Diversity of foraging strategies and responses to predator interference in seed-eating carabid beetles

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Abstract

The prediction of pest regulation by multi-predator communities often remains challenging because of variable and opposite effects of niche complementarity and predator interference. Carabid communities are regulating weeds in arable fields and include a mix of species ranging from granivores to predators that are obligate omnivores. It is not clear from field studies whether granivore and obligate omnivore species either contribute equally or are complementary in the process of weed suppression, and little is known about the impact of potential predator interference within carabid communities on weed suppression. We compared the weed seed foraging strategy of the granivore *Harpalus affinis* and the obligate omnivore *Poecilus cupreus*. Using no-choice test experiments, we compared their activity and seed acceptance for four weed species through a scoring of the proportion of tested individuals consuming weeds, their latency before the consumption of the first seed and the total number of seeds consumed. We then evaluated their seed acceptance for dandelion seed *Taraxacum officinale* under predator interference by using chemical cues of carabids and tested the impact of three treatments, namely cues of intraspecific competition, interspecific competition and intraguild predation. We found that the obligate omnivore *P. cupreus* was highly active, had a low latency before consuming its first seed but had an interest in only two of the four weed species. *P. cupreus* seed acceptance remained unchanged in the presence of predator cues. By contrast, *H. affinis* was slow to start its seed consumption, accepted equally seeds of the four weed species and significantly increased its seed consumption in the presence of cues mimicking intraguild predation. These findings indicate that the two species differ in their foraging strategies, and as such, could have different contributions to weed seed suppression. This novel result calls for further studies documenting the foraging strategy of carabid species that thrive in arable fields as this could significantly improve our understanding of the delivery of weed seed regulation.

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Introduction

The prediction of pest regulation by multi-predator communities remains difficult, notably because of the variable effects, both positive and negative, of generalist predator diversity on biocontrol that can arise either from predator niche complementarity or from predator interference (Straub, Finke, & Snyder 2008; Tylianakis & Romo 2010; Crowder & Jabbour 2014). Assessing the relative importance of both processes within predator communities could provide an explanatory mechanism for a relationship between predator diversity and the ecosystem function of biological control (Loreau 2001; Hines et al. 2015).

Seed-eating carabid beetles are common and abundant predators that contribute to weed control in arable fields (Bohan, Boursault, Brooks, & Petit 2011; Kulkarni, Dosdall, & Willenborg 2015). Differences in the relative importance of plant vs. animal prey in their diet mean that species can be placed along a continuum between more granivorous species that only feed occasionally on animal prey (i.e. opportunistic omnivores) to predators feeding both on plant and animal food (i.e. obligate omnivores) (Hengeveld 1979; Deroulers & Bretagnolle 2018). Granivore and obligate omnivore species coexist within carabid communities of arable fields, but the relative contribution of species exhibiting one diet or the other to weed suppression has not yet been resolved. Field studies analysing the links between carabid communities and co-occurring rates of seed predation have produced equivocal results. Some field studies demonstrated strong relationships between total seed-eating carabid abundance and seed predation rates (O'Rourke, Heggenstaller, Liebman, & Rice 2006; Menalled, Smith, Dauer, & Fox 2007; Petit, Trichard, Biju-Duval, McLaughlin, & Bohan 2017), suggesting that granivore and obligate omnivore species might contribute relatively equally to weed regulation and that predator interference is of limited importance. Other studies have highlighted the major role of granivore abundance (Trichard, Alignier, Biju-Duval, & Petit 2013; Diekötter, Wamser, Dörner, Wolters, & Birkhofer 2016) or, conversely, of obligate omnivore abundance (Bohan et al. 2011; Jonason, Smith, Bengtsson, & Birkhofer 2013). There is also field evidence that carabid species richness and/or diversity can be better predictors of seed predation rates than carabid abundances (Gaines & Gratton 2010; Jonason et al. 2013; Trichard et al. 2013), suggesting that there could be some level of complementarity between carabid species in weed regulation. These apparent contradictory findings might result from context-dependency, being determined by the composition of the carabid communities and the focal weed prey species. If we are to manage arable systems to promote weed regulation through changes in carabid communities, it appears necessary to clarify the relative contribution of granivore and obligate omnivore species to seed predation.

In controlled conditions, two key specific aspects may affect weed seed acceptance by a carabid species. First, one can hypothesise that an obligate omnivore species has a metabolic physiology that is not well adapted to the consumption and digestion of many different species of weed seeds (Lundgren & Lehman 2010) even if it requires seeds as food to increase its fitness (Saska & Jarošík 2001; Kulkarni et al. 2015). By contrast, a granivore species, being well-adapted to digesting plant material, might accept a wider range of weed seed species than an obligate omnivore species. Second, several studies indicate that predator interference is common among seed-eating carabid species, as evidenced in several studies using either true individuals (Griffith & Poulson 1993; Currie, Spence, & Niemelä 1996) or chemical cues (Guy, Bohan, Powers, & Reynolds 2008; Charalabidis, Dechaume-Moncharmont Petit, & Bohan 2017) to mimic predator interference. This might mean that the effort and time that an individual will invest in foraging for an acceptable feeding item will change according to the perceived intensity and risk of predator interference (Metcalfe, Huntingford, & Thorpe 1987; Ibrahim & Huntingford 1989; Jennions & Petrie 1997; Amita, Kawamori, & Matsushima 2010; Davis, Nufio, & Papaj 2011; Dechaume-Moncharmont, Brom, & Cézilly 2016). The impact of predator interference on prey consumption in carabids has rarely been documented and existing studies have produced equivocal results. Predator interference has been found to reduce per capita consumption of animal prey by carabids (Griffith & Poulson 1993; Lang, Rall, & Brose 2012), while predation risk has been shown to increase the consumption of weed seeds by carabids (Charalabidis et al. 2017) and vertebrate predators (Blubaugh, Widick, & Kaplan 2017).

