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

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18 **Abstract**

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

43 **Keywords:** Weed regulation; trophic guild; seed acceptance; latency; predation risk;

44 competition.

45

46 **Introduction**

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

55 Seed-eating carabid beetles are common and abundant predators that contribute to
56 weed control in arable fields (Bohan, Boursault, Brooks, & Petit, 2011; Kulkarni, Dossall, &
57 Willenborg, 2015). Differences in the relative importance of plant vs. animal prey in their diet
58 mean that species can be placed along a continuum between more granivorous species that
59 only feed occasionally on animal prey (i.e. opportunistic omnivores) to predators feeding both
60 on plant and animal food (i.e. obligate omnivores) (Deroulers & Bretagnolle, 2018;
61 Hengeveld, 1979). Granivore and obligate omnivore species coexist within carabid
62 communities of arable fields, but the relative contribution of species exhibiting one diet or the
63 other to weed suppression has not yet been resolved. Field studies analysing the links between
64 carabid communities and co-occurring rates of seed predation have produced equivocal
65 results. Some field studies demonstrated strong relationships between total seed-eating
66 carabid abundance and seed predation rates (Menalled, