

The consumption pattern of 28 species of carabid beetles (Carabidae) to a weed seed, *Viola arvensis*

P. Deroulers^{1*} and V. Bretagnolle^{1,2}

¹Centre d'Etudes Biologiques de Chizé, UMR7372, CNRS & Univ. La Rochelle, F-79360 Villiers-en-Bois, France; ²LTSER «Zone Atelier Plaine & Val de Sèvre», F-79360 Villiers-en-Bois, France

Abstract

Seedbank control has been the cornerstone of agricultural management practices. Regulating weeds by using their predators, as a weed control strategy, may be a prerequisite of decreasing herbicide use, and has thus attracted much research investigating the possible contribution of both vertebrates and invertebrates as weed seed predators. Carabid beetles are considered as one of the most important invertebrate seed predators in agroecosystems. We aimed at investigating carabid beetle preferences to a single prey type, seeds of *Viola arvensis*. We measured the consumption of seeds in 28 species of carabid beetles, under controlled experimental conditions. Two main tribes are identified in tested species, *Harpalini* with 12 species and *Pterostichini* with ten species. We found no relationships between species body mass and *Viola*'s seed consumption, nor with the ratio between mandible length and labrum width (ML/LW). However, trends became significant with the ratio ML/LW when restricting these analyses to species that ate at least five seeds. In addition, we detected a positive and significant relationship between consumption rate and occurrence in trapping sessions over the last 3 years. These results are in favor of weed seeds control by carabids. Clear limits of this study are the use of a single seed species and under control conditions. This experimentation calls for additional studies to check for consistencies in consumption against seed species.

Keywords: carabid beetles, tribe preferences, *Viola arvensis*, seed consumption, feeding experiments

(Accepted 10 May 2018)

Introduction

Carabid beetles show a wide range of feeding behavior and a continuum of diets, from complete carnivore to complete phytophage, with granivorous and omnivorous species lying between these extremes (Lundgren, 2009). Many carabid species are considered to be potentially important biological control agents (Lövei & Sunderland, 1996; Kromp, 1999; Kotze *et al.*, 2011). Pest control potential by carabid beetles, has for example, been established on both slugs (Bohan *et al.*, 2000; McKemey *et al.*, 2003), and aphids (Sunderland *et al.*, 1987;

Firlej *et al.*, 2013). Forsythe (1983) explored buccal parts of carabid beetles in relation to feeding habits and proposed three general feeding groups: carnivorous, polyphagous, and phytophagous, with several subgroups in each. Similarly, polyphagous feeders have different prey types according to the proventriculus morphology (Evans & Forsythe 1985; Chapman, 1985) and their mandibles (Forsythe, 1983). Phytophagous species typically show wide and rounded mandibles since they need powerful mandibular movements to crush plant materials such as leaves and seeds (Ingerson-Mahar, 2014).

In temperate agroecosystems, carabid beetles are a numerically abundant taxonomic group, with many of these being granivorous species (Zhang *et al.*, 1997). Therefore, several studies have investigated weed seed predation by carabid beetles (Honek *et al.*, 2003, 2005, 2006, 2007; Fawki & Toft, 2005; Petit *et al.*, 2014), typically using cafeteria-style experiments

*Author for correspondence

Phone: (+33)647085521

E-mail: paul.deroulers@hotmail.fr

(Saska *et al.*, 2010; Kulkarni *et al.*, 2015). The main granivorous carabid beetle species found in agroecosystems belong to two different tribes (Honek *et al.*, 2007): *Pterostichini* (genera *Amara*, *Zabrus*, *Pterostichus*) and *Harpalini* (*Harapalus*, *Ophonus*, *Pseudoophonus*), although other tribes present also contain granivorous species, e.g. *Trechini* or *Platinini* (Honek *et al.*, 2003, 2007; Hurst & Doberski, 2003). Carabid beetles are believed to play a role in the biocontrol of weed seeds (Honek *et al.*, 2003; Bohan *et al.*, 2011), but quantification of such a role largely remains elusive (see review in Kulkarni *et al.*, 2015). The lack of knowledge regarding this role may also result from the complexity of the carabid-weed seed system, which collectively comprises hundreds of species. Indeed, in our study site, more than 100 carabid beetle species have been identified in studies over the last 20 years, whilst the weed community contains at least 450 species. Carabid beetles (mouthparts morphology) and weed seed functional traits (i.e. physical and chemical defenses) probably further complicate the system (Davis *et al.*, 2008; Rusch *et al.*, 2015).

In our study, we explored a carabid interspecific variation in consumption whilst focusing on a single seed species. The aim was to elucidate how a carabid community was ordered in relation to their seed consumption to a weed species, which could be based on either their feeding habits or their phylogenetic classification.

Carabids morphological traits, as well as climatic conditions may impact on their consumption rate (Honek *et al.*, 2006; Rusch *et al.*, 2015; Russell *et al.*, 2017). Thus, we used standardized experimental conditions (Deroulers *et al.*, 2017), and selected two morphological traits of carabids, namely body size and the ratio of mandible length to labrum width (ML/LW), which are strongly related to feeding habits of carabid beetles (Forsythe, 1983). Thus, we verified whether the ratio ML/LW and body mass explained variation in seed consumption. Finally, we investigated whether consumption shown by the 28 species studies was related to their relative abundance in the field.

