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Seed requirements and consumption of *Amara montivaga*, a granivorous carabid (Coleoptera: Carabidae)

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Abstract. In this paper the requirements of the larvae of *Amara montivaga* Sturm, 1825 for feeding on seeds and its consumption of seeds were investigated. As this species is known to aggregate at sites where dandelion (*Taraxacum officinale* spp. agg.) is abundant and is shedding its seeds and these seeds are preferred by adult beetles in the laboratory, it is assumed that the larvae require dandelion seed to complete their development. In this study the larvae were reared on three different diets (insects, seed of *T. officinale* and seed of *Crepis biennis* L.), and mortality was measured in order to test this assumption. Most of the larvae completed their development on both seed diets but none on the insect diet. In addition, the mean daily consumption of dandelion seed was estimated to be 1.86±0.16 in L1, 4.08±0.47 in L2, and 6.65±0.68 in L3, respectively. It is concluded that there is a close trophic linkage between *A. montivaga* and dandelion and/or other Asteraceae with similar phenologies. This species aggregates at sites where dandelion is abundant at time when it is shedding its seeds, feeds on the florets in the flowers, prefers the seed of this plant over that of a range of other species, and most of the larvae fed on its seed successfully complete their development. *A. montivaga* can thus be considered as an obligatory granivore that is specialized in feeding on dandelion and other Asteraceae with seeds of a similar size and similar phenology in terms of seed production.

Key words. Seed predation, granivory, survival, seed consumption, Weibull function.

INTRODUCTION

Granivory, or seed predation, is when an animal, a granivore or seed predator, devours seeds to obtain nutrients. Obligatory or facultative granivores are important components of food webs (Lundgren 2009) as they are responsible for a substantial proportion of the seed loss during the life cycle of plant species (Janzen 1971). Despite the great number of studies published every year on granivory, the compositions of granivorous invertebrate assemblages in temperate ecosystems are poorly known. Besides the well known groups like ants, crickets, carabid beetles and slugs (Janzen 1971, Fenner & Thompson 2005), recent research indicates that the range of arthropods that consume substantial amounts of seed in the field is much greater than previously thought (Saska 2008, Koprdová et al. 2010, Lundgren et al. 2013).

Based on modelling it is concluded that an annual consumption by granivores of 50% of the seed of annual weeds would be sufficient to stop the increase in the populations of these plants. Studies that indicate such levels of seed predation, however, are scarce (Westerman et al. 2003, 2005). One such study documents that predation of dandelion (*Taraxacum officinale* spp. agg.) seed is as high as 95% when both pre- and post-dispersal predation of seed is combined (Honěk & Martinková 2005, Honěk et al. 2005). Dandelion is a perennial weed and its reproduction strategy differs from that of annual weeds in that the seeds are used for plant dispersal and so a high level of seed mortality may reduce the rate of spread of this plant. In the above and subsequent studies (Honěk et al. 2005, 2009) slugs, terrestrial isopods and carabid beetles were the most important granivores of seed after dispersal. *Amara montivaga* Sturm, 1805 is suggested to be the dominant carabid granivore at their study site, because it is the most abundant granivore in stands where dandelion is abundant and nearly absent in neighbouring dandelion-free stands (Honěk et al. 2005). Moreover, their peak in abundance coincides with the time of dandelion seed dispersal. This conclusion is also supported by the results of multi-choice laboratory experiment, in which this species prefers dandelion seed and that of other Asteraceae over the seed of other families (Honěk et al. 2005, 2007). Unpublished observation on adults of *A. montivaga* feeding on flowering florets within anthodia also support a trophic linkage between this species and dandelion and/or related Asteraceae*,* at least in the adult stage (own unpubl. obs.).

Most studies on seed consumption, however, are on predation by adults despite the fact that immature individuals may also destroy many seeds. For example, larvae of three species of carabid consume 1–50 seeds per day, depending on instar, species of carabid and seed species and size (Klimeš & Saska 2010), and in the case of the terrestrial isopod, *Armadillidium vulgare,* small immature individuals consume seeds in numbers proportional to their size (Saska 2008). Other studies indicate that granivory may be an obligatory strategy for some carabid larvae as they do not complete their development if not supplied with seed of the required species (Saska & Jarošík 2001, Saska 2004, Sasakawa 2009, Sasakawa et al. 2010). The most important dandelion granivore (Honěk et al. 2005), *A. montivaga*, is one of the species studied by Saska & Jarošík (2001) that did not develop well on a pure insect diet or mixed diet of insects and oat flakes, and rejected seeds of *Capsella bursa-pastoris*. The dietary requirements of the larvae of this species are unknown.

