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PREFERENCES OF CARABID BEETLES (COLEOPTERA: CARABIDAE) FOR HERBACEOUS SEEDS

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Preferences of seed predators may be an important factor that introduces bias in the results of seed predation studies. In this paper, we report on the experimentally established preferences of carabid beetles for seeds of herbaceous plants. The standard arrangement of 28 species of seeds from 13 families was offered to 37 species of carabids belonging to 5 tribes. The overall consumption was affected by the body mass more than by the body length and showed a quadratic relationship with the dry body mass of the carabid. The number of preferred species of seeds varied from 1 to 16, and in unspecialized species the ordered standardized consumptions formed an almost straight line with negative slope, while in specialized to highly specialized species the standardized consumption exponentially declined with increasing order of species. The most preferred seeds were *Taraxacum officinale*, *Capsella bursa-pastoris*, *Tripleurospermum inodorum* and *Descurainia sophia*, which were preferred by 28, 20, 19 and 19 species of carabids, respectively, while *Consolida regalis*, *Arctia lappa* and *Bidens tripartita* were not preferred by any of the studied carabids. We pinpoint that choice for a model seed species for a seed predation experiment in the field shall reflect the attractiveness of the seed for predators as seed identity may bring bias in the results.

Keywords: ground beetles, seed predation, granivory, food web, ecosystem service.

INTRODUCTION

Seed predation is ecosystem service the importance of which is rapidly gaining reputation among ecosystem network ecologists, agro-ecologists and plant population ecologists (e.g. Westerman *et al.* 2003*b*, Kulkarni *et al.* 2015, Blubaugh *et al.* 2016, Larios *et al.* 2017, Petit *et al.* 2017), but the road to adoption and utilization of this service in practical weed control in arable systems is still very long to go. One reason why including seed predation as a standard instrument in the weed management toolbox remains difficult is that it is highly variable and unpredictable in time and space (Westerman *et al.* 2003*b*, Saska *et al.* 2008, Petit *et al.* 2011, Kulkarni *et al.* 2015).

The literature showed cases when seed predators consumed up to 53–95% of the annual production of seeds of the studied weed species (Harrison *et al.* 2003, Westerman *et al.* 2003*b*, Honek *et al.* 2005, Westerman *et al.* 2011, Davis *et al.* 2013). Other studies have indicated that predation of 25–50% of annually produced seeds might slow down or stop the growth of a population of a weed (Firbank & Watkinson 1986, Westerman *et al.* 2005), which suggests that seed predators might be capable of managing the weed populations through reducing the input of seeds in the seed bank, which has been proven experimentally on a national scale (Bohan *et al.* 2011). Less optimistic results are provided by studies in which the observed seed predation was very low (Baraibar *et al.* 2012) or was temporally or spatially unrelated to densities of seed predators in the study fields (Saska *et al.* 2008). One might expect that density-dependence would occur between the intensity of seed predation and populations of seed predators (Bohan *et al.* 2011), but apparently there are many confounding factors at various scales that modulate this relationship (Fox *et al.* 2013, van der Laat *et al.* 2015, Diekotter *et al.* 2016, Petit *et al.* 2017) and make the predictions of the impact of seed predation on weed populations in particular field difficult, if not impossible.

We assume that composition of the community of seed predators represent a substantial source of blur in seed predation studies not because of the species identity *per se*, but more importantly because of the ecological functional traits through which particular species enter the food webs of arable fields. Besides vertebrates, such as birds and rodents, and other invertebrates, such as ants, crickets, terrestrial isopods and slugs, carabid beetles (Coleoptera: Carabidae) often represent the dominant component of the seed predation guild in arable fields of temperate climatic zone (Westerman *et al.* 2003*a*, Honek *et al.* 2005, Gaines & Gratton 2010, Bohan *et al.* 2011, Baraibar *et al.* 2012, van der Laat *et al.* 2015). Carabid beetles are enormously diverse not only in species numbers, but also in their trophic specializations, which range from rather strict specialist carnivores (e.g. *Loricera pilicornis*, genera *Notiophilus* and *Cychrus*) through generalist omnivores (e.g. *Poecilus cupreus*, *Pterostichus melanarius*) to obligatory (e.g. genus *Amara*) and strict granivores (e.g. genus *Ophonus*) (Brandmayr Zetto & Brandmayr 1975, Thiele 1977, Hengeveld 1980, Hurka 1996, Saska 2008*a*, Talarico *et al.* 2016). Various authors use different classifications of carabids according to their diet (e.g. Homburg *et al.* 2014, Hodecek *et al.* 2016, Magura & Lövei 2017, Nolte *et al.* 2017, Petit *et al.* 2017, Pizzolotto *et al.* 2018) when attempting to assess the functional community composition. Unfortunately, the dietary breadth of many species is poorly known, so the species are often classified differently across studies, which results in the fact that species are commonly placed in different trophic groups by particular authors. More information shall therefore be gained on carabid food, including seed, preferences in order to understand better the trophic position of the common carabid species of arable fields (Kulkarni *et al.* 2015), which would make the predictions of the impact of a carabid beetles-based seed predator community on weed seed populations in arable fields more trustworthy.

In this paper, we provide experimentally established seed preferences for 37 species of carabid beetles occurring in arable fields in Europe, and in this way, we contribute to better understanding of the food ecology of these species.