In this study, our aim was to investigate the existence of distinct foraging strategies in seed-eating carabids. Using no-choice experiments in laboratory microcosms, we characterised the foraging strategies of two seed-eating carabid species common in European arable fields, the granivore *Harpalus affinis* (Fabricius 1775) and the obligate omnivore *Poecilus cupreus* (Linnaeus, 1758). In our first experiment, we estimated seed acceptance in pairwise combinations of the two carabid species and four model weed species. We scored the proportion of individuals consuming weeds, individual latency to first seed acceptance, counts of seeds consumed and shelter use over 1 h and, additionally, counts of seeds consumed and shelter use after 13 h. We expected the two carabid species to differ in their pattern of seed acceptance. In our second experiment, we evaluated the impact of predator or competitor cues on seed acceptance of the two carabid species for seeds of *Taraxacum officinale* by comparing seed acceptance during 1 h under four treatment levels, i.e. no predator or competitor cues (control), intraspecific competition cues, interspecific competition cues and intraguild predation cues. Here we, expected the two carabid species to differ in their response to predator and competitor cues.

Materials and methods

The study system

The obligate omnivore, *P. cupreus* (∼11–12 mm), and the granivorous *H. affinis* (∼9–12 mm), are both medium-sized spring-breeding carabids that are common in arable fields. The four weed species, *Capsella bursa-pastoris* (L.) Medik. (dry weight 0.1 mg, length 0.8 mm), *Senecio vulgaris* L. (0.2 mg, 1.75 mm), *T. officinale* Weber (0.7 mg, 2.67 mm), *Viola arvensis* Murray (0.9 mg, 1.36 mm) were collected locally. These weeds are common in farmland and readily consumed by both carabid species, both in field and laboratory conditions (Petit, Boursault, & Bohan 2014; Trichard, Ricci, Ducourtieux & Petit 2014). For the experiments using predator and competitor cues, the granivorous *Pseudoophonus rufipes* (De Geer 1774, 11–16 mm) was chosen as the competitor species for both our focal species while *Pterostichus melanarius* (Illiger 1798, 12–19 mm), an obligate omnivore which also preys on other carabids (Currie et al. 1996) was chosen as the predator species.

Carabids were collected from traps, placed in rearing boxes and reared in controlled conditions (19 °C ± 1 °C, 60% humidity, 14:10 light:dark cycle). The rearing boxes were filled with field soil and a moistened paper tissue sheet. Water was provided ad libitum in an Eppendorf tube containing moistened cotton wool. The carabid species were held in separate boxes to prevent interspecific predation (Currie et al. 1996). At least 2 weeks prior to experimentation the boxes were moved to different rooms to prevent exposure and habituation to interspecific chemical signatures. Individuals were fed with the four tested weed seed species and the obligate omnivores were presented with *Tenebrio molitor* larva and frozen beef as an additional meat diet. Individuals were starved for 54 h prior to testing to produce individuals motivated to feed. Preliminary experimentation had shown that the 54 h duration did not affect survival or locomotory behaviours.

All seeds used in the experiments were soaked in clean water for 14 h prior to each experimental test, to become more palatable to and detectable by carabids (Law & Gallagher 2015).

General experimental design

We used no-choice tests, where only one seed species was presented to individuals (Dougherty & Shuker 2014). No-choice tests are widely used in behavioural ecology and assess the absolute acceptance level of a food item (Jennions & Petrie 1997; Rodríguez & Greenfield 2003; Murray, Withers, & Mansfield 2010; Rothbart & Hennig 2012; Reinhold & Schielzeth 2014). This method was selected over choice tests (cafeteria tests) because these only provide comparative estimates of acceptance of a food item. The experimental methodology of choice tests can artificially decrease or increase the attractiveness of a given food item, through a contrast effect with other items offered simultaneously (Raffa, Havill, & Nordheim 2002; Underwood, Chapman, & Crowe 2004; Larrinaga 2010; Murray et al. 2010; Dougherty & Shuker 2014; Edward 2014).

Experiments were conducted in a controlled room at 19 °C ± 1 °C and 60% humidity. Each individual was tested alone and once. To avoid a potential effect of date/hour and the status of individuals, all treatments and both sexes were tested each day in a random order. To avoid any possible behavioural modification via volatile olfactory cues, the two carabid species were always tested on separate days.

Acceptance of weed seeds without olfactory disturbance

Experimental setting

Individuals were placed in small plastic arenas (9 × 5 cm diameter × height) which contained a moist paper tissue (hiding place), water provided ad libitum and 20 seeds evenly positioned and were monitored for 13 h. We tested a total of 80 *H. affinis* and 72 *P. cupreus*, respectively. The number of males and females tested for each weed species is presented in Table 1.

During the first hour, we recorded: (i) the proportion of individuals eating; (ii) the latency to first seed acceptance, as the time from the first movement of an individual until it accepts the first seed; (iii) the number of seeds consumed; and, (iv) individual shelter usage, as the total number of sampling time points where individuals were under the moist paper tissue (head not visible). In addition, the number of seeds consumed and individual shelter usage were recorded at 2 h, 3 h, 4 h, 5 h, and 13 h. Damaged seeds and the debris from eaten seeds were removed at each sampling time point to avoid double accounting.

