instar were usually 2–2.5 times longer, except in *Amara spreta* and *A. tibialis* where the 3rd instar lasted only slightly longer than did the 1st and 2nd larval instars.

The variance in developmental times of the 1st instar larvae significantly increased with increasing development duration. Thus, the development of the 1st instar larvae of *A. aenea* fed mealworms was fast and varied between 5–6 d, that of *A. familiaris* was slow and varied between 6–12 d. The increase in mean developmental time was caused by a longer developmental time of some individuals. Therefore, with inappropriate foods, the distribution of developmental time was asymmetric and significantly right skewed (skewness = 1.11; $P = 7.05E-09$). The standardized residuals increased toward the right end

when plotted against ranked normal deviates. For instance, on the preferred seed diet about 70% of the larvae of *A. familiaris* and *A. similata* spent only 4 d in the 1st larval instar, while two individuals of *A. montivaga* fed a mixed diet of mealworms and oat flakes spent 14 and 16 d in this instar. Many species were unable to complete their development on the diets offered.

Amara aenea appeared omnivorous. Its larvae reached the 3rd instar both when fed mealworms or seeds of *Capsella bursa-pastoris*, but the development was significantly faster with seed than insect diet, both in the 1st ($F = 8.87$; $df = 1, 16$; $P = 0.009$) and 2nd ($F = 41.78$; $df = 1, 12$; $P = 3.10E-05$) larval instars.

Amara familiaris and *A. similata* were both granivorous, unable to complete the development when reared on a diet of mealworms. Mortality of the 1st instar larvae fed mealworms was higher than in other species (Fig. 1). Mortality suffered by *A. familiaris* and *A. similata* did not differ significantly from that of *A. montivaga* and *A. aenea* (Table 2). *A. familiaris* developed successfully on seeds of *Stellaria media*. All larvae reared on seeds of *C. bursa-pastoris* died during the 1st larval instar, whereas the mortality with *S. media* was negligible. All but one individual reached the 2nd and 3rd larval instar. Their developmental rates in the 1st larval instar were significantly faster than those of larvae fed mealworms ($F = 141.7$; $df = 1, 26$; $P = 5.01E-12$). All the larvae but one of *A. similata* fed seeds of *C. bursa-pastoris* reached the 2nd or 3rd larval

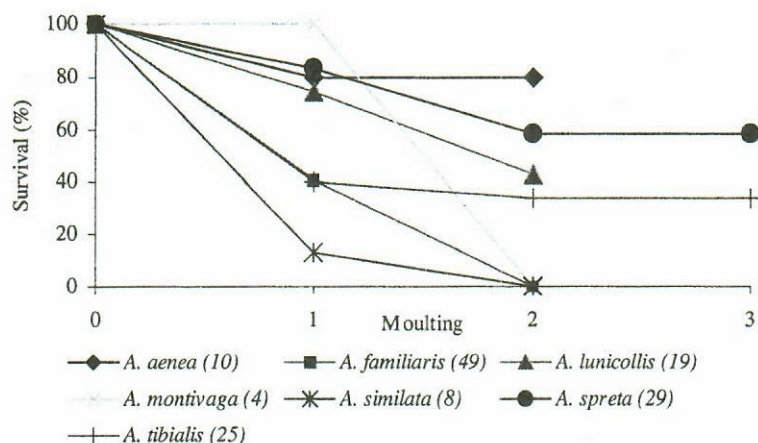


Fig. 1. Survival of larvae of *Amara* species reared on mealworms. Figures in parentheses are numbers of 1st instar larvae

instar. The developmental rate of *A. similata* fed seeds of *C. bursa-pastoris* was very fast, both in the 1st (Fig. 2) and 2nd (Fig. 3) larval instar, and the 1st instar of this species developed significantly faster than that of the omnivorous *A. aenea* (Fig. 2). Mortality of *A. similata* was significantly lower ($\chi^2 = 36.27$; $df = 1$; $P = 1.72E-09$) and developmental rate in the 1st instar significantly faster ($F = 67.72$; $df = 1, 33$; $P = 1.67E-09$) when fed seeds of *C. bursa-pastoris* instead of mealworms.