MATERIAL AND METHODS

Carabid beetles

Seed preferences were estimated for adults of 37 species of carabid beetles (Table 1) belonging to the tribes Zabrini (18 species), Harpalini (15 spp.), Pterostichini (1 sp.), Platynini (2 spp.) and Trechini (1 sp.). All species are locally and temporarily common in cultivated land (fields and their margins, gardens, orchards, fallow fields, etc.). Their average body length ranged from ca 4 to 16 mm (Hurka 1996), based on which the average dry body mass was calculated using the formula of Jarošík (1989). The beetles were collected in Prague-Ruzyně (Czech Republic), Štúrovo (Slovakia), Moča (Slovakia), Wageningen (The Netherlands) and Vienna (Austria) (Table 1), by pitfall trapping or hand collecting by Pavel Saska and/or Alois Honěk. After collecting the beetles were stored in 0.5 litre plastic bottles filled with folded moist filter paper and transported to the laboratory. Individuals from outside the Czech Republic were sent (delivery time < 4 days) in plastic bottles (100 ml) filled with a mixture of moist filter paper and sand. In the laboratory, the adults were stored for 3–5 days in the dark at temperatures of 5–7 °C. This cold storage prevented cannibalism and standardised the level of hunger. The beetles were then removed from the cold, randomly assigned into groups of 10 and immediately used in preference experiments. They were not sexed.

Seeds

Preference essays were based on seeds of 28 species of dicotyledoneous herbaceous species belonging to 13 families (Table 2, Kubát 2002). All species are growing on arable land, in ruderal habitats and along field and woody margins so the seeds may be encountered by the species of carabids used in the experiment. The selection of seed species was deliberate to cover a range of seed weights from 0.1 to 8.7 mg evenly. The seeds were collected in 1999–2000 at several localities within 30 km of Prague. The seeds were dried under room conditions (25–28 °C, 40% r.h.) for 3–4 weeks, then stored frozen until used in the preference experiments. Seed mass (Table 2) of each batch of seed was determined by weighing 100 air dried seeds on Sartorius balances to a precision of 10^{-5} g.

Preference experiments

The preference experiments were conducted from April to October, 2001–2013 (Table 1). The seeds were exposed to carabid predation in small tin trays (28 mm in diameter, surface area 6.2 cm^2, 6 mm deep, Honek *et al.* 2003, 2007, Saska *et al.* 2014*a*). The trays were filled with white modelling clay (Plasticina JOVI®, Barcelona, Spain) and the seeds were pressed into the modelling clay to half their transverse width so they could be easily picked up by the beetles. The number of seeds per tray was 15 for large or 30 for small seeds (Table 2). Preference experiments took place in Petri dishes (250 mm in diameter, 50 mm deep),

Table 1. List of carabid species used in the experiment. Abbreviations: average body length taken from Hurka (1996), and is used for calculating dry body mass (Mass) after Jarošík (1989). N – number of replicated experiments.

Species	Tribus	Length [mm]	Mass [mg]	Site	Date	N
Acupalpus meridianus (Linnaeus)	Harpalini	3.6	0.9	Prague	25.8.2001	5
Amara aenea (DeGeer)	Zabrini	7.5	6.3	Prague	22.4.2001	5
Amara anthobia A. Villa et G.B. Villa	Zabrini	6.4	4.1	Vienna	2.6.2002	5
Amara apricaria (Paykull)	Zabrini	7.4	6	Prague	19.10.2001	3
Amara aulica (Panzer)	Zabrini	12.5	24.1	Prague	19.8.2001	5
Amara bifrons (Gyllenhal)	Zabrini	6.3	3.9	Prague	19.8.2001	5
Amara consularis (Duftschmid)	Zabrini	8.3	8.2	Prague	2.9.2001	5
Amara convexior Stephens	Zabrini	7.7	6.7	Prague	20.6.2013	5
Amara convexiuscula (Marsham)	Zabrini	11.4	18.9	Prague	2.9.2001	3
Amara eurynota (Panzer)	Zabrini	10.4	14.8	Prague	8.10.2001	5
Amara familiaris (Duftschmid)	Zabrini	6.4	4.1	Prague	22.7.2001	4
Amara ingenua (Duftschmid)	Zabrini	9.6	12	Prague	19.10.2001	5
Amara littorea C. G. Thomson	Zabrini	7.7	6.7	Prague	23.6.2002	5
Amara montivaga Sturm	Zabrini	8.2	7.9	Prague	20.5.2003	5
Amara ovata (Fabricius)	Zabrini	9	10.1	Prague	16.7.2001	5
Amara sabulosa (Audient-Serville)	Zabrini	6.8	4.8	Prague	3.10.2001	3
Amara similata (Gyllenhal)	Zabrini	8.7	9.3	Prague	10.6.2001	5
Amara spreta Dejean	Zabrini	7.8	6.9	Wageningen	30.5.2004	5
Anisodactylus signatus (Panzer)	Harpalini	12.5	24.1	Prague	2.6.2001	5
Calathus ambiguus (Paykull)	Platynini	10.2	14.1	Prague	25.10.2001	1

Table 1 (continued)

