

DO PROPERTIES AND SPECIES OF WEED SEEDS AFFECT THEIR CONSUMPTION BY CARABID BEETLES?

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Seed predators are an integral part of agroecosystems, where they can reduce the populations of weeds. The preference of predators for seeds and the observed predation rate may be affected by the properties of seeds (e.g. taxonomy, chemical composition, physical defence). In this work, we focused on seed consumption of *Taraxacum officinale* Web. and *Stellaria media* (L.) Vill., from France and the Czech Republic, by three species of ground beetle that are seed predators (Coleoptera: Carabidae): *Poecilus cupreus* (L.), *Pterostichus melanarius* (Illiger) and *Anchomenus dorsalis* (Pontoppidan). The seed species were offered in arenas, simultaneously, under three different experimental manipulations of moisture and seed coat conditions: dry and intact, water-imbibed and intact, and water-imbibed with a damaged seed coat. Seed consumption was checked after 0.5, 1, 2, 24, and 48 hrs of exposure. *Anchomenus dorsalis* largely refused to feed on seeds. *Taraxacum officinale* seeds with damaged coats were most preferred by the remaining two species of carabids. The consumption by *P. cupreus* of *T. officinale* seeds with damaged coats increased from 0.18% after 0.5 hrs to 83.83% after 48 hrs, and by *P. melanarius* from 13.76% after 0.5 hrs to 76.77% after 48 hrs. Seeds of *S. media* were consumed less. There was a significant difference in consumption rates due to the country of origin of the seeds, but there were no differences between the carabid sexes. That carabids preferred water-imbibed and damaged seeds may suggest an involvement of olfactory clues in the seed selection process, and/or shorter seed-handling times.

Keywords: carabid beetle, weed seeds, preference, imbibed seeds, seed predator, granivory.

INTRODUCTION

Ground beetles are one of the most important seed predator groups in agroecosystems (TOOLEY & BRUST 2002, GALLANDT *et al.* 2005, HONEK *et al.* 2005). Seeds constitute a vital part of the diet for both adults and larvae (SASKA 2005, 2008, KLIMES & SASKA 2010). Seed predators can remove 18 to 70% of seeds produced annually (WESTERMAN *et al.* 2003) thus they can reduce the input of seeds into the soil bank in arable fields (BOHAN *et al.* 2011). Numerous factors affect seed predation and selection by carabid beetles, such as seed size

(FORSYTHE 1983, ACORN & BALL 1991), seed mass (HONEK *et al.* 2007), seed coat thickness (LUNDGREN & ROSENTRATER 2007), chemical composition (BEWLEY & BLACK 1982, JANZEN 1982, HULME 1996), time after ripening of the seeds (SASKA *et al.* 2019a), the hardness of seeds (VAN DER MEIJ & BOUT 2000) and state of seed imbibition (LAW & GALLAGHER 2015), amongst others. One understudied effect is the geographical origin of the seed. Both physical and chemical properties of seeds may vary among locations (WIDMER *et al.* 2007, HE *et al.* 2020), which may influence the seed choice by granivores (HONEK *et al.* 2011).

The attributes of the ground beetle predator may also affect seed consumption. There is a positive correlation between the mass of the carabid and the mass of the most preferred seeds (HONEK *et al.* 2006, SASKA *et al.* 2019b). The sex of the carabid also influences seed consumption, with females consuming more seeds than males (MARSHALL & MOONEN 2002, SASAKAWA 2010, SASKA *et al.* 2010, KULKARNI *et al.* 2015), probably because they require more energy for reproduction. Dietary preferences are also influenced by the evolutionary history of carabids: species of the tribe Zabrini prefer seeds of Asteraceae, while those of the tribe Harpalini may feed upon seeds of the Violaceae and other Asteraceae usually not selected by the Zabrini (HONEK *et al.* 2007, SASKA *et al.* 2019b).

Carabids seem to use olfactory (LAW & GALLAGHER 2015) and tactile cues (KIELTY *et al.* 1996) when searching for seeds. The type or amount of chemical cues released from seeds might be affected by conditions of the seeds, e.g. the state of the seed coat or the levels of imbibition. Many seed predators are not able to detect seeds with an impermeable coat, most likely because chemical cues are not released from the seed (VANDER WALL 1998). Beetles appear to prefer water-imbibed seeds over the dry seeds (KULKARNI *et al.* 2016, 2017) because the olfactory cues of the previous are stronger and the handling time of these seeds is also shorter (personal observation).