Food specializations of other species may be referred from differences in mortality and developmental rates of the 1st and 2nd instars.

Three other species are probably granivorous. Larvae of *Amara nitida*, which were reared on the seeds of *Capsella bursa-pastoris*, developed rapidly and with no mortality. The developmental rate of this species was intermediate and did not differ significantly from that of the granivorous *A. similata* and omnivorous *A. aenea*, both in the 1st (Fig. 2) and 2nd instar (Fig. 3). This species is therefore omnivorous or granivorous in the larval stage. Larvae of *A. saphyrea* were only reared on a mixed diet of mealworms and oat flakes. The development was poor and only one individual of 29 reached the 3rd instar. Mortality of *A. saphyrea* on the mixed diet was marginally ($\chi^2 = 3.492$; $df = 1$; $P = 0.06$) higher than that of *A. montivaga*, but their developmental rates in the 1st instar did not differ

significantly ($F = 0.1014$; $df = 1, 19$; $P = 0.75$). Larvae of *A. montivaga* reared on mealworms all died before moulting to the 3rd instar. Mortality was significantly higher (Fig. 1, Table 2) and developmental rate in the 1st instar significantly lower (Fig. 4) than those recorded for *A. spreata*. However, all larvae of *A. montivaga* reared on seeds of *C. bursa-pastoris* died in the 1st instar. Mortality and developmental rates ($F = 3.495$; $df = 1, 12$; $P = 0.086$) of the 1st instar larvae reared on mealworms and the mixed diet did not differ significantly. All larvae reared on these diets died before reaching the 3rd instar, except for two individuals reared on the mixed diet.

A. lunicollis and *A. tibialis* are also both potentially omnivorous in the larval stage as they reached the 3rd instar, but mortality was significantly higher and developmental rate slower than that of the most carnivorous species, *A. spreata* (Table 2). Larvae of these three species were only reared on mealworms (Table 1). However, in comparison with *A. spreata* and the omnivorous *A. aenea*, the developmental rate of larvae of *A. lunicollis* and *A. tibialis* was slower and the mortality higher. The 1st larval instar of *A. tibialis* developed significantly slower than that of *A. aenea* and *A. spreata*, and *A. lunicollis* slower than *A. spreata* and faster than *A. familiaris* (Fig. 4). *A. tibialis* had a significantly higher mortality than *A. spreata*, and both species a lower mortality than *A. sim-*

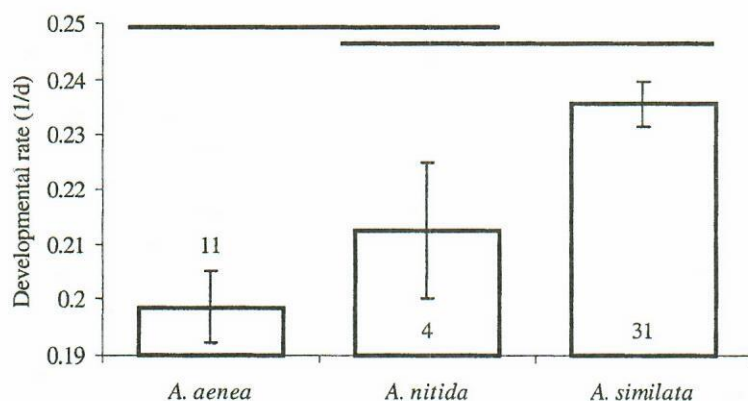


Fig. 2. Mean developmental rates (per days) \pm standard errors (bars) of 1st instar larvae fed seeds of *Capsella bursa-pastoris*. Horizontal lines indicate species not significantly different by LSD test. Figures – numbers of larvae. $F = 11.22$; $df = 2.45$; $P = 0.0001$

Table 2. The significance of differences in mortality of larvae of *Amara* species reared on mealworms