Species	Tribus	Length [mm]	Mass [mg]	Site	Date	N
Calathus fuscipes (Goeze)	Platynini	11.7	20.2	Prague	19.8.2001	5
Harpalus affinis (Schrank)	Harpalini	10.2	14.1	Prague	16.7.2001	5
Harpalus atratus Latreille	Harpalini	9.6	12	Prague	2.8.2008	3
Harpalus distinguendus (Duftschmid)	Harpalini	9.7	12.3	Prague	16.7.2001	5
Harpalus honestus (Duftschmid)	Harpalini	9.2	10.7	Prague	2.8.2008	3
Harpalus luteicornis (Duftschmid)	Harpalini	7.5	6.3	Prague	6.9.2003	5
Harpalus rubripes (Duftschmid)	Harpalini	10.3	14.4	Prague	18.7.2006	5
Harpalus signaticornis (Duftschmid)	Harpalini	6.9	5	Prague	16.7.2001	5
Harpalus subcylindricus Dejean	Harpalini	7.1	5.4	Prague	27.6.2008	3
Ophonus azureus (Fabricius)	Harpalini	7.8	6.9	Prague	16.7.2001	3
Parophonus maculicornis (Duftschmid)	Harpalini	6.6	4.5	Vienna	2.6.2002	1
Pseudoophonus griseus (Panzer)	Harpalini	10.5	15.2	Moča	13.8.2008	5
Pseudoophonus rufipes (DeGeer)	Harpalini	13.8	31.3	Prague	17.7.2001	5
Pterostichus melanarius (Illiger)	Pterostichini	15.7	43.9	Prague	18.8.2006	5
Stenolophus teutonus (Schrank)	Harpalini	6.6	4.5	Wageningen	30.5.2004	3
Trechus quadristriatus (Schrank)	Trechini	3.9	1.1	Prague	11.9.2001	5
Zabrus tenebrioides (Goeze)	Zabrini	14.6	36.3	Štúrovo	18.6.2003	5

each containing a 1 cm layer of sieved soil (mesh diameter 4 mm) which did not contain any seeds from the soil bank. The trays were pressed to the soil so that the clay surface was flush with that of the soil. The trays were arranged in a standard order (Table 1) and exposed in two concentric circles – the outer circle consisted of 19 trays at c. 0.5 cm inter-

Table 2. List of seed species used in the experiment. Order indicates the arrangement of particular species – 1-19 were in the outer circle and 20-28 in the inner circle.

Species	Family	Mass [mg]	Order	N seeds per tray
Amaranthus retroflexus L.	Amaranthaceae	0.53	17	30
Arctium lappa L.	Asteraceae	8.72	16	15
Arenaria serpyllifolia agg.	Caryophyllaceae	0.05	7	30
Bidens tripartita L.	Asteraceae	2.69	22	15
Campanula trachelium L.	Campanulaceae	0.18	2	30
Capsella bursa-pastoris (L.) Med.	Brassicaceae	0.23	15	30
Chenopodium album L.	Amaranthaceae	0.70	27	30
Cichorium intybus L.	Asteraceae	1.09	26	30
Cirsium arvense (L.) Scop.	Asteraceae	0.79	11	30
Consolida regalis S.F.Gray	Ranunculaceae	1.38	21	15
Crepis biennis L	Asteraceae	0.67	1	30
Descurainia sophia (L.) Prantl	Brassicaceae	0.11	3	30
Fumaria officinalis L.	Fumariaceae	3.01	25	15
Galinsoga parviflora Cav.	Asteraceae	0.17	5	30
Galium aparine L.	Rubiaceae	6.64	10	15
Lapsana communis L.	Asteraceae	1.38	20	30
Leonurus cardiaca L.	Lamiaceae	0.64	13	30
Lepidium ruderale L.	Brassicaceae	0.21	8	30
Melilotus albus Med.	Fabaceae	1.81	24	30
Potentilla argentea L.	Rosaceae	0.08	6	30
Silene latifolia ssp. *alba* (Mill.) Greuter et Burdet	Caryophyllaceae	0.79	19	30
Sisymbrium loeselii L.	Brassicaceae	0.08	28	30
Stellaria media (L.) Vill.	Caryophyllaceae	0.42	14	30
Taraxacum officinale agg.	Asteraceae	0.48	18	30
Thlaspi arvense L.	Brassicaceae	0.97	9	30
Tripleurospermum inodorum (L.) Schultz-Bip.	Asteraceae	0.32	4	30
Urtica dioica L.	Urticaceae	0.14	23	30
Viola arvensis Murray	Violaceae	0.46	12	30

vals, while the inner circle consisted of 9 trays, similarly spaced. The circles were separated by c. 2.5 cm of bare ground. Before introducing the beetles, the soil in each Petri dish was moistened with 50 ml of tap water and a piece of moist cotton wool provided a source of water for the beetles. For most species, this experiment was replicated five times (5 Petri dishes with ten beetles in each), except for less common species for which there were fewer replicates (Table 1). The experiments were done in a room in which the temperature fluctuated between 25–27 °C, relative humidity in the Petri dishes was 100% and the natural photoperiod increased from 14.5 h light (day length plus civil twilight) : 9.5 h dark (April 14) to 17 h light : 7 h dark (June 23), then decreased to 11 h light : 13 h dark (Oct. 30). Each run continued for five days and the numbers of remaining seeds per tray were recorded daily. Missing seeds and those of which > 50% was consumed were considered eaten. The trays were replaced if >50% of the seed was removed. The total number of seeds consumed per tray was summed over the 5-day period.

Data analysis

The following expressions of seed consumption were used:

The total seed consumption (T_S) is the mean number of all seeds consumed by a species over the experimental period.