Statistical analysis

The proportion of individuals eating and/or using a shelter (i.e shelter usage) were modelled with generalized linear models using a binomial distribution. If the seed species effect was significant, the difference between seed species was analysed using exact Fisher's test for the null hypothesis of odds-ratio OR=1 based on the 'twoby2' function from 'Epi' package (Carstensen, Plummer, Laara, & Hills 2017). Latency to first seed acceptance was analysed using Cox proportional hazard models in the 'cox.ph' function from the 'survival' package (Therneau 2015) and effect size indices and the corresponding 95% confidence intervals reported to allow meta-analysis or comparisons in future studies (Nakagawa & Cuthill 2007; Lakens 2013). The measure of effect size for all latencies was the hazard ratio estimated as the exponential of the regression coefficient, exp(beta), of the Cox model (Dechaume Moncharmont, Decourtye, Hennequet-Hantier, Pons, & Pham-Delègue 2003). The total number of seeds consumed was analysed using beta regres-

Table 1. Acceptance of weed seeds without olfactory disturbance: Observed mean and SE per carabid species and sex during the first hour of test for the four species of weeds.

	Poecilus cupreus		Harpalus affinis	
	Males	Females	Males	Females
T. officinale				
# individuals tested	9	9	10	10
% individuals consuming	89 (±11)	89 (±11)	40 (±16)	10 (±10)
Latency 1st seed (seconds)	809 (±395)	1026 (±470)	2455 (±489)	3392 (±207)
Mean # seeds consumed	5.6 (±1)	5.2 (±1.1)	3.6 (±1.6)	0.4(±0.4)
Shelter use (%)	22 (±15)	11 (±11)	50 (±17)	90 (±10)
S. vulgaris				
# individuals tested	9	9	10	10
% individuals consuming	78 (±15)	67 (±17)	40 (±16)	18 (±12)
Latency 1st seed (seconds)	1519 (±500)	1519 (±546)	2502 (±496)	3348 (±181)
Mean # seeds consumed	6.9 (±1.8)	6.7 (±2.2)	2.4 (±1.2)	0.4 (±0.3)
Shelter use (%)	11 (±11)	11 (±11)	50 (±17)	82 (±12)
V. arvensis				
# individuals tested	9	9	10	10
% individuals consuming	100	89 (±11)	20 (±13)	22 (±15)
Latency 1st seed (seconds)	566 (±159)	1186 (±362)	3200 (±276)	3265 (±259)
Mean # seed consumed	3.9 (±1.1)	2.3 (±0.8)	0.6 (±0.3)	0.8 (±0.7)
Shelter use (%)	0 (±0)	22 (±15)	50 (±17)	78 (±15)
C. bursa-pastoris				
# individuals tested	9	9	10	10
% individuals consuming	33 (±17)	22 (±15)	20 (±13)	10 (±10)
Latency 1st seed (seconds)	2531 (±538)	3038 (±383)	2974 (±420)	3563 (±37)
Mean # seeds consumed	1.4 (±1)	3.1 (±2.1)	1.8 (±1.2)	0.3 (±0.3)
Shelter use (%)	11(±11)	22 (±15)	60 (±16)	80 (±13)

sions with the function 'betareg' from the 'betareg' package (Cribari-Neto & Zeileis 2010). If the weed species effect was significant, differences between specific pairs of weeds were tested using post-hoc multiple comparisons with Tukey adjustment. Data were analysed in R version 3.3.2 (R Development Core Team 2016).

Effect of predator and competitor cues on seed acceptance

Experimental setting

The experiment was conducted on *P. cupreus* and results were compared with those obtained for *H. affinis*, reported in Charalabidis et al. (2017). Using the method of Armsworth, Bohan, Powers, Glen, and Symondson (2005), predators and competitors were simulated with chemical cues. It has been shown that walking carabids leave olfactory cues along their path of movement and that these cues can induce behavioural change in carabids and in their prey (Armsworth et al. 2005; Guy et al. 2008; Charalabidis et al. 2017). This method was preferred over the use of actual competitors or predators which would have not allowed to separate the weed seed consumption of the focal individual from that of the competitor or predator. Moreover, mating-related behaviours, which might have occurred in the intraspecific competition treat-

ment, or predatory interactions, which might have occurred in the predation treatment, would have distracted individuals from foraging.

Predator and competitor cues were simulated by placing in the arena a white filter paper impregnated with non-volatile cuticular carabid hydrocarbon chemical cues using the method of Armsworth et al. (2005). To produce an appropriate level of stimulus on the filter paper (Guy et al. 2008), 20 carabids (10 females and 10 males) were released to walk over the papers for 24 h (Armsworth et al. 2005). Chemical cues from either *H. affinis* or *P. cupreus*, or *P. rufipes* or *P. melanarius* were used to simulate respectively intraspecific competition, interspecific competition and intraguild predation. For the control treatment clean test papers, with no carabid chemical cues, were used.

Individuals were tested in 18 cm diameter arenas, namely a petri dish positioned on the filter paper on which 20 seeds of *T. officinale* were arranged in two concentric circles of 10 seeds of respectively 5 and 16 cm diameter.