Materials and methods

Literature survey

Based on a literature review of carabid beetles feeding habits and diet (reviewed in table 1), we classified the tested species according to main feeding habits groups, from species almost strictly carnivorous, to intermediate polyphagous species (feeding on seeds) and finally phytophagous species, which are mainly granivorous. Tribes of each species were also noted to allow comparison of consumption according to phylogeny.

Feeding experiments

We tested the most common carabid beetles found in the Long Term Social Ecological Research – Zone Atelier Plaine et Val de Sèvre (LTSER-ZAPVS). The LTSER site covers approximately 450 km² of an intensively managed agricultural landscape, mostly dedicated to cereal crop production, located in western France, South of Niort (79, Deux-Sèvre department) (Bretagnolle *et al.*, 2017). Adult carabid beetles were collected alive with pitfall traps placed in the fields that were known to provide high capture rates and high species diversity, from April to August in 2015 and 2016. Traps were filled with soil pebbles placed at the bottom of the trap to provide shelter for

trapped arthropods. Each trap was emptied daily to avoid cannibalism or predation. Carabid beetles were then brought back to the laboratory and placed in a room kept at a temperature of 20–23°C. Specimens were stored in plastic boxes (diameter: 5.5 cm, height: 6.5 cm) with moist cotton, and fed with weed seeds and crushed dried cat food (Purina®, Friskies®) to prevent cannibalism. Specimens were stored in this way until we collected five individuals of the same species. Due to limitations in the capture rate for scarce carabid beetle species, some of the tests were occasionally performed on a smaller number of individuals.

All feeding experiments were carried out in climatic chambers set to optimize carabid beetle predation activity (humidity: 70%, temperature: 25°C, day/night conditions: 17/7 h) (Honek *et al.*, 2003; Eskelson *et al.*, 2011; Petit *et al.*, 2014). Before consumption measures, carabid beetles were left to starve for 72 h in order to standardize the level of satiation amongst individuals (Sunderland *et al.*, 1987; Lövei *et al.*, 1990). All individuals were weighted to assess body mass before and after the experimentation.

The initial number of seeds offered to carabids during experimentation was 50, in order to match the average field seed density (2000 seeds per m²) from our study site (Powolny, 2012). Seeds were placed in a 63.60 cm² area, corresponding to 25% of the experimental box and covered by 5 mm of sand in order to hide seeds (granulometry: 300 µm, color: chocolate; Le marchand de sable, Challans 85). All tests were conducted with *Viola arvensis*, a common dicotyledonous annual weed found in the study site (Gaba *et al.*, 2010; Meiss *et al.*, 2010). This species is known to be attractive (and accessible) to carabids because of their high lipid content (Bretagnolle *et al.*, 2015) and thin seed coat. Seeds were obtained from Herbiseed® (Twyford, the UK).

We used plastic boxes (11 × 23 × 8 cm) with rounded corners and with six screened openings on the sides (mesh: 1 × 1 mm) that provided good air circulation within the box. All tests were carried out with one individual in one box. Moist cotton and a paper shelter (5 × 4 cm) were placed in the plastic box. After 24 h of experimentation, the remaining seeds were counted; missing seeds and those consumed >50% were considered to be eaten (Honek *et al.*, 2005). After each test, in order to erase any smell from previous individuals (Kielty *et al.*, 1996), all boxes were washed with water and black soap.

Carabid beetles occurrence and morphological traits measurements

Carabid beetles were also trapped on the LTSER-ZAPVS in order to study occurrence. To estimate occurrence, we used data collected in a previous study where data were collected over 3 years (2014, 2015, and 2016) with samples collected across 635 fields (see Marrec *et al.*, 2015, Caro *et al.*, 2016). Between four (2015 and 2016) and five (2014) traps per experimental field (around 1250 m²) were utilized. Two traps were placed in the field's border and two (2014) or three placed in the core. Pitfall traps consisted of plastic cups (8.5 cm in diameter and 7 cm deep) and were filled with a solution containing ten drops of odorless soap and 10 g of salt per liter of water to improve insect preservation. Pitfall traps were left in place for four trapping effective days during two trapping sessions with a 1-month interval between. Beetles were brought back to the laboratory, stored in alcohol, and identified at species level.

The morphological traits measured focused on those that could impact on weed seed consumption, such as body mass

Table 1. Feeding preferences of 28 carabid beetle species tested during our experimentation based on literature survey (Larochele, 1990; Honek *et al.*, 2003; Lundgren, 2009).