The mean individual consumption (I_S) is T_S divided by the number of individuals and duration of the experiment, so it expresses the number of seeds eaten by an individual per day.

The total mass consumption (T_M) is the mean seed mass consumed by a carabid species over the experimental period.

The mean individual mass consumption (I_M) is T_M divided by the number of individuals and duration of the experiment, so it expresses the seed mass eaten by an individual per day.

Specific consumption (C_S) is I_M divided by the dry body mass of a particular carabid species.

For each carabid species, a standardized consumption was also calculated so for each seed species the actual seed consumption was expressed as the proportion of maximum consumption by the carabid species in seed numbers. From this each species of seed was assigned as "preferred" (P) when the standardized consumption was at least 0.2 of the maximum consumption, "consumed" (C) when the standardized consumption was between 0.2 and 0.05 of the maximum consumption, and "rejected" (R) when the standardized consumption was below 0.05 of the maximum consumption. The threshold of 0.2 between P and C species was chosen *post hoc* based on the visualization of the ranked preferences as the around this value the line of ordered standardized preferences often broke. The threshold of 0.05 distinguishing C and R species was chosen arbitrarily as standardized consumption below this value represented randomly picked seeds.

Linear and quadratic regression (Pekár & Brabec 2009) were used to test the relationships between the consumption variables and carabid dry body mass and body length in R 3.3.3 (R Development Team 2017).

RESULTS

Overall consumption and preferences greatly varied among species of carabids. The T_S ranged from ca 34 to 1272 seeds over the experimental pe-

Table 3. Seed consumption by 37 carabid species and their dietary breadth. T_S – total seed consumption [N seeds]; I_S – mean individual consumption [N seeds ind^{-1} day^{-1}]; T_M – total mass consumption [mg seeds]; I_M – mean individual mass consumption [mg seeds ind^{-1} day^{-1}]; C_S – specific consumption [mg seeds ind^{-1} day^{-1} mg beetle^{-1}]. P – number of preferred species; C – number of consumed species; R – number of rejected species.

Species	T_S	I_S	T_M	I_M	C_S	Preference		
						P	C	R
A. meridianus	46.0	0.92	8.11	0.162	0.180	6	3	19
A. aenea	706.8	14.14	204.49	4.090	0.654	9	3	16
A. anthobia	408.8	8.18	133.58	2.672	0.649	5	3	20
A. apricaria	129.3	2.59	71.26	1.425	0.236	3	5	20
A. aulica	329.6	6.59	407.88	8.158	0.339	2	10	16
A. bifrons	154.4	3.09	59.49	1.190	0.301	1	5	22
A. consularis	140.6	2.81	74.58	1.492	0.183	5	8	15
A. convexior	387.4	7.75	111.85	2.237	0.334	8	7	13
A. convexiuscula	923.7	18.47	530.78	10.616	0.562	11	12	5
A. eurynota	902.6	18.05	386.34	7.727	0.521	12	8	8
A. familiaris	485.3	9.71	166.01	3.320	0.807	6	5	17
A. ingenua	484.4	9.69	282.56	5.651	0.471	8	8	12
A. littorea	910.6	18.21	332.61	6.652	0.992	9	5	14
A. montivaga	326.6	6.53	189.42	3.788	0.479	2	1	25
A. ovata	825.6	16.51	347.08	6.942	0.686	9	4	15
A. sabulosa	181.0	3.62	64.13	1.283	0.266	3	5	20
A. similata	1221.4	24.43	391.20	7.824	0.846	12	2	14
A. spreta	657.8	13.16	202.43	4.049	0.584	8	4	16
A. signatus	1271.8	25.44	789.04	15.781	0.655	16	8	4
C. ambiguus	70.0	1.40	38.08	0.762	0.054	3	2	23
C. fuscipes	49.0	0.98	18.65	0.373	0.018	10	6	12
H. affinis	694.2	13.88	419.57	8.391	0.596	13	10	5
H. atratus	801.0	16.02	513.67	10.273	0.856	8	12	8
H. distinguendus	1004.6	20.09	498.72	9.974	0.811	15	6	7
H. honestus	653.7	13.07	313.38	6.268	0.586	11	8	9
H. luteicornis	342.0	6.84	158.94	3.179	0.508	8	13	7
H. rubripes	507.2	10.14	418.08	8.362	0.581	9	11	8
H. signaticornis	418.0	8.36	152.71	3.054	0.609	6	13	9
H. subcylindricus	493.7	9.87	131.20	2.624	0.486	10	6	12
O. azureus	72.3	1.45	169.73	3.395	0.489	5	6	17
P. maculicornis	369.0	7.38	83.69	1.674	0.375	6	6	16

Table 3 (continued)

Species	T_S	I_S	T_M	I_M	C_S	Preference		
						P	C	R
P. griseus	1228.6	24.57	570.25	11.405	0.750	14	6	8
P. rufipes	778.0	15.56	578.91	11.578	0.370	9	12	7
P. melanarius	90.2	1.80	70.77	1.415	0.032	4	9	15
S. teutonus	365.3	7.31	74.46	1.489	0.334	9	3	16
T. quadristriatus	34.2	0.68	5.64	0.113	0.101	3	3	22
Z. tenebrioides	466.6	9.33	350.56	7.011	0.193	5	5	18
Mean	511.7±58.82	10.2±1.18	251.9±32.31	5.0±0.64	0.5±0.04			