As experiments were conducted during the reproductive season of carabids, cues left by conspecifics on the impregnated paper of the intraspecific competition treatment could also be perceived as sexual olfactory cues and could induce mating-related behaviours and distract individuals from foraging. In order to disentangle the behaviours due to perceived

Table 2. Effect of predator and competitor cues on seed acceptance: observed mean (and SE) per carabid species and sex for each olfactory cues treatment. Values for *H. affinis* are derived from Charalabidis et al. (2017) .

| | *Poecilus cupreus* | | *Harpalus affinis* | |
	Males	Females	Males	Females
Control				
# individuals tested	35	36	39	31
% individuals consuming	86 (±6)	72 (±7)	36 (±8)	42 (±9)
Handling time (seconds)	750 (±95)	563 (±143)	397 (±60)	335 (±24)
Latency 1st seed (seconds)	1007 (±211)	1617 (±246)	2533 (±249)	2158 (±313)
Mean # seed consumed	3.0 (±0.4)	3.3 (±0.5)	1.6 (±0.5)	2.2 (±0.5)
% of space used	62 (±4)	74 (±3)	64 (±3)	67 (±3)
Intraspecific competition				
# individuals tested	36	36	39	32
% individuals consuming	72 (±7)	61 (±8)	46 (±8)	53 (±9)
Handling time (seconds)	717 (±118)	608 (±75)	511 (±69)	354 (±41)
Latency 1st seed (seconds)	1355 (±249)	1756 (±262)	2090 (±278)	1784 (±313)
Mean # seed consumed	2.9 (±0.4)	2.6 (±0.4)	1.2 (±0.3)	1.5 (±0.4)
% of space used	63 (±3)	66 (±3)	59 (±3)	58 (±3)
Interspecific competition				
# individuals tested	36	36	43	32
% individuals consuming	86 (±6)	72 (±8)	46 (±8)	50 (±9)
Handling time (seconds)	614 (±55)	421 (±55)	493 (±65)	281 (±25)
Latency 1st seed (seconds)	1034 (±211)	1418 (±245)	2135 (±256)	1915 (±308)
Mean # seed consumed	3.1 (±0.3)	2.7 (±0.4)	1.4 (±0.3)	2.4 (±0.6)
% of space used	67 (±3)	70 (±3)	67 (±3)	71 (±3)
Predation				
# individuals tested	36	36	43	31
% individuals consuming	75 (±7)	72 (±8)	60 (±7)	71 (±8)
Handling time (seconds)	665 (±80)	529 (±60)	430 (±54)	361 (±28)
Latency 1st seed (seconds)	1162 (±243)	1558 (±244)	1527 (±261)	1070 (±296)
Mean # seed consumed	3.1 (±0.4)	2.6 (±0.4)	3.0 (±0.5)	3.3 (±0.7)
% of space used	68 (±3)	71 (±4)	68 (±3)	64 (±3)

food competitors from those due to perceived sexual competitors, we treated interspecific competition as a control for these potential sexual olfactory interactions. Test individuals were placed under a plastic pot at the centre of the arena for 8 min prior to the start of each replicate test, the pot was then removed and the test individuals were observed and filmed for one hour using a monochrome video camera (Imaging Source DMK 31AU03) suspended over the arena. A total of 287 *P. cupreus* individuals were split into four treatment groups: control, intraspecific competition, interspecific competition and predation. Results were compared to those obtained with 290 *H. affinis* individuals split into similar groups and reported in Charalabidis et al. (2017). The numbers of males and females tested in each treatment are presented in Table 2.

After 1 h, seed acceptance was assessed by scoring: i) the proportion of individuals that had consumed at least one seed; ii) the latency to first seed acceptance; and, iii) the number of seeds consumed. The videos were used to score seed handling time, measured as the duration of consumption of a single seed, and individual space use evaluated in Ethovision (Noldus Information Technology, Wageningen, The Nether-

lands) as the number of 1×1 cm cells of the arena visited at least once.

Statistical analyses

Latency to first seed acceptance and seed handling time were analysed, as before, using the Cox proportional hazard models. The total number of seeds consumed was modelled as a generalized linear model assuming a negative binomial distribution with zero-inflation, in the 'zeroinfl' function from the 'pscl' package (Jackman 2015). Individual space use was analysed using ANOVA. For each analysis, sex effect and treatment interactions were tested. Data were analysed in R version 3.3.2 (R Development Core Team 2016).

Results

Acceptance of weed seeds without olfactory disturbance

Estimates for the variables recorded during the first hour of the experiment are presented in Table 1. Potential sex

effects and of interactions between sex and weed species are presented in the appendices (see Appendix A: Table 1 in Supplementary material) and are mentioned in the text where the results are significant.

For *P. cupreus*, the proportion of individuals consuming seeds differed between weed species ($\chi^2 = 24.41$, df = 3, P < 0.001) and was lower for *C. bursa-pastoris* than for *S. vulgaris* (P = 0.016), *T. officinale* (P = 0.0042) and *V. arvensis* (P = 0.002) (see Appendix A: Table 2 in Supplementary material). Individuals accepted their first seed of *C. bursa-pastoris* significantly later than in *S. vulgaris* (P = 0.0085), *T. officinale* (P < 0.001) and *V. arvensis* (P < 0.001) (see Appendix A: Table 3 in Supplementary material). The amount of seeds consumed differed between weed species during the first hour ($\chi^2 = 11.58$, df = 3, P = 0.0090, Fig. 1), with more *T. officinale* consumed than *C. bursa-pastoris* (P = 0.013, see Appendix A: Table 4 in Supplementary material). There was also a significant difference at 13 h ($\chi^2 = 41.17$, df = 3, P < 0.001, Fig. 1) for pairs of weed species (see Appendix A: Table 4 in Supplementary material). *T. officinale* was consumed more than *C. bursa pastoris* (P < 0.001) and *V. arvensis* (P < 0.001) while *S. vulgaris* was consumed more than *C. bursa-pastoris* (P < 0.001) and *V. arvensis* (P = 0.001). Females used the shelter more than males ($\chi^2 = 8.45$, df = 1, P = 0.0036) and shelter usage was not affected by the weed species ($\chi^2 = 1.26$, df = 3, P = 0.74), with no interaction between weed species and sex of individuals ($\chi^2 = 5.76$, df = 3, P = 0.12).