There is a lack of information about the preferences of carabids for seed species in interaction with water-imbibed seeds or seeds with a damaged seed coat. In this study, we conducted a multiple-choice test to determine the preference of the three carabid species: *Pterostichus melanarius*, *Poecilus cupreus* and *Anchomenus dorsalis*. Although the representatives of the genera *Pterostichus*, *Poecilus* and *Anchomenus* are commonly regarded as predominantly carnivorous species, they have been frequently observed to consume seeds (GOLDSCHMIDT & TOFT 1997, HONEK *et al.* 2003, HURST & DOBERSKI 2003, DEROULERS & BRETAGNOLLE 2019). The presence of plant DNA in carabid regurgitates of *P. melanarius* and *P. rufipes* was found to be substantial (>70% of individuals) and independent of carabid species, sex, region and the time of sampling (FREI *et al.* 2019). In particular, *P. melanarius* has been described as a generalist predator (BOHAN *et al.* 2000, LANGAN *et al.* 2004, BARGMANN *et al.* 2016), but this species also consumes weed seeds (TOOLEY *et al.* 1999, HONEK *et al.* 2003). *P. melanarius* has been found to readily accept fresh, dry and im-

bibed seeds of *Brassica napus* (KOPRDOVA *et al.* 2012). On average, *P. melanarius* consumed three seeds of *S. media* seeds in 48 hrs in a cafeteria test (TOOLEY *et al.* 1999). *P. cupreus* is known as an omnivorous species (LÖVEI & SUNDERLAND 1996, HONEK *et al.* 2003, BARGMANN *et al.* 2016, SASKA *et al.* 2019b). Very little is known about seed consumption of *A. dorsalis*. This species consumed 1.7 ± 1.4 seeds of *Capsella bursa-pastoris* during a three days experiment (HONEK *et al.* 2003). Because it is one of the dominant species in European agroecosystems, the capacity of this species to eat seeds is worth exploring.

The preferences of the three different conditions of seeds (dry/intact, imbibed/intact and imbibed/damaged) were tested on three different species of carabids, separately for each sex. We expected: (i) carabid species-specific responses to particular species of seed; (ii) specific responses to the different seed conditions; (iii) sex-specific consumption; and (iv) that geographical origin of the seeds would affect consumption.

MATERIAL AND METHODS

Ground beetles

Three species of carabids were used in this study: *Pterostichus melanarius*, *Poecilus cupreus* and *Anchomenus dorsalis*. These species were selected because they are amongst the most abundant carabids in arable fields in France. The ground beetles were collected using pitfall traps from two field edges on the INRAe experimental farm near Dijon, France (47.233°N, 5.097°E) between the end of September and October 2018. We used 160 trapped individuals of each species for the experiments. Beetle identification was made according to HURKA (1996). Carabids were starved for 3 days before the trial. The beetles were individually kept in plastic containers (7.5 cm in diameter) covered with a lid at room temperature to standardise their hunger level (LUNDGREN & ROSENTRATER 2007) and water was provided by placing a wet cotton roll on the bottom.

Seeds

We used seeds of *Taraxacum officinale* (Asteraceae) and *Stellaria media* (Caryophyllaceae); species that have previously been used for experimentation with adults as well as larvae of carabid beetles (HONEK *et al.* 2005, SASKA 2008, PETIT *et al.* 2014). The seeds of *T. officinale* are obconic achenes 2.5 x 0.9 mm long on average (BOJNANSKÝ & FARGAŠOVÁ 2007), and are rich in proteins (25.65%), lipids (27.86%) and carbohydrates (23.05%) (BRETAGNOLLE *et al.* 2016). The seeds of *S. media* are round, ca. 1 mm diameter (BOJNANSKÝ & FARGAŠOVÁ 2007), and have lower protein (16.44%) and lipid (5.19%) content than *T. officinale*, but are higher in carbohydrate (65.22%) (BRETAGNOLLE *et al.* 2016). Seeds from the Czech Republic (collected near to CRI, Prague, 50.086°N, 14.302°E) and France (collected near to INRAe Dijon, 47.316°N, 5.068°E) were used. All seeds were dried at room temperature (22 °C) for 4 weeks. Plant identification was made according to KUBÁT *et al.* (2002).