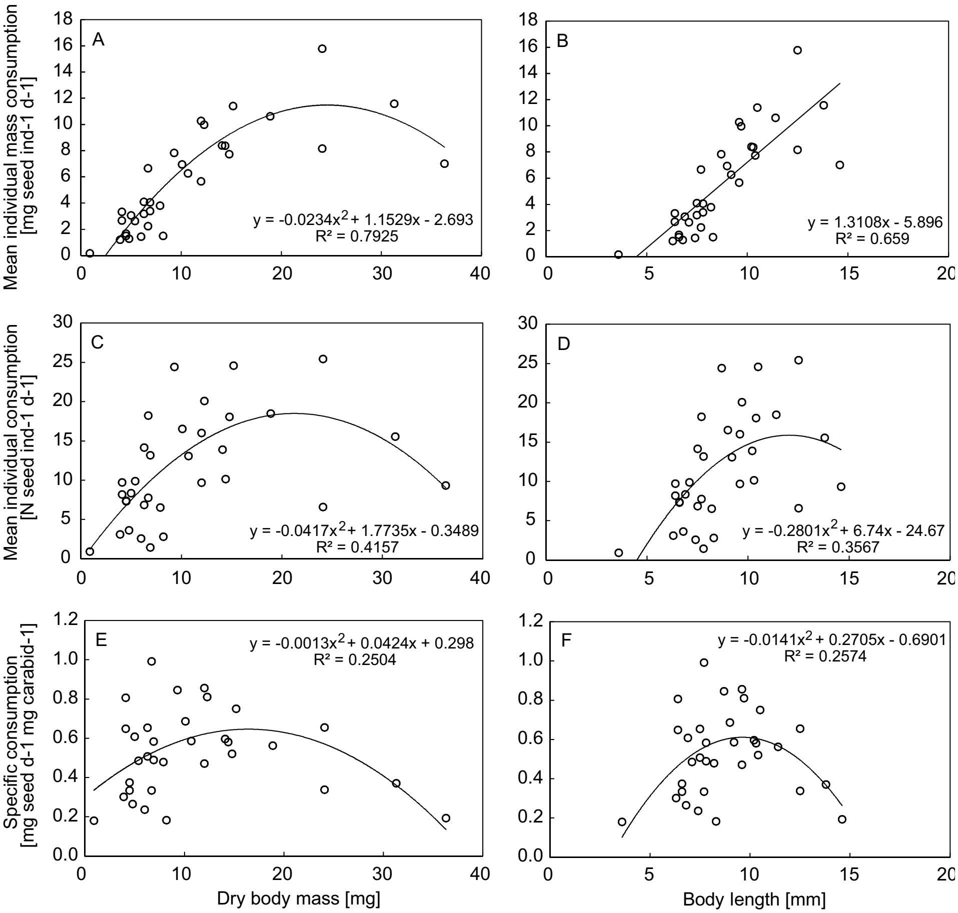

Fig. 1. Variation in seed consumption with carabid dry body mass (A, C, E) and body length (B, D, F). Seed consumption expressed as mean individual mass consumption (A, B), mean individual consumption (C, D) and specific consumption (E, F)

Table 4. Matrix of seed species by carabid species according to carabid preferences, preferred species are marked as •. Carabids and seeds are ordered according to their taxonomic affiliation (See Tables 1 and 2). Abbreviations: Ar = *A. retroflexus*, Ca = *C. album*, Al = *A. lappa*, Bt = *B. tripartita*, Ci = *C. intybus*, Cr = *C. arvense*, Cb = *C. biennis*, Gp = *G. parviflora*, Lc = *L. communis*, To = *T. officinale* agg., Ti = *T. inodorum*, Cu = *C. bursa-pastoris*, Ds = *D. sophia*, Lr = *L. ruderale*, Sl = *S. loeselii*, Ta= *T. arvense*, Ct = *C. trachelium*, As = *A. serpyllifolia* agg., Sl= *S. latifolia* ssp. *alba*, Sm= *S. media*, Mo = *M. officinalis*, Fo = *F. officinalis*, La = *L. cardiaca*, Ce = *C. regalis*, Pa= *P. argentea*, Ga= *G. aparine*, Ud= *U. dioica*, Va= *V. arvensis*

	Ar	Ca	Al	Bt	Ci	Cr	Cb	Gp	Lc	To	Ti	Cu	Ds	Lr	Sl	Ta	Ct	As	Sl	Sm	Mo	Fo	La	Ce	Pa	Ga	Ud	Va
A. aenea										•	•	•	•	•			•	•	•	•								
A. anthobia										•		•	•	•						•								
A. apricaria						•				•										•								
A. aulica					•	•																						
A. bifrons										•																		
A. consularis						•				•							•		•	•								
A. convexior								•		•	•		•	•			•	•									•	
A. convexiuscula					•	•	•	•		•	•						•		•						•		•	•
A. eurynota						•		•		•	•	•	•	•	•	•			•	•							•	
A. familiaris												•	•	•				•	•	•								
A. ingenua					•	•		•		•	•								•								•	•
A. littorea										•		•	•	•	•	•	•			•							•	
A. montivaga							•			•																		
A. ovata										•		•	•	•	•	•			•	•							•	
A. sabulosa								•		•	•																	
A. similata										•	•	•	•	•	•	•	•	•	•	•							•	
A. spreta								•		•	•	•	•	•					•	•								
Z. tenebrioides					•		•			•	•								•									
T. quadristriatus												•		•	•													
P. melanarius						•	•			•																		•