For *H. affinis*, the weed species did not affect either the proportion of individuals eating ($\chi^2 = 1.33$, df = 3, P = 0.72), the latency to first seed consumption ($\chi^2 = 1.56$, df = 3, P = 0.67), or the mean amount of seeds consumed in the first hour ($\chi^2 = 0.66$, df = 3, P = 0.88, Fig. 1) and at 13 h ($\chi^2 = 4.74$, df = 3, P = 0.19, Fig. 1). Females used the shelter more than males ($\chi^2 = 54.12$, df = 1, P < 0.001) and shelter usage was not affected by the weed species ($\chi^2 = 2.04$, df = 3, P = 0.56) with no interaction between weed species and sex of individuals ($\chi^2 = 2.83$, df = 3, P = 0.42).

The two carabid species differed in their seed acceptance for the four weed species in the first hour and at 13 h. In the first hour, the proportion of individuals of *P. cupreus* that had consumed *S. vulgaris* ($\chi^2 = 7.64$, df = 1, P = 0.0057), *V. arvensis* ($\chi^2 = 17.21$, df = 1, P < 0.001) and *T. officinale* ($\chi^2 = 23.33$, df = 1, P < 0.001) was higher than that of *H. affinis*. The two carabid species differed in their latency to first seed acceptance ($\chi^2 = 48.77$, df = 1, P < 0.001) with *P. cupreus* accepting the first seed earlier than *H. affinis* for the four weed species (hazard ratio for *P. cupreus* compared with *H. affinis* = 6.1, 95%CI = [3.52, 10.60], P < 0.001). At the end of the experiment, *H. affinis* had consumed more weed seeds than *P. cupreus* ($\chi^2 = 17.67$, df = 1, P < 0.001), with mean amounts of 14.6 and 11 seeds at 13 h, respectively. The two carabids also differed in their mean consumption of specific weed seeds ($\chi^2 = 9.08$, df = 3, P = 0.028). *H. affinis* consumed more seeds of *C. bursa-pastoris* ($\chi^2 = 20.72$, df = 1, P < 0.001) and *V. arvensis* ($\chi^2 = 12.17$, df = 1, P < 0.001) than *P. cupreus*. Conversely, *P. cupreus* consumed more seeds of *T. officinale*

($\chi^2 = 16.37$, df = 1, P < 0.001) than *H. affinis*. The two carabid species did not differ in their mean consumption of *S. vulgaris* ($\chi^2 = 0.23$, df = 1, P = 0.63). *H. affinis* females ($\chi^2 = 156.33$, df = 1, P < 0.001) and males ($\chi^2 = 71.55$, df = 1, P < 0.001) used the shelter more often than *P. cupreus* individuals.

Effect of predator and competitor cues on seed acceptance

Variable estimates per carabid species and sex for each treatment are presented in Table 2. Results for potential sex effect and interactions between sex and the treatments are presented in Appendix A: Table 5 in Supplementary material.

For *P. cupreus*, irrespective of treatment, the proportion of males consuming seeds was higher than that of females ($\chi^2 = 4.1$, df = 1, P = 0.04). Females accepted their first seed later ($\chi^2 = 8.09$, df = 1, P = 0.004), consumed seeds faster ($\chi^2 = 7.8$, df = 1, P = 0.005) and had a higher space use ($F_{1,285} = 4.33$, P = 0.038) than males. Treatment had no significant effect on the proportion of individuals consuming seeds ($\chi^2 = 3.91$, df = 3, P = 0.27), the latency to first seed acceptance ($\chi^2 = 1.99$, df = 3, P = 0.57, Fig. 2A), the mean amount of seeds consumed ($\chi^2 = 5.10$, df = 6, P = 0.53, Fig. 2B), seed handling time ($\chi^2 = 3.46$, df = 3, P = 0.32) and space use ($F_{1,283} = 0.73$, P = 0.53).

For comparison, identical analyses conducted on *H. affinis* and reported in Charalabidis et al. (2017) were as follows. Irrespective of treatment, *H. affinis* females consumed more seeds than males ($\chi^2 = 16.45$, df = 1, P < 0.001). A treatment effect was observed on the proportion of individuals consuming weeds ($\chi^2 = 10.62$, df = 3, P = 0.014), the latency to first seed consumption ($\chi^2 = 12.6$, df = 3, P < 0.001, Fig. 2A), the total number of seeds consumed ($\chi^2 = 17.22$, df = 6, P = 0.0085, Fig. 2B). More individuals consumed weed seeds with predator cues than in the control (P = 0.0025, odds-ratio = 2.94, 95%CI = [1.49, 5.79]). Latency was lower with predator cues than in the other treatments (control: P < 0.001, hazard ratio = 2.22, 95%CI = [1.38, 3.56]; intraspecific competition: P = 0.032, hazard ratio = 1.59, 95%CI = [1.02, 2.47]; interspecific competition: P = 0.020, hazard ratio = 1.67, 95%CI = [1.08, 2.57], Fig. 2A). *H. affinis* consumed more seeds with predator cues than in the other treatments (control P = 0.030; intraspecific competition P = 0.031; interspecific competition P = 0.019 (Fig. 2B)) with a sex effect ($\chi^2 = 6.58$, df = 2, P = 0.037), but no interaction between sex and treatment ($\chi^2 = 1.47$, df = 6, P = 0.96). Handling time did not vary with treatment ($\chi^2 = 1.40$, df = 3, P = 0.71). Space use differed between treatments ($F_{3,257} = 3.95$, P = 0.0088) and was higher under interspecific competition than under intraspecific competition ($F_{3,257} = 3.36$, P = 0.019).