In this paper the dietary requirements of larvae of *A. montivaga* are studied, focusing on seeds of Asteraceae as the possible diet. This test is in line with the hypothesis of Saska & Jarošík (2001) who speculate that larvae of this species are granivorous but with unknown seed requirements, and the findings of Honěk et al. (2005) for adults. It is assumed that seed of Asteraceae, particularly those of dandelion, are also a suitable diet for larvae and that they will prefer this seed in laboratory tests and aggregate in patches of dandelion in the field (see above). The consumption of this seed is also measured for each larval instar.

MATERIAL AND METHODS

Amara montivaga Sturm, 1825 is a small carabid, 7.1–9.0 mm long, usually a dark metallic green in colour, which prefers unshaded habitats such as meadows and pastures at moderate altitudes, where it can be locally abundant (Hůrka 1996). It is classified as an adaptable species by Hůrka et al. (1996) based on their habitat quality requirements. The parental adults were collected in Prague-Ruzyně, 20.5.2005, in a mown lawn densely infested with dandelion (*Taraxacum officinale*) using pitfall traps (plastic cups 7 cm in diameter set into ground). The adults were kept in pairs in Petri dishes (10 cm in diameter, 2 cm high) filled to a depth of 1 cm with sieved garden soil. The seeds of *Taraxacum* and pieces of *Tenebrio molitor* larvae were provided as food. The dishes with adults were checked twice a week and eggs were transferred to a new dish. The Petri dishes for eggs were of the same size as those used for adults but filled to a depth of 0.5 cm with a moist mixture of plaster of Paris and charcoal (Saska & Honěk 2003). In this way moisture could be kept at an optimum level and the eggs could be monitored until they hatched.

Hatchling larvae were transferred to small Petri dishes (6 cm in diameter and 1 cm high) filled to a depth of 0.5 cm with sieved soil that did not contain any seed. The larvae were assigned to one of the three dietary treatments and each treatment was replicated 20 times. The larvae were fed either with pieces of *Tenebrio molitor* larvae, seeds of *T. officinale* or seeds of *Crepis biennis*. The *T. molitor* larvae were taken from a laboratory colony maintained at the Crop Research Institute, and the seeds of both plants were collected on site. The food was offered in excess. The dishes with larvae were kept at 21 °C and under a long day photoperiod (17L:7D) and checked regularly until they died or pupated. The data were analyzed using the survival analysis in R package, v. 2.15.2 (R Core Team 2014). In this analysis each individual was assigned “1” if it died and “0” if it survived the experiment and instar was used as a time unit (Saska & Jarošík 2001). The survreg function from the survival library (Therneau 2014) was used to perform the test, first fitted by an exponential and then by a Weibull distribution function; both models were then compared based on the log-likelihood ratio using the χ^2 distribution (Saska 2005). The significance of the models was assessed based on z statistics (Crawley 2005). The

Table 1. The effect of diet on the survival of larvae of *A. montivaga*. The full model contains all treatment levels, while in the reduced model the treatments levels that do not differ significantly from each other were combined. Value – natural logarithm of the mean time to death measured in each instar as estimated by the model. Same letters behind the p-value indicate diets significantly not different from each other

diet	value±s.e.	z	p	
full model (exponential) – log-likelihood: –74.8 full model (Weibull) – log-likelihood: –54.1				
Crepis	1.415±0.133	10.619	<0.001*	a
insects	0.552±0.170	5.549	<0.001**	b
Taraxacum	1.427±0.179	10.688	0.945**	a
reduced model (Weibull) – log-likelihood: –54.1				
Crepis+Taraxacum	1.420±0.099	14.390	<0.001*	a
insects	0.550±0.145	8.390	<0.001**	b

* difference from 0; ** difference from the first-listed term (*Crepis* in the full model and *Crepis+Taraxacum* in the reduced model)

treatments that were not significantly different were combined and the adequacy of this model simplification was assessed based on the log-likelihood ratio using the χ^2 distribution (Crawley 2005).

In the second experiment, larvae of each instar were kept individually under the same conditions as described above, but there was moist filter paper on the bottom of the Petri dishes (Klimeš & Saska 2010). Each larva was provided with a defined number of seeds of dandelion and the consumption monitored for three consecutive days. The following numbers of seeds were offered: 10 to L1 and 20 to L2 and L3, which were based on the sizes of the larvae. If more than 50% of the seeds in each dish was consumed, they were replenished to the initial number. The consumption was expressed as the mean daily consumption.