Tribes	Genus	Species	Carnivorous	Polyphagous	Phytophagous (granivorous)	Observation number
Pterostichini	<i>Amara</i>	<i>aena</i>			x	1
Pterostichini	<i>Amara</i>	<i>apricaria</i>		x	x	13
Pterostichini	<i>Amara</i>	<i>consularis</i>	x		x	1
Pterostichini	<i>Amara</i>	<i>similata</i>			x	11
Platinini	<i>Anchomenus</i>	<i>dorsalis</i>	x	x		2
Harpalini	<i>Anisodactylus</i>	<i>signatus</i>	x	x		9
Brachinini	<i>Brachinus</i>	<i>crepitans</i>	x	x		3
Brachinini	<i>Brachinus</i>	<i>sclopete</i>	x			1
Pterostichini	<i>Calathus</i>	<i>fuscipes</i>	x	x		15
Harpalini	<i>Dixus</i>	<i>clypeatus</i>			x	3
Harpalini	<i>Harpalus</i>	<i>affinis</i>		x	x	25
Harpalini	<i>Harpalus</i>	<i>atratus</i>		x	x	4
Harpalini	<i>Harpalus</i>	<i>dimidiatus</i>		x	x	4
Harpalini	<i>Harpalus</i>	<i>distinguendus</i>		x	x	10
Harpalini	<i>Harpalus</i>	<i>tardus</i>			x	2
Bembidiini	<i>Metallina</i>	<i>spp</i>	x			1
Nebriini	<i>Nebria</i>	<i>salina</i>	x			1
Notiophilini	<i>Notiophilus</i>	<i>spp</i>	x			9
Harpalini	<i>Ophonus</i>	<i>sabulicola</i>			x	1
Pterostichini	<i>Poecilus</i>	<i>cupreus</i>		x		14
Harpalini	<i>Pseudoophonus</i>	<i>calceatus</i>		x	x	11
Harpalini	<i>Pseudoophonus</i>	<i>rufipes</i>		x	x	50 and more
Pterostichini	<i>Pterostichus</i>	<i>anthracinus</i>	x	x		1
Pterostichini	<i>Pterostichus</i>	<i>madidus</i>	x	x	x	31
Pterostichini	<i>Pterostichus</i>	<i>melanarius</i>	x	x		47
Harpalini	<i>Scybalicus</i>	<i>oblongiusculus</i>			x	1
Harpalini	<i>Semiophonus</i>	<i>signaticornis</i>		x	x	1
Pterostichini	<i>Zabrus</i>	<i>tenebroides</i>			x	50 and more

or size (see Honek *et al.*, 2007), and mandibles (Forsythe, 1983). Since the latter are asymmetrical in carabid beetles, we systematically measured the left mandible, as well as the labrum width. These measurements were then used to calculate the following ratio: ML/LW. This ratio is considered to be a good proxy to estimate robustness and strength of mandibles in carabid beetles (Brandmayr *et al.*, 1998). We used an average measurement for each carabid beetle species. Mandible length and labrum width were measured on dead individuals from 2013 collected in a previous study. Individuals were selected randomly irrespective of the crop that they were trapped within. We used trapped individuals from random years (2011 and 2012) to avoid any year effect on trait measurement. All individuals had been conserved in alcohol ethyl 96 surfin (99.9% of ethanol). Body and trait measurements were performed using a stereo microscope (Leica Microsystems M50) equipped with an integrated high-definition microscope camera (Leica IC80 HD). Ten carabid species were not measured in 2013; we therefore measured individuals trapped in 2016 following the same process to provide data for our study.

Statistical analyses

All tests were performed on R 3.2.5 (R Development Core Team, 2013). A preliminary analysis was completed to test the relationships between selected morphological traits (body mass and ratio ML/LW) with a spearman correlation test. We then analyzed the variation of seed consumption between carabid beetle species using generalized linear model with Poisson's error included. Since some species ate very few seeds, we fixed two threshold values of consumption to

analyze the effects of each morphological trait on seeds consumption. Then, to analyze the effects of body mass and of the ratio ML/LW on seeds consumption, we varied the threshold value, from zero (including all species) to at least five seeds consumed. Then, the effect of body mass and ratio ML/LW on seed consumption was analyzed using a linear model. Similar analyses were conducted between carabid beetle occurrence (caught in traps in 2014, 2015, and 2016) and *V. arvensis* seed consumption observed in our experiments.

Results

In total, 225 carabid individuals from 28 different species were tested to measure their consumption on *V. arvensis* seeds. Two main tribes were identified, *Harpalini* with 12 species and *Pterostichini* with ten species. Other tribes represented comprised one or two species (*Platinini*, *Brachinini*, *Bembidiini*, *Nebriini*, *Notiophilini*). Feeding habits found in our literature survey showed different classifications for carabid species. Five species were classified as strict carnivorous. Only *Poecilus cupreus* was classified as a strictly polyphagous species. Eight species were classified as strictly phytophagous, especially for *Amara* species (between three and four individuals tested for each species). All other species were classified either as carnivorous–polyphagous or polyphagous–phytophagous.

There were obvious variations in the consumption shown by different beetle species for the seed (fig. 1). Ten of the 12 species tested in *Harpalini* tribes seemed to actively seek and eat *Viola* seeds (five seeds or more). For species of the *Pterostichini* tribe, individuals ate on average between 0 and 3.28 seeds.