There was an effect of carabid species and treatment on the proportion of individuals consuming seeds ($\chi^2 = 8.82$, df = 3, P = 0.032). More individuals of *P. cupreus* consumed seeds in the control ($\chi^2 = 24.44$, df = 1, P < 0.001), intraspecific competition ($\chi^2 = 4.45$, df = 1, P = 0.035) and interspecific
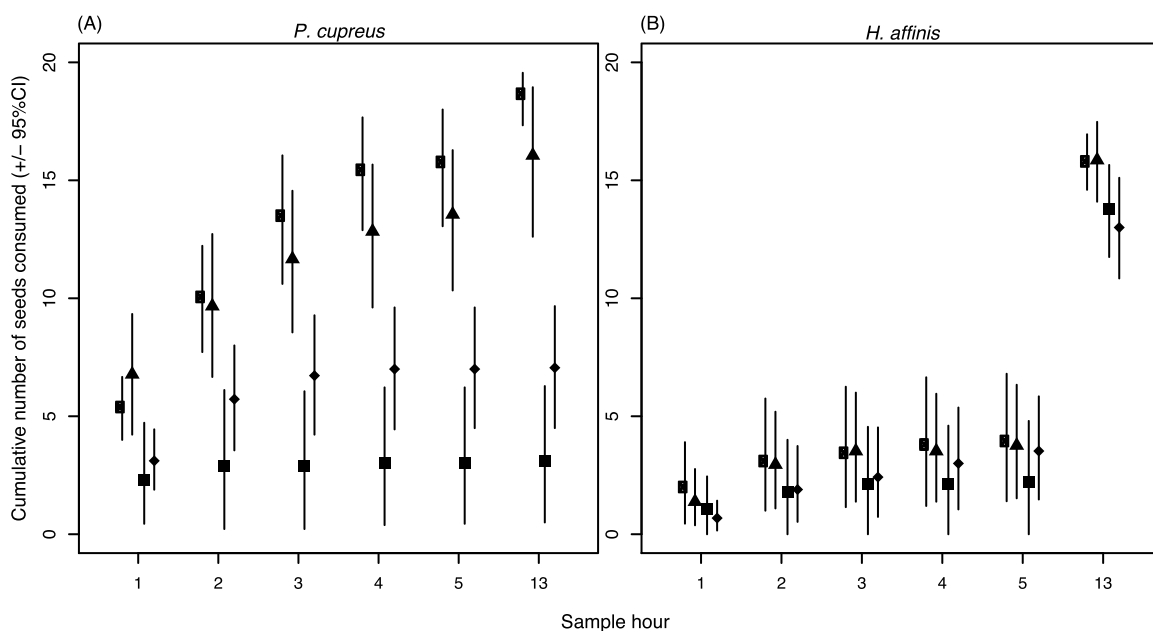
Fig. 1. Cumulative number of seeds consumed (bootstrapped ±95%CI) by *P. cupreus* (A) and *H. affinis* (B) individuals at each sample date for seeds of *T. officinale* (●), *S. vulgaris* (▲), *C. bursa-pastoris* (■) and *V. arvensis* (♦).

competition treatments than *H. affinis* ($\chi^2 = 15.77$, df = 1, P < 0.001). There was no significant difference in seed consumption by the two carabid species under predation ($\chi^2 = 1.31$, df = 1, P = 0.25). Latency to first seed acceptance differed between the two carabid species ($\chi^2 = 8.14$, df = 3, P = 0.043). *P. cupreus* started consuming seeds earlier than *H. affinis* in all four treatments (control: $\chi^2 = 28.76$, df = 1, P < 0.001; intraspecific competition: $\chi^2 = 4.51$, df = 1, P = 0.034; interspecific competition: $\chi^2 = 22.66$, df = 1, P < 0.001 and predation: $\chi^2 = 4.51$, df = 1, P = 0.034). Moreover, across treatments *P. cupreus* individuals spent more time handling seeds of *T. officinale* than individuals of *H. affinis* ($\chi^2_1 = 33.60$, df = 1, P < 0.001, results for the control: $\chi^2 = 8.46$, df = 1, P = 0.0036; predation: $\chi^2 = 12.60$, df = 1, P < 0.001; intraspecific competition: $\chi^2 = 7.65$, df = 1, P = 0.0057; interspecific competition: $\chi^2 = 4.45$, df = 1, P = 0.035). There was no interaction between carabid species and treatment ($\chi^2 = 2.26$, df = 3, P = 0.52). The proportion of space used did not differ between the two carabid species ($F_{1,543} = 3.06$, P = 0.08). There was no interaction between carabid species and treatment ($F_{3,540} = 0.51$, P = 0.67).