Experiment design

The effects of seed species, conditions, location of origin and the sex of the beetles, and all interactions, on seed consumption by ground beetles, were tested in a multi-choice experiment. The experimental arenas consisted of Petri dishes (14 cm in diameter) lined with moist filter paper on the bottom. Both species of seeds, *T. officinale* and *S. media*, were placed simultaneously in each arena. Three seed conditions were used: dry/intact, imbibed/intact and imbibed/damaged. To assure that the dry treatment seeds remain dry at the time of exposure, they were placed into the arena immediately before the start of the trial. The water-imbibed seeds were left to soak on wet filter paper for 24 hrs before the start of the trial. The imbibed/damaged seeds were first imbibed on filter paper for 24 hrs, after which a small hole was made through the seed coat using an entomological pin number 0 (0.35 mm in diameter), so the seeds remained viable (confirmed by conducting a parallel germination test on a subset of 20 seeds per species and country; data not shown). Each condition was replicated five times per dish, so 30 seeds were presented at a time (Fig. 1). The French and Czech seeds were examined separately. The photoperiod was set for 10 hrs light/14 hrs dark and constant temperature of 17 °C, in order to prevent any temperature effect on seed consumption (SASKA *et al.* 2010). The experiment was conducted from the end of October to the beginning of December 2018. Individual beetles were released into arenas and the remaining seeds were counted after 0.5, 1, 2, 24, and 48 hrs. Any seed that was more than half-eaten was considered eaten and removed, as were the empty seed coats.

Statistical analysis

The statistical analysis was performed by generalised mixed effects models in R version 3.5.3 (R Core Team) using the package *glmmTMB* (Brooks *et al.* 2017). Since *A. dorsalis* ate very few seeds (a total of 89 out of the 4800 seeds offered), the data for this species were not analysed. The preferences of *P. melanarius* and *P. cupreus* were tested separately. Since the data contained a high proportion of zeros, we fitted models using the binomial and beta-binomial distributions, with or without terms that accounted for zero-inflation, and with or without arena as a random factor (because the consumptions of different seed conditions within the same arena were not independent from each other). Models based on beta-binomial distribution without the zero-inflation term and with random effect were superior (justified by the change in Akaike Information Criterion). As the preferred models did not show any signs of overdispersion and zero-inflation (checked using the DHARMA

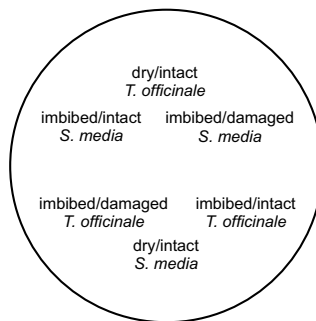


Fig. 1. Design of the testing arena

package; HARTIG 2016), beta-binomial models were used in the subsequent steps of model simplification. Significance of individual terms in the models was assessed using the Anova function from the car package (FOX & WEISBERG 2019).

RESULTS

Seed consumption was affected by seeds species and conditions, and it varied between the carabid species (Table 1). For *P. melanarius*, seed preference was affected by seed conditions, species and geographical origin. There were also significant two- and three-way interactions between seed conditions and seed origin, and seed species, seed conditions and geographical origin (Table 2). Seeds of *T. officinale* were preferred more than *S. media*. Dry/intact seeds were consumed significantly less than imbibed/intact and imbibed/damaged seeds. The seeds from France were consumed significantly more than the Czech seeds. There was no effect of the sex of the beetle (Table 2).

Poecilus cupreus also preferred seeds of *T. officinale*. Dry/intact seeds were the least consumed seed conditions followed by imbibed/intact seeds. There was a significant interaction between seed species and seed conditions, as well between seed conditions and seed origin (Table 3). There was also no significant difference in consumption between the sexes of the beetles.