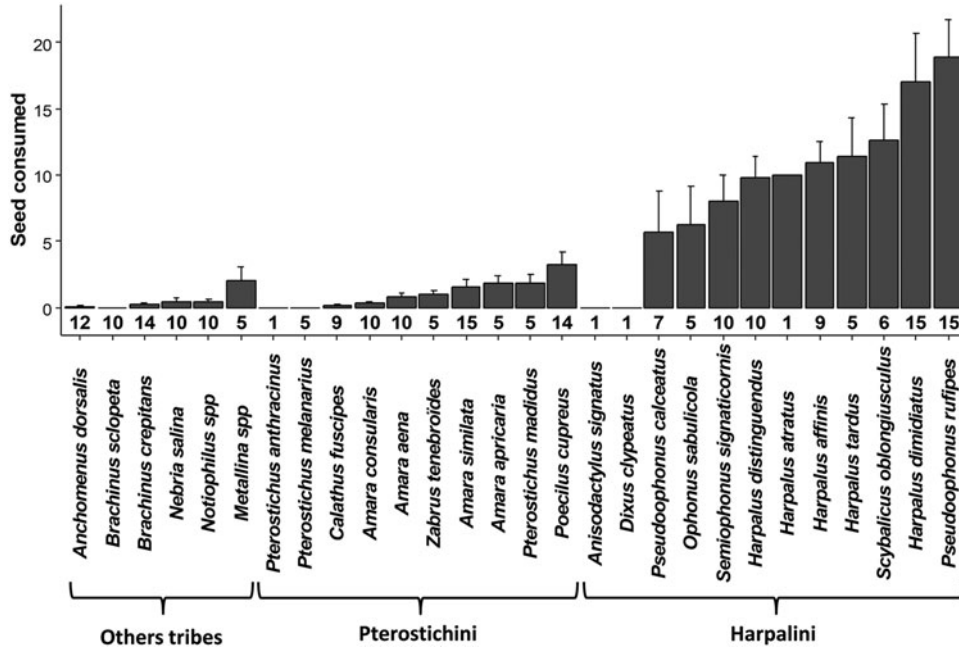


Fig. 1. Mean seed intake of *Viola arvensis* consumed by 28 carabid beetle species (± 1 SE), with the number of individuals tested on the bottom of the histogram for each species. Species are grouped according to their tribe, within tribe they are classified from the lowest consumer to the highest.

There was no correlation between body mass and the ratio ML/LW ($S = 2949$; $P = 0.62$). However, relationships between body mass and mandible length ($S = 622.59$; $P < 0.0001$) and body mass and labrum width ($S = 1655.8$; $P < 0.01$) were observed. We found no effect of body mass on *Viola* seed consumption when all species were included in the analysis ($F = 0.231$; $df = 1$; $P = 0.635$; fig. 2a). Similarly, there was no effect of body mass on seed consumption within species which ate more than five seeds ($F = 3.27$; $df = 1$; $P = 0.108$). No relationship was observed for ML/LW ratio when all species were included ($F = 0.56$; $df = 1$; $P = 0.462$). However, there

was a significant positive correlation for species which had eaten more than five seeds ($F = 9.58$; $df = 1$; $R^2 = 0.49$; $P = 0.015$; fig. 2b).

Occurrence of species from field site that consumed *V. arvensis* seeds

Across 3 years, 86 carabid beetle species were trapped at our study site (fig. 3a). The dominant species, *P. cupreus* showed a frequency of occurrence of 69% in cultivated fields, followed by *Anchomenus dorsalis* (57%). Of these 86 species, the

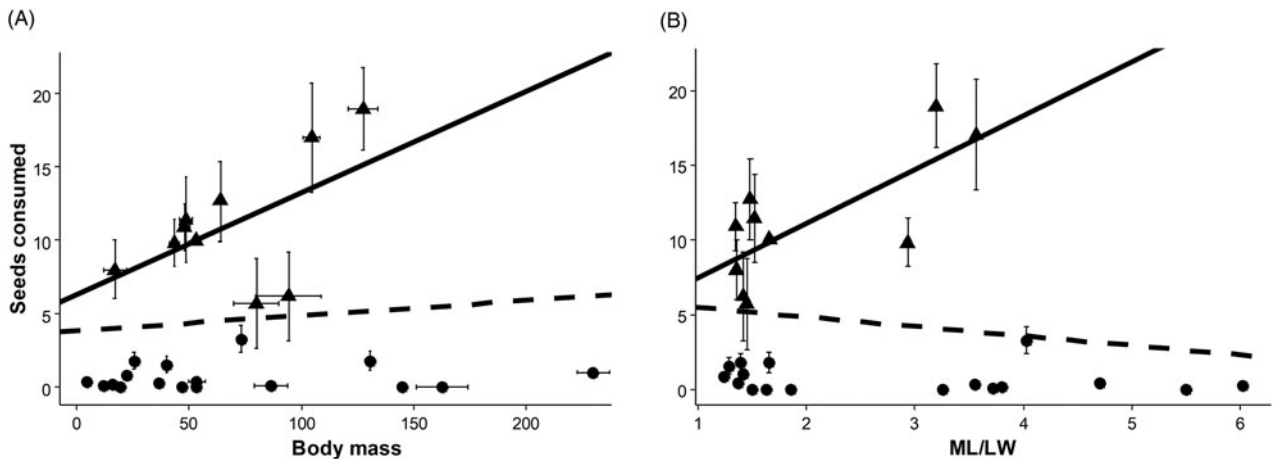


Fig. 2. Mean consumption rate of *Viola arvensis* seeds (± 1 SE) in relation to morphological traits of body mass (± 1 SE) and buccal parts. (a) Seed consumption in relation to body mass; (b) seed consumption in relation to the ratio between the mandible length and the labrum width. The dashed line represents the relationship when all species are considered, whilst the solid line represents only species that consumed at least five seeds.