Species	<i>A. aenea</i>	<i>A. spreta</i>	<i>A. lunicollis</i>	<i>A. tibialis</i>	<i>A. montivaga</i>	<i>A. familiaris</i>	<i>A. similata</i>
<i>A. aenea</i> (10)	–						
<i>A. spreta</i> (29)	NS	–					
<i>A. lunicollis</i> (19)	NS	NS	–				
<i>A. tibialis</i> (25)	NS	*	NS	–			
<i>A. montivaga</i> (4)	NS	*	NS	NS	–		
<i>A. familiaris</i> (49)	NS	*	*	*	NS	–	
<i>A. similata</i> (8)	NS	*	*	*	NS	NS	–

LSD test, $\chi^2 = 66.98$; $df = 6$; $P = 1.70E-12$ Figures in parentheses are numbers of 1st instar larvae; NS = not significant; * = significant at $P < 0.05$

ilata and *A. familiaris* (Fig. 1, Table 2). *A. spreta* had the fastest development of those reared on an insect diet in the 1st (Fig. 4) and 2nd (Fig. 5) larval instars. Developmental rate in the 1st instar was significantly faster than in all other species except *A. aenea* (Fig. 4), and in the 2nd instar except for *A. tibialis* and *A. lunicollis* (Fig. 5). Mortality in the 1st instar fed mealworms was not as low as that of *A. aenea* (Fig. 1, Table 2), and did not differ from that recorded for *A. aenea* and *A. lunicollis*. These results indicate that larvae of *A. lunicollis*, *A. tibialis* and *A. spre-*

ta might be omnivorous, although the latter is probably the most carnivorous.

DISCUSSION

Granivory was recently (JØRGENSEN & TOFT 1997) demonstrated as optimum food specialization in larvae of *Amara similata*, which survived best when fed *Capsella bursa-pastoris* seeds, but were unable to finish development on a diet of insects.

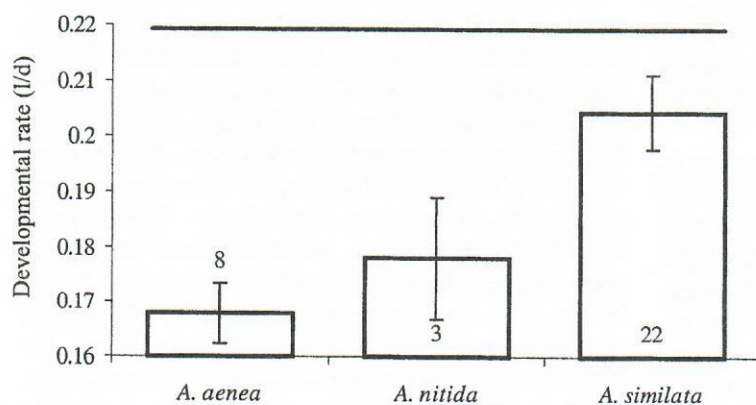


Fig. 3. Mean developmental rates (per days) \pm standard errors (bars) of 1st instar larvae fed seeds of *Capsella bursa-pastoris*. Otherwise as in Fig. 2. $F = 5.514$; $df = 2.32$; $P = 0.009$

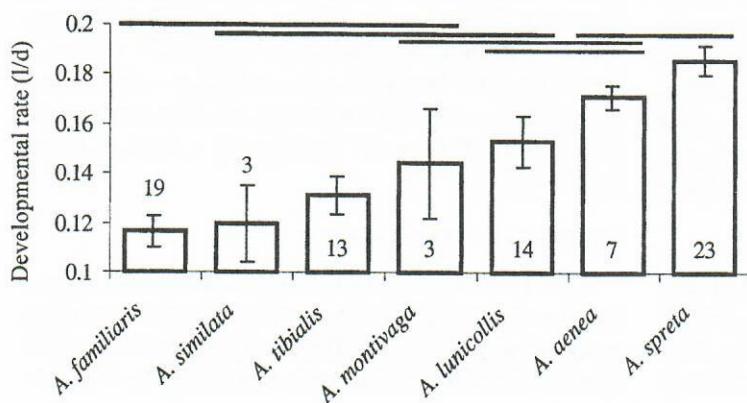


Fig. 4. Mean developmental rates (per days) \pm standard errors (bars) of 1st instar larvae fed mealworms. Other-wise as in Fig. 2. $F = 12.33$; $df = 6.81$; $P = 8.19E-10$