Table 1. The mean proportions (95% confidence intervals) of consumed seeds by two species of carabids in 48 hrs.

Species of carabids/ Condition of seeds	<i>Stellaria media</i>		<i>Taraxacum officinale</i>	
	France	Czech Republic	France	Czech Republic
<i>Pterostichus melanarius</i>				
Imbibed/damaged	0.401 (0.304, 0.507)	0.208 (0.142, 0.294)	0.712 (0.571, 0.821)	0.761 (0.629, 0.856)
Dry/intact	0.312 (0.226, 0.412)	0.096 (0.059, 0.151)	0.803 (0.683, 0.886)	0.187 (0.107, 0.304)
Imbibed/intact	0.217 (0.149, 0.304)	0.166 (0.110, 0.241)	0.67 (0.522, 0.790)	0.224 (0.132, 0.353)
<i>Poecilus cupreus</i>				
Imbibed/damaged	0.196 (0.113, 0.317)	0.102 (0.054, 0.187)	0.853 (0.656, 0.946)	0.702 (0.456, 0.868)
Dry/intact	0.144 (0.080, 0.245)	0.061 (0.030, 0.119)	0.843 (0.642, 0.942)	0.361 (0.168, 0.612)
Imbibed/intact	0.135 (0.075, 0.232)	0.078 (0.039, 0.149)	0.751 (0.506, 0.899)	0.241 (0.101, 0.474)

Table 2. The minimum model for the seed preference of *Pterostichus melanarius* determined after 48 hrs. Generalised mixed-effects model with beta-binomial distribution was used.

Variables	χ^2	Df	P
Seed species	181.872	1	<0.001
Seed conditions	45.223	2	<0.001
Seed origin	14.207	1	<0.001
Seed species \times Seed conditions	2.799	2	0.246
Seed species \times Seed origin	3.421	1	0.064
Seed conditions \times Seed origin	36.934	2	<0.001
Seed species \times Seed conditions \times Seed origin	26.784	2	<0.001

The cumulative proportion of seeds consumed increased over time (Fig. 2). The most preferred seeds were those of *T. officinale* with imbibed/damaged seed coat. The consumption of these seeds differed between carabid species: *P. cupreus* consumed 0.18% of the seeds after 0.5 hrs, while *P. melanarius* consumed 13.76% of the seeds over the same time period. The consumption of these seeds, regardless of seed origin, gradually increased and *P. cupreus* and *P. melanarius* consumed 83.83% and 76.77% of seeds after 48 hrs, respectively.

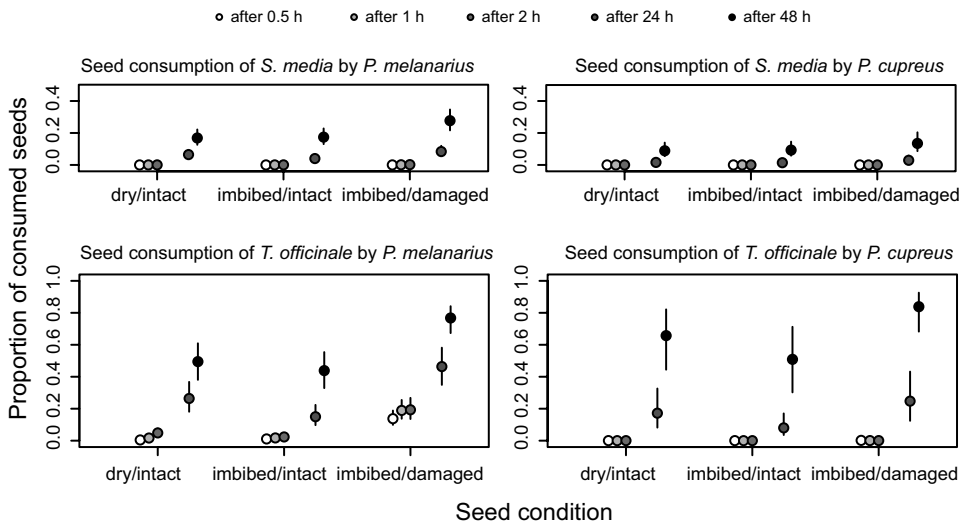


Fig. 2. Average cumulative consumption rate by carabids during the time of 0.5, 1, 2, 24, and 48 hrs. Each point represents the mean consumption, and the vertical bars represent 95% confidence interval. Points within particular seed condition are spaced based on log(time of exposure). Note that the ranges of y-axis differ between the top and bottom panels.