RESULTS

A Weibull distribution function fitted the data significantly better than an exponential function (–2×log-likelihood ratio=41.39, df=1, p<0.001), which indicates that the probability of survival of larvae changed over time. Therefore, the Weibull distribution function was used in all subsequent analyses. Although the larvae consumed all the diets offered, the diet significantly affected their

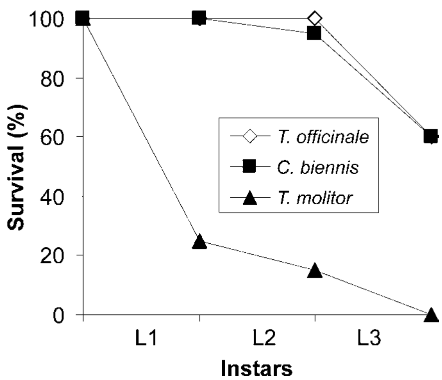

Fig. 1. The survival curves for *A. montivaga* larvae fed on three different diets.

survival (χ^2=43.89, df=2, p<0.001). While survival was high on both seed diets (60% survived until the third instar), it was poor on the insect diet as none survived to pupate (Table 1; Fig. 1). The seed diets did not differ significantly in their effect on the survival of *A. montivaga* larvae (Table 1; Fig. 1), as the reduced and full model did not differ significantly (–2×log-likelihood ratio=0.005, df=1, p=0.945).

The daily mean consumption (±s.e.) of dandelion seeds increased with instar of *A. montivaga*, and was 1.86±0.16 in L1, 4.08±0.47 in L2, and 6.65±0.68 in L3, respectively.

DISCUSSION

In this contribution the preference of larvae of *Amara montivaga* for feeding on seeds of Asteraceae, notably *T. officinale*, is demonstrated for the first time. It is shown that seeds of *T. officinale* and *C. biennis* were a suitable diet for larvae but not a pure insect diet of *T. molitor* larvae. This result complements already published data based on which the hypothesis of a trophic link between *A. montivaga* and Asteraceae seeds was erected (Saska & Jarošík 2001, Honěk et al. 2005). It is concluded that *A. montivaga* is a granivorous species, which specializes on seeds of dandelion and other related Asteraceae and both as an adult and a larva, aggregates at sites where dandelion is abundant and at time when it disperses its seeds (Honěk et al. 2005), feeds on flowering florets (own unpubl. obs.), prefers this seed to that of other species of plants (Honěk et al. 2005, 2007) and develops well on this seed (and related and similarly shaped seed of *C. biennis*) in the larval stage. This specialization thus includes all phases of the life cycle. The only part of the life cycle for which data are missing is oviposition, but the linkage of this trait to dandelion or other Asteraceae can also be expected. Unpublished observations (own unpubl. obs.) indicate that only individuals collected at the time of maximum seed dispersal laid eggs, while females collected earlier laid only very few if any eggs. Thus, the linkage to dandelion and perhaps other Asteraceae of the same phenology seems to be complex.

The mean daily values of seed consumption by larvae measured in this study are comparable to those previously reported in the literature. Indeed there is only one available study (Klimeš & Saska 2010) in which larvae of three carabid species of comparable size, *Amara aenea*, *A. familiaris* and *A. similata*, were fed seeds of dandelion. Larvae of *A. familiaris*, a specialist on *Stellaria media* (L.) Vill. hardly consumed any of the seed but those of the other two species readily consumed dandelion seeds (Klimeš & Saska 2010). The first instar larvae of *A. montivaga* studied here consumed more seeds than *A. aenea* and *A. similata*, while the second instar larvae of all three species consumed seeds in similar numbers. Surprisingly, the third instar larvae of *A. montivaga* consumed less seed of dandelion than either *A. aenea* or *A. similata*. This difference in consumption may be related to differences in size and possibly also to behavioural adaptations for seed opening that may have developed in the specialist *A. montivaga*. In the first instar the head capsule of *A. montivaga* is the largest of the three species (Saska 2004), which may help the larva to open seed that is almost as large as the whole body of the larva at this stage. The somewhat lower consumption of the third instar of *A. montivaga* compared to *A. aenea* and *A. similata* may be related to possible differences in optimum growth rates of these species. Growth rate describes how the body size increases per unit time and is related to the amount of food required, i.e. consumption. While the larva of *A. montivaga* is relatively large (Saska 2004) compared to the mean adult size the final size can be achieved slowly, whereas the larvae of the other two species have to grow faster to attain their final size and thus consume more food per day.

It is concluded that *A. montivaga* is a specialist feeder on the seeds of Asteraceae, mainly *T. officinale*, both in the adult and larval stages. Currently it is one of the few granivorous species of Carabidae for which the role of its food plant is so well described.

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