Table 4 (continued)

	Ar	Ca	Al	Bt	Ci	Cr	Cb	Gp	Lc	To	Ti	Cu	Ds	Lr	Sl	Ta	Ct	As	Sl	Sm	Mo	Fo	La	Ce	Pa	Ga	Ud	Va
C. ambiguus										•		•		•														
C. fuscipes						•					•	•	•				•	•		•	•		•		•			
A. meridianus												•	•	•	•		•	•										
A. signatus	•	•			•	•	•	•	•	•	•					•	•		•				•		•		•	•
H. affinis	•				•	•		•		•	•	•			•	•			•				•				•	•
H. atratus	•	•			•	•						•								•			•					•
H. distinguendus		•			•	•	•	•		•	•	•	•	•			•		•				•				•	•
H. honestus	•					•		•			•	•	•	•						•			•				•	•
H. luteicornis						•	•	•		•	•	•							•									•
H. rubripes		•			•	•		•		•	•										•	•						•
H. signaticornis								•		•		•	•												•			•
H. subcylindricus								•		•	•	•	•	•	•		•										•	•
O. azureus						•					•		•			•										•		
P. maculicornis								•		•			•	•			•										•	
P. griseus	•	•			•	•		•		•			•	•			•		•				•		•		•	•
P. rufipes	•	•			•	•				•	•								•								•	•
S. teutonus								•				•	•	•			•	•		•					•		•	
Frequency of preference	6	6	0	0	11	18	7	17	1	28	19	20	19	18	8	7	14	7	16	14	2	1	7	0	6	1	16	14

riod, which is equivalent to less than 1 and more than 24 seeds per individual and day (Table 3). The T_M of particular species varied from 6 to 789 mg seeds over the experimental period, which is equivalent to the range of ca 0.1 to almost 16 mg seeds per individual and day (Table 3). C_S varied from ca 0.02 to 0.99 mg of seeds per day and mg of dry mass of the carabid (Table 3).

Consumption was affected by the body size, while body mass seemed to be a better predictor of the consumption than body length (Fig. 1). Also, species not belonging to the tribes Harpalini or Zabrini tended to eat seeds of the offered species only reluctantly (Table 3), so these were excluded from further analyses. I_M showed a strong quadratic relationship with dry body mass of the carabid (Fig. 1*a*) with a maximum consumption achieved by carabids that were around 25 mg of carabid dry body mass, and positive linear relationship with body length (Fig. 1*b*). The quadratic relationship between the I_S and dry body mass was also significant but less strong (Fig. 1*c*) or weak in the case body length (Fig. 1*d*), and between C_S and dry body mass or body length it was still significant but very week (Figs 1*e*, *f*).

The preferences and their breadths also varied with carabid species (Tables 3 & 4). The number of preferred species of seeds varied from 1 to 16 (Tables 3 & 4). In species which were unspecialized (i.e. preferred many species of seeds) the standardized consumptions were organized along an almost straight line with negative slope, while in specialized to highly specialized

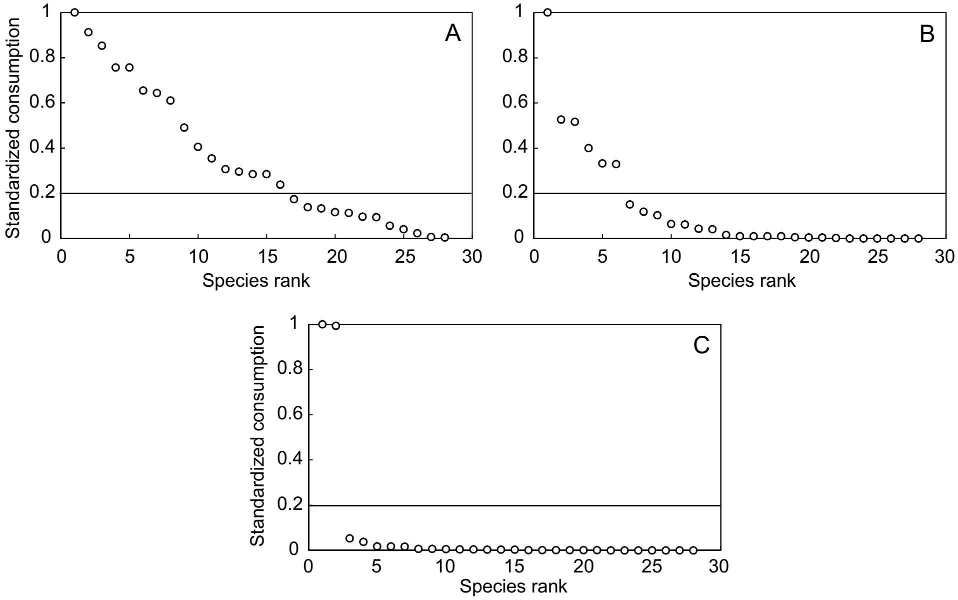

Fig. 2. Ranked standardized consumption of seeds. (A) *Anisodactylus binotatus*; (B) *Amara familiaris*; (C) *Amara montivaga*