Table 3. The minimum model for the seed preference of *Poecilus cupreus* determined after 48 hrs. Generalised mixed-effects model with beta-binomial distribution was used.

Variables	χ^2	Df	P
Seed species	293.469	1	<0.001
Seed conditions	26.124	2	<0.001
Seed origin	4.347	1	0.037
Seed species \times Seed conditions	7.039	2	0.029
Seed conditions \times Seed origin	6.462	2	0.039

The seed consumption of *S. media* was lower than the consumption of *T. officinale*. The most preferred seeds of the *S. media* sets were the imbibed/damaged conditions. Consumption after 48 hrs, irrespective of the origin of the seeds, was 13.46% of seeds for *P. cupreus*, and 27.69% of seeds for *P. melanarius*.

DISCUSSION

In this study, the seed preferences of two omnivorous carabid species were found to depend on the seed species, conditions and the geographical origin of the seeds. *Pterostichus melanarius* and *Poecilus cupreus* consumed a rather high number of seeds of *Taraxacum officinale* in our study, and both consumed more of the water-imbibed than dry seeds. In other studies, carabids also made significant preference choices for imbibed seeds (HURST & DOBERSKI 2003, KULKARNI *et al.* 2016).

Several mechanisms could explain why the dry and unimbibed seeds were less consumed by carabids (Fig. 2). These seeds release less olfactory volatiles than those that are imbibed (PAULSEN *et al.* 2013) and more attractive to predators. Dry and unimbibed seeds may also deter seed predators (CARDINA *et al.* 1996), because of the chemical compounds in the seed coat. Alternatively, it may be that the effect of imbibition on the hardness or thickness of the seed coat (LUNDGREN & ROSENTRATER 2007), is to soften the seed coat making penetration by the carabids relatively easier. The seeds of *S. media* have stronger and harder seed coats than *T. officinale*, which may partly explain the higher predation of seeds of *T. officinale* observed. Another mechanism may be related to the chemical properties of seeds which are not changed during imbibition, such as the volatile compounds (PAULSEN *et al.* 2013), waxes and other secondary metabolites that are present (JANZEN 1982). Both mechanisms may also explain the increase in consumption in the case of imbibed seeds with damaged coats. It is possible that the handling time of these seeds by the carabids was shorter (MIKHEEV & WANZENBÖCK 2010), although this was not measured in our study.

On average, after one day of seed exposure, consumption by *P. melanarius* was 3.44 seeds of *T. officinale* and 1.9 seeds of *S. media*, and that by *P. cupreus* was 2.46 seeds of *T. officinale* and 0.3 seeds of *S. media*. The daily consumption of *T. officinale* is lower than observed by (PETIT *et al.* 2014). The consumption rates observed here could be negatively affected by the relatively late time of the year that the experiment was conducted in October. Although the experiment was carried out in the laboratory, the beetles were collected in the field near the end of their period of seasonal activity. The predation rate has been found both to be low in the winter months (CARDINA *et al.* 1996) and to decline from late summer (HONEK *et al.* 2003). The season of the experiment could also affect the consumption by the different beetle sexes (HONEK *et al.* 2006) because in the autumn females no longer need energy for reproduction.

Current information about carabid selection for seeds with different geographical origin is limited. HONEK *et al.* (2011) demonstrated that the locale of seed origin played an important role in preferences of carabids. In our study, the origin of the seed significantly affected seed consumption and preferences by both species of carabids (Tables 1 & 2). The French beetles used in our study preferred French seeds; unfortunately, we could not make the same comparison with Czech beetles since these were not available at the time of the experiment. Differential consumption by origin might be explained by micro-species of plants (MOGIE & FORD 1988). Perhaps seeds from particular geographical regions differ e.g. in starch (WIDMER *et al.* 2007) or oil content (HE *et al.* 2020) to which local carabids respond, and this aspect of seed-predator interaction deserves further attention.

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