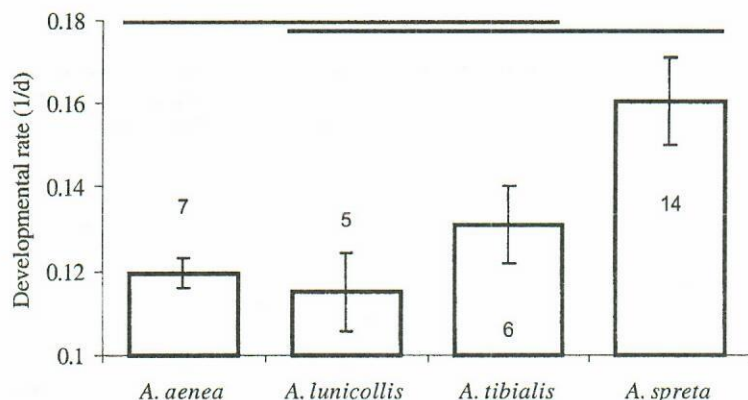


Fig. 5. Mean developmental rates (per days) \pm standard errors (bars) of 1st instar larvae fed mealworms. Otherwise as in Fig. 2. $F=4.359$; $df=3.31$; $P=0.011$

Our results revealed differences in larval food requirements among nine closely related *Amara* species. We confirmed granivory of *A. similata* in the larval stage, and demonstrated the specialization of *A. familiaris* on the seeds of *Stellaria media*. Larvae of *A. nitida*, *A. montivaga* and *A. saphyrea* are probably granivorous.

Larvae of *Amara aenea* are certainly omnivorous as they developed successfully on seeds or insect diet. This agrees with the habits of the adults, which are often observed feeding on plants (e.g. KLEINE 1912; BURMEISTER 1939). Three other species (*A. lunicollis*, *A. tibialis* and *A. sprete*) are potentially omnivorous in the larval stage. The latter species is probably the most carnivorous. Omnivorous feeding habits of larvae of *A. famelica* (HŮRKA 1998) and carnivory of the larvae of representatives of *A. communis* species-aggregate (HŮRKA & JAROŠÍK 2001) and *A. proxima* (HŮRKA 1998) have been already recorded, and omnivory of *A. littorea* has been suggested (HŮRKA 1998).

Carnivory is generally considered as the plesiomorphic character state for the larvae of carabids (HŮRKA 1996). The evolution of granivory was associated with increase in developmental time and mortality on an insect diet, probably as a consequence of decreasing ability of digestion (ALLEN & HAGLEY 1982; JØRGENSEN & TOFT 1997). Consequently, species probably lost their ability to complete the post-embryonic development on an insect diet. With regards to our results (striking differences in food requirements in closely related species) we consider larval granivory as an apomorphic character of several species of the subgenus *Amara*. Thus, granivory might have developed in particular species several times in parallel. Future analysis of the morphological features (e.g. shape of the mandibles) that were recently used for estimation of feeding habits of larval carabids (ZETTO BRANDMAYR *et al.* 1998) might support our opinion.

Granivorous (*A. similata*, *A. familiaris*) and omnivorous (*A. aenea*) species are abundant on arable land (e.g. JAROŠÍK & HŮRKA 1986; LUKA *et al.* 1998; HONĚK & JAROŠÍK 2000). Their predation on seeds of weedy plants dispersed on the ground may be an important factor of

weed population biology. Our results indicated that the larvae also feed on seeds and thus significantly contribute to the total seed predation. Therefore, the granivorous larvae of particular *Amara* species are potential weed control agents on agricultural land.