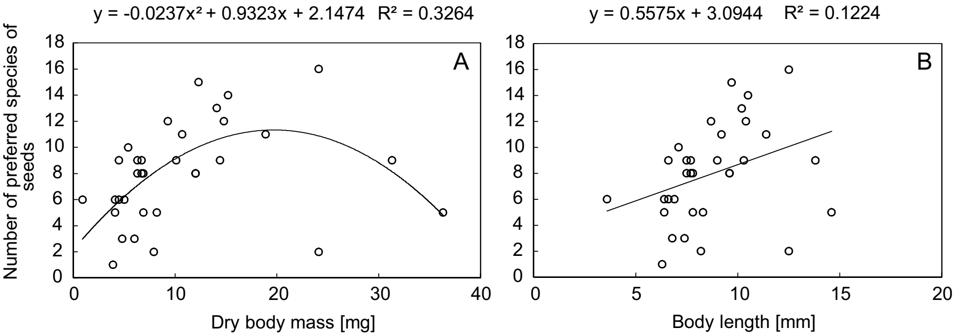

Fig. 3. Variation in the breadth of preferences with dry body mass (A) and body length (B)

species (i.e. those that preferred only a few species of seeds) the standardized consumption exponentially declined with increasing order of species (Fig. 2). The breadth of preference for seed seemed to show a quadratic pattern with dry body mass and a linear one with body length (Fig. 3), but the relationships were rather week. On the other hand, the breadth of preferences was strongly positively related to the I_S (Fig. 4*a*) and less strongly but still significantly so with I_M and C_S (Figs 4*b, c*).

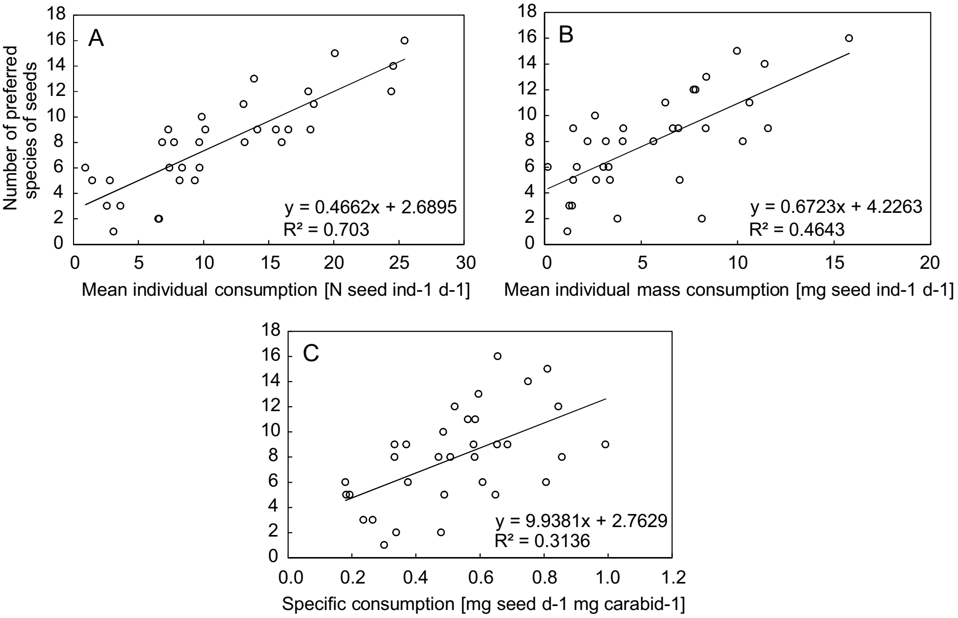

Fig. 4. Variation in the breadth of preferences with consumption. (A) Mean individual consumption; (B) mean individual mass consumption; (C) specific consumption

Also, particular seed species differed in their attractiveness for carabid beetles as the frequency of being preferred largely varied among the species of seeds (Table 4). The most preferred ones were *T. officinale*, *C. bursa-pastoris*, *T. inodorum* and *D. sophia*, which were preferred by 28, 20, 19 and 19 species of carabids, respectively, while *C. regalis*, *A. lappa* and *B. tripartita* were the most rejected as they were not preferred by any of the studied carabid, followed by *G. aparine*, *F. officinalis* and *L. communis*, each being preferred by only one species of carabids (Table 4).

DISCUSSION

We show in this paper that seed consumption, seed preferences and the breadths of seed preferences differ among the species of carabids and that these differences were observed in groups that are generally regarded as granivorous or at least in which seeds constitute an important part of their diet (Zabrini and Harpalini).

Seed consumption varied with the body size of the beetles and the observed patterns were analogous to what was previously described in the literature (Honek *et al.* 2007). We demonstrated quadratic relationships for consumption and body size metrics, i.e. dry body mass and body length, except for the combination of body length and I_M, which however may be an artefact of missing data for carabids longer than 15 mm in our study. Body length was in general worse predictor of consumption patterns than dry body mass, possibly because body mass reflects better the need for energy intake of an individual. The existence of such quadratic relationships indicates that small and large species of carabids ate fewer seeds compared to the intermediate ones at both absolute and relative (to body size) scale. One might ask why this was the case. We think that the answer to this question can be deduced from the fact that also the number of preferred species, i.e. the breadth of preferences, showed the same pattern. In other words, smaller and larger species of carabids not only ate fewer seeds but also preferred fewer species of seeds compared to middle-sized ones. We think that this relates to the size ratio of the carabid species with the seeds offered in this study. Hence small carabids on average preferred smaller seed species which they were capable to grasp and crush, and large species preferred larger seed species as they were incapable to hold smaller seeds in their mouthparts. On the contrary, middle-sized species are able to utilize not only the species of seeds intermediate in size but also small and larger ones, which has resulted in overall higher consumption and lower specificity for species of seeds.