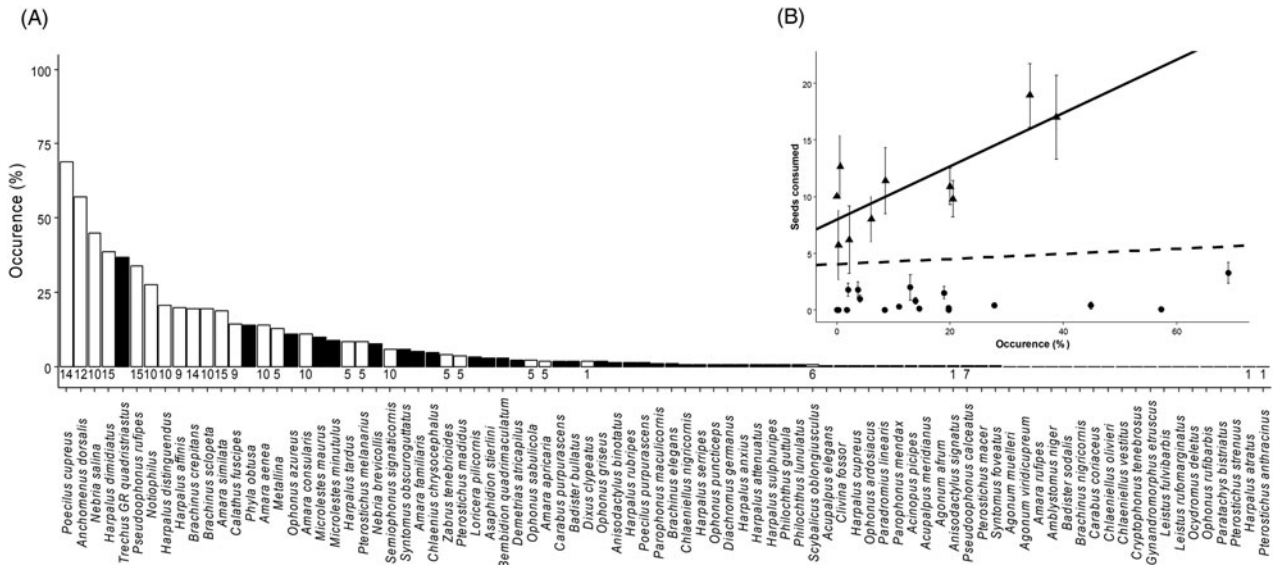


Fig. 3. (a) Occurrence of 86 carabid beetles captured in the LTSER 'Zone Atelier Plaine & Val de Sèvre' over 3 years (2014–2016), among which 28 have been tested to measure their consumption rate of *Viola arvensis* seeds (in white + number of individuals tested on the bottom of the histogram), other species are in black; (b) seed consumption rate in relation to the frequency of occurrence (two thresholds as in fig. 2: dashed line when all species are considered and solid line when species ate at least five seeds).

consumption of *Viola* seeds could be measured for 26 of them, since *Pterostichus anthracinus* and *Harpalus atratus* were not trapped in spring/summer over these 3 years. Again, there was no overall correlation between occurrence and consumption rate ($F = 0.13$; $df = 1$; $P = 0.72$), but restricting the analysis to species which had eaten more than five seeds yielded a significant positive correlation ($R^2 = 0.59$; $df = 1$; $P < 0.01$; fig. 3b). Therefore, amongst carabid species that ate *Viola* seeds, the most common carabid species (from our study site) were those that consumed seeds at a higher rate of consumption. Specifically, *Harpalus dimidiatus* and *Pseudoophonus rufipes* were, respectively, the fourth and sixth most common amongst the 86 carabid beetle species found in the study area.

Discussion

Three feeding groups are usually recognized for carabid beetles: polyphagous predators, carnivorous predators, and phytophagous species (Thiele, 1977; Forsythe, 1983; Dajoz, 2002). But carabids are also claimed to be mainly polyphagous predators in some studies (Kotze *et al.*, 2011). We found that the claimed carnivorous species actually consumed seeds (e.g. *Nebria salina* consumed on average 0.4 seeds) as much as species known as strict and obligate granivorous and seed eaters, like *Amara similata* (average 1.5 seeds). The genus *Pterostichus* is known as a generalist carnivore (Pollet & Desender, 1985, 1986), although Hurst & Doberski (2003) indicated that *Pterostichus madidus* is a potential predator of weed seeds. Conversely, species within the genus *Amara*, which did not consume *V. arvensis* seeds during our experiments, is believed to be a strong seed consumer (Toft & Bilde, 2002; Fawki *et al.*, 2005). However, Boursault (2012) also found that *Amara* does not eat *Viola* seeds, perhaps because this genus prefers *Brassicaceae* seeds (Thiele, 1977). Another possibility is that the composition of the bacterial guts symbionts

could result in an inability of *Amara* species to consume seeds of *Viola* (Lundgren & Lehman 2010). Our results were in close agreement with regard to other genera such as *Harpalus*, *Ophonus*, and *Pseudoophonus* species, which are regarded as high consumers of seeds (Tooley *et al.*, 1999; Toft & Bilde, 2002). Our results also showed a phylogenetic signal on seeds consumption (species of the same tribes showed similar abilities to consume *Viola* seeds). The tribe *Harpalini* (e.g. *Harpalus*, *Ophonus*, and *Pseudoophonus*) appears less specialized than the tribe *Pterostichini* (*Amara*, *Zabrus*) (Brandmayr, 1990; Honek *et al.*, 2007). Thus, they may consume a wider range of weed seed species than specialist granivorous species from *Pterostichini*.

It is possible that *V. arvensis* is a 'peculiar' seed, with a chemical composition which is not suitable for some carabid beetle species (e.g. *Amara* spp.). In addition, weed seeds differ in mechanical traits, in particular regarding the seed coat hardness (Lundgren & Rosentrater, 2007; Davis *et al.*, 2008; Gaba *et al.*, 2014). Furthermore, the buccal apparatus is different according to carabid beetle species. Thus, their abilities to consume weed seeds is variable (Forsythe, 1983). Therefore, some carabid beetle species which did not eat *V. arvensis* seed may be able to consume other weed seed species (Honek *et al.*, 2007).

Body mass and ratio of ML/LW were poor predictors of seed consumption. However, the correlation between the ratio of ML/LW and consumption became significant when restricted to species which ate more than five seeds. Indeed, all these species belong to the recognized category of strict phytophagous species, with mandibles being wider and stouter than for the other species (Forsythe, 1983). Therefore, at least in seed predator specialists, consumption increased with both body mass and the degree of specialization in morphological traits. For these species, we found a positive correlation between their consumption toward seeds and their occurrence. Indirectly, these results imply that carabids may

contribute to weed seed control. Limitations of our study primarily relate to the use of a single seed species and the specific control conditions that we chose to use. Our study also did not consider the species' trophic network position within the specialist–generalist gradient (Thébault & Fontaine, 2008), or the effects of natural conditions on seed consumption by carabid beetles. However, our study provides a comparative assessment among a fairly large range of carabid species. It would be valuable to extend such studies to investigate the consumption for other seed species.

Acknowledgements

The authors thank Gaétanne Leprovost who provided trait measurements, Isabelle Badenhauer for help in measurements, Marilyn Roncoroni who helped in species identification and for sharing her knowledge on ground beetles. Many thanks to Edoardo Tedesco and Charlotte Gibson who read and improved this manuscript. Many thanks too for their help, to Alexis Harismendy and Simon Emeriau. PHD funding was obtained from Conseil Départemental Des Deux-Sèvres and Région Poitou Charentes. This study took place under and was funded by ANR AGROBIOSE and LISEA foundation projects.

References

- Bohan, D.A., Bohan, A.C., Glen, D.M., Symondson, W.O., Wiltshire, C.W. & Hughes, L. (2000) Spatial dynamics of predation by carabid beetles on slugs. *Journal of Animal Ecology* **69**, 367–379.
- Bohan, D.A., Boursault, A., Brooks, D.R. & Petit, S. (2011) National-scale regulation of the weed seedbank by carabid predators. *Journal of Applied Ecology* **48**, 888–898.
- Boursault, A. (2012) *Caractérisation des relations trophiques entre composantes d'un agroécosystème : le cas de la prédation des graines d'adventices par les Carabidae*. Doctoral dissertation, Université de Bourgogne.
- Brandmayr, T.Z. (1990) Spermophagous (seed-eating) ground beetles: first comparison of the diet and ecology of the harpaline genera *Harpalus* and *Ophonus* (Col., Carabidae). pp. 307–316 in Stork, N. (Ed.) *The Role of Ground Beetles in Ecological and Environmental Studies*. Andover, Intercept.
- Brandmayr, T.Z., Giglio, A., Marano, I. & Brandmayr, P. (1998) Morphofunctional and ecological features in carabid (Coleoptera) larvae. *Museo Regionale di Scienze Naturali, Torino* 449–490.
- Bretagnolle, V., Berthet, E., Gross, N., Gauffre, B., Plumejeaud, C., Houte, S., Badenhauer, I., Monceau, K., Aliier, F., Monestiez, P. & Gaba, S. (2017) Biodiversity, ecosystem services and citizen science: the value of long term monitoring in farmland landscapes for sustainable agriculture. *Science of the Total Environment*.
- Bretagnolle, V., Matejcek, A., Gregoire, S., Reboud, X. & Gaba, S. (2015) Determination of fatty acids content, global antioxidant activity and energy value of weed seeds from agricultural fields in France. *Weed Research* **56**, 78–95.
- Caro, G., Marrec, R., Gauffre, B., Roncoroni, M., Augiron, S. & Bretagnolle, V. (2016) Multi-scale effects of agri-environment schemes on carabid beetles in intensive farmland. *Agriculture, Ecosystems & Environment* **229**, 48–56.
- Chapman, R.F. (1985) Structure of the digestive system. pp. 165–211 in Kerkut, G.A. & Gilbert, L.I. (Eds) *Regulation: Digestion, Nutrition, Excretion*. Pergamon Press. ISBN: 9780080308050.
- Dajoz, R. (2002) *Les coléoptères Carabidés et Ténébrionidés: Ecologie et Biologie*. Paris, Éditions Tec & Doc. ISBN: 2-7430-0539-4.
- Davis, A.S., Schutte, B.J., Iannuzzi, J. & Renner, K.A. (2008) Chemical and physical defense of weed seeds in relation to soil seedbank persistence. *Weed Science* **56**(5), 676–684.
- Deroulers, P., Gauffre, B., Emeriau, S., Harismendy, A. & Bretagnolle, V. (2017) Towards a standardized experimental protocol to investigate interactions between weed seeds and ground beetles (Carabidae, Coleoptera). *Arthropods and Plant Interactions*.
- Eskelson, M.J., Chapman, E.G., Archbold, D.D., Obrycki, J.J. & Harwood, J.D. (2011) Molecular identification of predation by carabid beetles on exotic and native slugs in a strawberry agroecosystem. *Biological Control* **56**(3), 245–253.
- Evans, M.E.G. & Forsythe, T.G. (1985) Feeding mechanisms, and their variation in form, of some adult ground-beetles (Coleoptera: Caraboidea). *Journal of Zoology*, **206**(1), 113–143.
- Fawki, S. & Toft, S. (2005) Food preferences and the value of animal food for the carabid beetle *Amara similata* (Gyll.) (Col., Carabidae). *Journal of Applied Entomology* **129**(9–10), 551–556.
- Firlej, A., Doyon, J., Harwood, J.D. & Brodeur, J. (2013) A multi-approach study to delineate interactions between carabid beetles and soybean aphids. *Environmental Entomology*, **42**(1), 89–96.
- Forsythe, T.G. (1983) Mouthparts and feeding of certain ground beetles (Coleoptera: Carabidae). *Zoological Journal of the Linnean Society* **79**(4), 319–376.
- Gaba, S., Chauvel, B., Dessaint, F., Bretagnolle, V. & Petit, S. (2010) Weed species richness in winter wheat increases with landscape heterogeneity. *Agriculture, Ecosystems & Environment* **138**(3), 318–323.
- Gaba, S., Collas, C., Powolny, T., Bretagnolle, F. & Bretagnolle, V. (2014) Skylarks trade size and energy content in weed seeds to maximize total ingested lipid biomass. *Behavioural Processes* **108**, 142–150.
- Honek, A., Martinkova, Z. & Jarosik, V. (2003) Ground beetles (Carabidae) as seed predators. *European Journal of Entomology* **100**(4), 531–544.
- Honek, A., Martinkova, Z. & Saska, P. (2005). Post-dispersal predation of *Taraxacum officinale* (dandelion) seed. *Journal of Ecology* **93**(2), 345–352.
- Honek, A., Saska, P. & Martinkova, Z. (2006) Seasonal variation in seed predation by adult carabid beetles. *Entomologia Experimentalis et Applicata* **118**(2), 157–162.
- Honek, A., Martinkova, Z., Saska, P. & Pekar, S. (2007) Size and taxonomic constraints determine the seed preferences of Carabidae (Coleoptera). *Basic and Applied Ecology* **8**(4), 343–353.
- Hurst, C. & Doberski, J. (2003) Wild flower seed predation by *Pterostichus madidus* (Carabidae: Coleoptera). *Annals of Applied Biology*, **142**(2), 251–254.
- Ingerson-Mahar, J.M. (2014) *Relating diet and morphology of the head, mandibles and proventriculus in adult carabid beetles*. Doctoral dissertation, The State University of New Jersey.
- Kielty, J.P., Allen-Williams, L.J., Underwood, N. & Eastwood, E. A. (1996) Behavioral responses of three species of ground beetle (Coleoptera: Carabidae) to olfactory cues associated with prey and habitat. *Journal of Insect Behavior* **9**(2), 237–250.
- Kotze, D.J., Brandmayr, P., Casale, A., Dauffy-Richard, E., Dekoninck, W., Koivula, M.J., Lövei, G.L., Mossakowski, D., Noordijk, J., Paarmann, W., Pizzoloo, J., Szyszko, J., Taboada, A., Turin, H., Venn, S., Vermeulen, R. & Zetto, T. (2011) Forty years of carabid beetle research in Europe – from taxonomy,

- biology, ecology and population studies to bioindication, habitat assessment and conservation. *ZooKeys* **100**, 55–148.
- Kromp, B.** (1999) Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agriculture, Ecosystems & Environment* **74**(1), 187–228.
- Kulkarni, S.S., Dossall, L.M. & Willenborg, C.J.** (2015) The role of ground beetles (Coleoptera: Carabidae) in weed seed consumption: a review. *Weed Science* **63**(2), 335–376.
- Larochelle, A.** (1990) *The Food of Carabid Beetles: (coleoptera: Carabidae, Including Cicindelinae)*. Association des entomologistes amateurs du Québec.
- Lövei, G.L. & Sunderland, K.D.** (1996). Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual review of entomology* **41**(1), 231–256.
- Lövei, G.L., Sopp, P.I. & Sunderland, K.D.** (1990) Digestion rate in relation to alternative feeding in three species of polyphagous predators. *Ecological Entomology* **15**(3), 293–300.
- Lundgren, J.G.** (2009) *Relationships of Natural Enemies and non-Prey Foods*, vol. 7. Springer Science & Business Media, New York.
- Lundgren, J.G. & Lehman, R.M.** (2010) Bacterial gut symbionts contribute to seed digestion in an omnivorous beetle. *PLoS ONE* **5**(5), e10831.
- Lundgren, J.G. & Rosentrater, K.A.** (2007) The strength of seeds and their destruction by granivorous insects. *Arthropod-Plant Interactions* **1**(2), 93–99.
- Marrec, R., Badenhausser, I., Bretagnolle, V., Börger, L., Roncoroni, M., Guillon, N. & Gauffre, B.** (2015) Crop succession and habitat preferences drive the distribution and abundance of carabid beetles in an agricultural landscape. *Agriculture, Ecosystems & Environment* **199**, 282–289.
- McKemey, A.R., Symondson, W.O.C. & Glen, D.M.** (2003) Predation and prey size choice by the carabid beetle *Pterostichus melanarius* (Coleoptera: Carabidae): the dangers of extrapolating from laboratory to field. *Bulletin of Entomological Research* **93**(3), 227–234.
- Meiss, H., Médiène, S., Waldhardt, R., Caneill, J. & Munier-Jolain, N.** (2010) Contrasting weed species composition in perennial alfalfas and six annual crops: implications for integrated weed management. *Agronomy for Sustainable Development* **30**(3), 657–666.
- Petit, S., Boursault, A. & Bohan, D.A.** (2014) Weed seed choice by carabid beetles (Coleoptera: Carabidae): linking field measurements with laboratory diet assessments. *European Journal of Entomology* **111**(5), 615.
- Pollet, M. & Desender, K.** (1985) Adult and larval feeding ecology in *Pterostichus melanarius* Ill. (Coleoptera, Carabidae). *Rijksuniversiteit Faculteit Landbouwwetenschappen Gent* **37**(2), 581–594.
- Pollet, M. & Desender, K.** (1986) Prey selection in carabid beetles (Coleoptera, Carabidae): are diet activity patterns of predators and prey synchronized. *Meded Fac Landbouwwet Rijksuniv Gent* **51**, 957–971.
- Powolny, T.** (2012) *Faire face à l'hiver-Quelles réponses à l'hétérogénéité de la ressource en agroécosystème? L'exemple de l'alouette des champs (Alauda arvensis)*. Doctoral dissertation, Université de Poitiers.
- R Development Core Team** (2013) *R: A Language and Environment for Statistical Computing*. Vienna, Austria, R Foundation for Statistical Computing. ISBN 3-900051-07-0, Available online at <http://www.R-project.org>.
- Rusch, A., Birkhofer, K., Bommarco, R., Smith, H.G. & Ekbom, B.** (2015) Predator body sizes and habitat preferences predict predation rates in an agroecosystem. *Basic and Applied Ecology* **16**(3), 250–259.
- Russell, M.C., Lambrinos, J., Records, E. & Ellen, G.** (2017) Seasonal shifts in ground beetle (Coleoptera: Carabidae) species and functional composition maintain prey consumption in Western Oregon agricultural landscapes. *Biological Control* **106**, 54–63.
- Saska, P., Martinkova, Z. & Honek, A.** (2010) Temperature and rate of seed consumption by ground beetles (Carabidae). *Biological Control* **52**(2), 91–95.
- Sunderland, K.D., Crook, N.E., Stacey, D.L. & Fuller, B.J.** (1987) A study of feeding by polyphagous predators on cereal aphids using ELISA and gut dissection. *Journal of Applied Ecology* **24**, 907–933.
- Thébault, E. & Fontaine, C.** (2008) Does asymmetric specialization differ between mutualistic and trophic networks? *Oikos* **117** (4), 555–563.
- Thiele, H.U.** (1977) *Carabid Beetles in Their Environments: A Study on Habit Selection by Adaptations in Physiology and Behaviour*. Translated by Joy Wieser. Springer-Verlag, Berlin.
- Toft, S. & Bilde, T.** (2002) Carabid diets and food value. pp. 81–110 in Holland, J.M. (Ed.) *Agroecology of Carabid Beetles*. Andover, Hampshire, UK.
- Tooley, J.A., Froud Williams, R.J., Boatman, N.D., Holland, J.M., Boatman, N.D., Davies, D.H.K., Chaney, K., Feber, R., Snoo, G.R. & Sparks, T.H.** (1999). Weed seed predation in arable field margins by carabid beetles (Carabidae: Coleoptera). *Aspects of Applied Biology* **54**, 211–216.
- Zhang, J., Drummond, F. A., Liebman, M. & Hartke, A.** (1997). Insect predation of seeds and plant population dynamics. *Maine Agricultural and Forest Experiment Station Technical Bulletin* **163**.