Discussion

Seed acceptance for four weed species

P. cupreus and *H. affinis* differed in their relative acceptance for the four weed species, with subsequent differences in seed diet breadth. *P. cupreus* exhibited a high level of seed acceptance for *T. officinale* and *S. vulgaris* seeds. Individuals accepted seeds earlier and ate more seeds, and a higher total

proportion of individuals consumed seeds. This high acceptance by *P. cupreus* for *T. officinale* and *S. vulgaris* might be explained by their ease of consumption. Conversely, the other two weed species were less accepted. We observed that *P. cupreus* individuals had difficulties handling seeds of *V. arvensis* and often lost these seeds; as a result, the initial interest of *P. cupreus* in *V. arvensis* declined dramatically after the first hour of the experiment, i.e. these seeds were subsequently discarded. The same behaviour was observed for seeds of *C. bursa-pastoris*. Ease of consumption could be explained by an allometric compatibility between the size of the mandibles of the carabid and the size of the seed species (Honek, Martinkova, Saska, & Pekar 2007). *P. cupreus* individuals might be too large (in comparison to *H. affinis)* to consume *V. arvensis* but can handle well seeds of *T. officinale* that are twice as long as those of *V. arvensis* for the same weight. The lack of interest of *P. cupreus* individuals in seeds of *V. arvensis* might also be explained by the lower digestibility of *V. arvensis* seeds (Hengeveld 1987; Lundgren & Lehman 2010; Schmid, Lehman, Brözel, & Lundgren 2014).

In contrast, the granivore *H. affinis* consumed all seed species similarly, with equal levels of seed acceptance. *Harpalini* species have been described as unspecialized feeders of seeds (Forsythe 1983; Acorn & Ball 1991; Zetto Brandmayr, Giglio, Marano, & Brandmayr 1998; Kulkarni et al. 2015) and *Harpalus* sp. have evolved broad mandibles with massive adductors that are able to readily crush seeds (Zetto Brandmayr et al. 1998; Paarmann, Faust, Arndt, Lüchtrath, & Rohe 2006). The greater ability of *H. affinis* to consume seeds, as compared to *P. cupreus*, is illustrated by a markedly different handling time for *T. officinale*, a
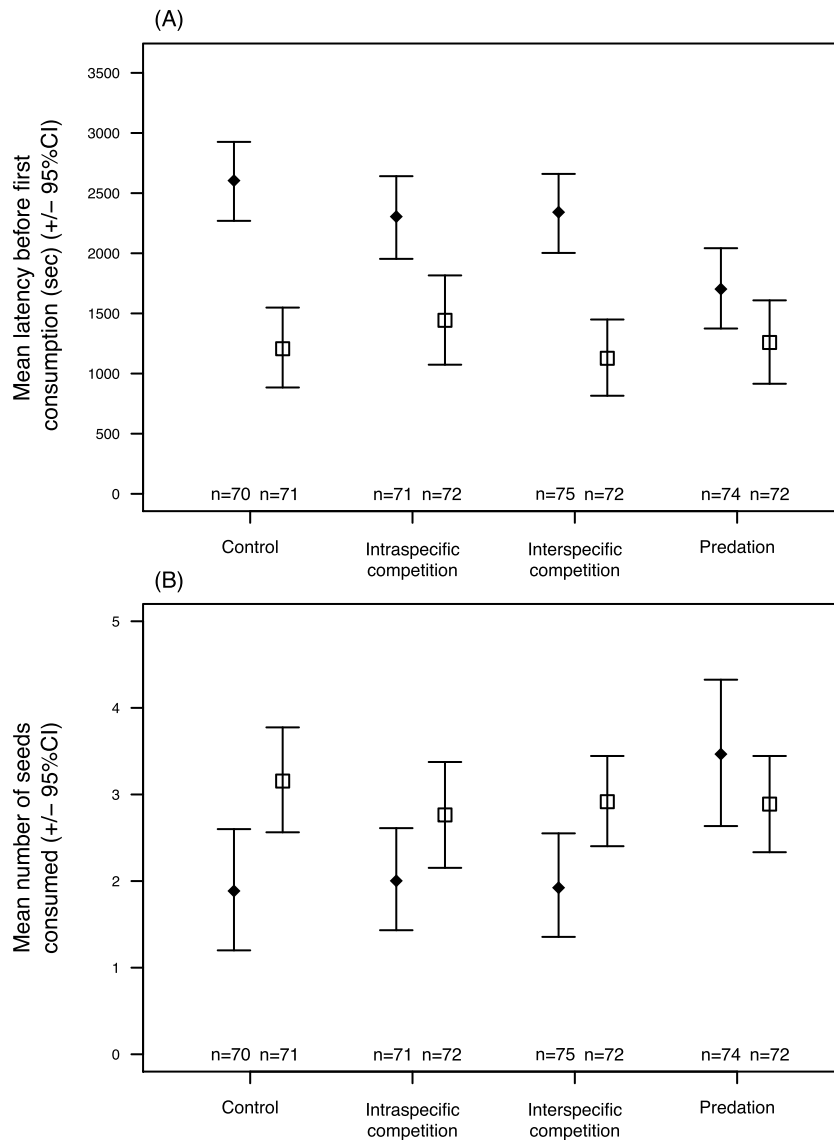
Fig. 2. (A) Mean latency to first seed acceptance (bootstrapped ±95%CI) in each treatment for *H. affinis* (♦) and *P. cupreus* (□), (B) mean number of seeds consumed (bootstrapped ±95%CI) by *H. affinis* (♦) and *P. cupreus* (□) individuals during the hour of the test in each treatment. The sample sizes are shown above the x-axis. Values for *H. affinis* are derived from Charalabidis et al. (2017).