Another reason why less specialized species of carabids consumed overall larger amounts of seeds might relate to the fact that they could be less efficient in obtaining nutrients from the food they eat than more specialized species (Dethier 1954, Slansky & Scriber 1985) so they are predestined to eat a variety of foods and in larger amounts to meet their energy requirements (Waldbauer & Friedman 1991).

In this study the preferences of individual species were estimated based on the multi-choice, or cafeteria, experiment, which is a frequently used approach (Honek *et al.* 2003, 2007, Saska *et al.* 2014*a*). This kind of experiments basically provide relative preferences as the choice for a seed may be influenced by the presence of another seed species (Charalabidis *et al.* 2017). We believe that this is not a problem for estimating the real preferences that occur in the field as the seeds of species that were heavily eaten in this study were regularly replenished so they were presented in excess during the entire experiment. The only problem might arise in the case when the seed species included in the array would not be those that carabids normally come across in the field, or if by chance a preferred species would not be included. The species of seeds included in this study can be frequently encountered by most of the species of carabids, but as the seed selection was made a priori, it is possible that some of the seeds important for carabids were neglected. On purpose we did not include seeds of the families Poaceae and Apiaceae, which are known to be preferred by the species of the subgenus *Zezea* (genus *Amara*, Hurka 1996) and genus *Ophonus* (Brandmayr Zetto & Brandmayr 1975), respectively, but do not stick well in the modelling clay we used to carry the seeds (Saska *et al.* 2014*a*, A. Honěk, unpublished observation). The other approach of determining preferences includes the no-choice experiment, i.e. providing just one species of seeds at a time. In this way, the willingness to accept, or chose, the seed would provide a measure of preference for particular seed (Charalabidis *et al.* 2017). However, such a design, despite providing some benefits (Charalabidis *et al.* 2017), represents simplified situation from the field conditions when more species of seeds, or types of prey in general, are available at a time at the scale of the daily radius of movement by an individual.

The preferences were measured under a situation of presenting the seeds to 10 conspecific individuals at the same time. Potentially the risk of intraspecific competition might affect the consumption at individual level, however the recent paper of Charalabidis *et al.* (2017) has shown on the example of *H. affinis*, a species that is also included in this study, and under no-choice situation, that intraspecific competition was not perceived as a risk in terms of the number of seeds eaten. If intraspecific competition may affect the actual preference is not known, but given that many species have the preference clearly determined, we assume it has only a minor effect if any.

Preferences varied among the species of carabids notably. The species of Harpalini were generally less selective and preferred more species of seeds than the species of Zabrini (Honek *et al.* 2007), but we cannot discriminate the taxonomic effect from the size effect as the species of Harpalini included in the study were on average larger than those of Zabrini. But, some affinities to seeds can be observed at the level of carabid tribes, such as that several Harpalini exclusively preferred both species of *Amaranthaceae* and *L. cardiaca*. In Zabrini, some differences can also be observed among spring and autumn reproducing species. Besides a pool of species commonly preferred at the genus level, the autumn reproducing species *Amara* preferred seeds of *C. intybus* and *C. arvense*, while the spring breeding species preferred seeds of *Brassicaceae*. This may relate to the period of seed shed (Kubát 2002) and carabid phenology – species reproducing in spring predominantly preferred seeds of plants that are massively shed in spring and early summer, while those reproducing in autumn seemed to prefer seeds that are available in autumn. The notable exception in this study is represented by *A. eurynota*, which belonged to the most generalist species of the genus and preferred species of seeds typical for spring and autumn species of *Amara*. The reason can be found in the fact that it is the only known winter breeding species of the subgenus *Amara*, which starts reproducing in late autumn (Saska 2004, Saska *et al.* 2014b) and continues laying eggs over winter if conditions are suitable, until very early spring (Bílý 1972).

There are several close interactions observed in this study for which literature support exists. In this study, *A. aulica* preferred only two species of seeds, both of *Asteraceae*, which is in line with the field observation of adult feeding and laboratory tests made on larvae (Saska 2005). Similarly, *A. montivaga* preferred another two species of *Asteraceae* in this as well as in another studies (Honek *et al.* 2005, Saska 2015). Other trophic links are suggested by the data, i.e. preference of *O. azureus* for seeds of *G. aparine*.

In this study, we contributed to understanding the food preferences of an array of arable field inhabiting carabid species. Besides the notoriously known tribes of seed-eating carabids, Zabrini and Harpalini, we also included species of other genera. Although the seed consumption by these species was not overwhelming, they may occasionally eat seeds also in the field and in some circumstances, they may appear to be important granivores (Koprdova *et al.* 2008, Saska 2008*b*). The inconstant attractiveness of seeds to carabid beetles shall be considered when planning the seed predation studies in the field as choosing the "wrong" seed may obscure the results. We recommend *T. officinalis*, *C. arvense*, *T. inodorum* and *C. bursa-pastoris* as promising model species of weeds for such studies due to the fact they are preferred by a wide range of carabid species.

Besides the seed properties studied in this study (seed mass) and mentioned above (phenological match), other seed traits might be responsible for such a variable attractiveness of seeds to carabids. These may include variability in e.g. nutritional content, mechanical or chemical protection, or stimulating cues elicited from the seeds. These factors are investigated in ongoing research.

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