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Appendix I: The origin of reared specimens

Amara aenea (De Geer) – Bohemia centr., Praha-Kunratice, 22. iv. 1998, P. Saska leg., four females (4f) and (+) two males (2m); *Amara familiaris* (Duftschmid) – Slovakia occ., Borský Mikuláš, 3. iv. 1997, Z. Papoušek leg., 1f + 3m; Moravia mer., Sedlec nr. Mikulov, 24. v. 1999, P. Saska leg., 3f + 1m; *Amara lunicollis* Schiödt – Boh. bor.-or., Vrchlabí, 20. iv. 1997, P. Saska leg., 1f + 2m; *Amara montivaga* Sturm – Boh. bor.-or., Vrchlabí, 2. v. 1997, P. Saska leg., 6f + 4m; Boh. bor.-or., Vrchlabí, 16. v. 1998, P. Saska leg., 1f + 1m; Boh. centr., Praha-Radotín, 3. v. 1999, P. Saska leg., 2f + 1m; *Amara nitida* Sturm – Boh. bor.-or., Vrchlabí, 2. v. 1997, 24. iv.-16. v. 1998, P. Saska leg., 5f + 1m; *Amara saphyrea* Dejean – Slov. mer., Štúrovo – Hegy Fárok, 9. v. 1999, K. Hůrka leg., 19f + 5m; *Amara similata* (Gyllenhal) – Mor. mer., Sedlec nr. Mikulov, 23. v. 1997, P. Saska leg., 2f; Boh. centr., Vlašim, 15. v. 1999, L. Přenosilová leg., 2f; Mor. mer., Sedlec nr. Mikulov, 24. v. 1999, P. Saska leg., 8f + 3m; *Amara sprete* Dejean – Boh. centr., Travčice, 15. v. 1997, K. Hůrka leg., 1f + 2m; *Amara tibialis* (Paykull) – Boh. centr., Travčice, 15. v. 1997, K. Hůrka leg., 3f + 2m.

Appendix II: Survival analysis

The differences in survival were fitted by a likelihood function described by two parameters, mean time to death μ , and shape parameter α . The mean time to death was the time to when 50% of the larvae had died. The shape pa-

rameter indicated the appearance of the mortality curve. Proportion P of larvae that died as a function of time (t) was described as

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

where: $\lambda = \mu^{-\alpha}$

The model indicates on exponential distribution of survivorship if α is equal to 1, and to Weibull distribution if α significantly differs from 1. In Weibull distribution, $\alpha < 1$ indicates decrease in death rate with increasing time, and $\alpha > 1$ increase in death rate with time.

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Souhrn

SASKA P., JAROŠÍK V. (2001): **Laboratorní studie potravních nároků larev devíti druhů rodu *Amara* (Coleoptera: Carabidae)**. *Plant Protect. Sci.*, **37**: 103–110.

Potravní nároky devíti příbuzných druhů rodu *Amara* (Coleoptera: Carabidae) byly podrobeny zkoumání v laboratorních chovech. Jako typy potravy byly nabízeny: kousky larev potměníka moučného (*T. molitor*), smíšená potrava z kousků larev *T. molitor* a ovesných vloček, semena kokošky pastušky (*Capsella bursa-pastoris*) a ptačince žabince (*Stellaria media*). Od počátku prvního instaru byla denně zaznamenávána mortalita a délka vývoje. Na základě našich výsledků byly u tří druhů objeveny potravní nároky larev: omnivorní u *Amara aenea* a granivorní u *A. similata* a *A. familiaris*. Larvy *A. familiaris* se ukázaly jako specialisté na semena druhu *Stellaria media*. Potravní specializace ostatních druhů se nepodařilo spolehlivě prokázat. Výsledky ovšem naznačují, že larvy zejména polních druhů jsou významnými predátory semen některých plevelů. Dále je diskutován původ granivorie u rodu *Amara*; ta je považována za evoluční novinku některých druhů.

Klíčová slova: *Amara*; larvy; potravní nároky; semena polních plevelů; původ granivorie

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