weed otherwise preferred by *P. cupreus*. While *P. cupreus* consumed more seeds of *T. officinale* in total than *H. affinis* did, *P. cupreus* individuals had longer handling times for seeds of this weed. The ability of *H. affinis* individuals to feed on several species of seeds, regardless of their shape or size, is a benefit for a granivore, which subsists predominantly on seeds (Kamenova, Leroux, Polin, & Plantegenest 2017) and requires these food items throughout its period of activity. Discarding seeds might result in strong opportunity costs (Stephens 2008) either because of competition (Dechaume-Moncharmont et al. 2016) or because uneaten seeds enter the seed bank and become unavailable. Our study also showed that *H. affinis* was much slower at commencing the consumption of weed seeds than *P. cupreus*. During the first five hours of the first experiment, *P. cupreus* accepted

their first seed earlier and ate significantly more seeds than *H. affinis*, irrespective of the weed species, and a similar pattern was observed in the control treatment of the predator cue experiment. This apparent lower initial interest for seeds by *H. affinis* is unlikely to be due to the weed species offered, as these weed species have been found to be 'preferred' by *H. affinis* in multiple choice-test studies (Honek, Saska, & Martinkova 2006; Honek et al. 2007; Saska, Martinkova, & Honek 2010; Honek, Martinkova, & Saska 2011; Petit et al. 2014). Rather, the pattern might simply result from a lower activity in *H. affinis* than in *P. cupreus* (Thiele 1977). Smaller species, such as *H. affinis* have been found to be less active than larger species like *P. cupreus* (Greenslade 1964; Luff 1975; Lang 2000). We also observed that most *H. affinis*

individuals sought shelter and hid during the first experiment, with subsequently less time to forage actively for seeds.

Response to predator and competitive cues

As hypothesized, we detected contrasting responses to competitor and predator cues in the two carabid species. *P. cupreus* did not adjust its level of seed acceptance when facing predator cues. Conversely, *H. affinis* significantly increased its level of seed acceptance in the presence of predator cues, with individuals reducing their latency to first seed acceptance by half and almost doubling their mean seed consumption in comparison to the control treatment. This is consistent with other research showing an increase in seed acceptance in carabids exposed to predator cues (Blubaugh et al. 2017) and with the hypothesis that predator cues could increase acceptance of a food item (Metcalfe et al. 1987; Leaver & Daly 2003; Perea, González, San Miguel, & Gil 2011). In situations of predatory interference, individuals would tend to reduce the effort or energy used to assess a resource and therefore accept more of the encountered food items, irrespective of their quality. This ability to adjust feeding item acceptance when faced with a predation risk would enable *H. affinis* to maintain its feeding income, especially in arable situations where carabid predators such *P. melanarius* are common and abundant. In contrast, situations of intraspecific and interspecific competition triggered no behavioural adjustment in *H. affinis*, even if competition could expose individuals to the loss of reasonably good quality resource items (Dechaume-Moncharmont et al. 2016).

The lack of change in the level of seed acceptance by *P. cupreus* under competition may be related to its status as an obligate omnivore. Since *P. cupreus* can rely on both plant and animal prey we can speculate that under predation, individuals might always be able to switch to other food types that are not shared with the competitor, thus not requiring to increase their seed acceptance in order to maintain their energetic income. We would have expected a change in seed acceptance in response to a predation risk, since an encounter with a potential predator is more directly lethal than the opportunity costs resulting from competition. It is possible that *P. cupreus* perceived the olfactory cues of *P. melanarius* as cues of a potential feeding competitor, rather than that of a predator, as both species can act as carnivores (Brooks et al. 2012) and consume seeds (Lundgren 2009). It is also possible that the interest of *P. cupreus* in *T. officinale* seeds in the control treatment was already as high as possible, with individuals consuming any available seeds quickly and to satiety. Finally, we cannot exclude the possibility that while olfactory cues have proved useful to induce behavioural response in carabids (Guy et al. 2008), *P. cupreus* does not rely on olfactory cues alone to assess risks, but may rather rely on mechanical cues (Kratina, Vos, Bateman, & Anholt 2009). Hence, individuals may have not perceived odours as effective cues of risks in our study.

Implications of contrasted foraging strategies for weed biocontrol

The present study focused on two carabid species, an obligate omnivore and a granivore and provides evidence that the two species exhibit different seed foraging strategies. Although the two strategies described here cannot be generalised to the trophic guild level, the two carabid species tested here are the two most abundant species and often co-occur within carabid communities sampled regionally. As such, and provided that the strategies we observed in controlled conditions apply in field conditions, one can speculate that the two foraging strategies described here could coexist in arable fields. Although we observed that the two strategies overlap, as shown by the shared high interest of *P. cupreus* and *H. affinis* for dandelion seeds, they would also appear quite complementary in terms of the respective ranges of seed species eaten, and in terms of timing of seed consumption. Future studies characterizing the foraging strategies of granivore and obligate omnivore carabid species should assess whether the two strategies described here are generic and/or if other foraging strategies exist in seed-eating carabid beetles. Gaining such knowledge would enable scientists to test for potential behaviourally-based niche complementarity in seed-eating carabid assemblages and to quantify its effect on seed suppression.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.baae.2019.02.003.

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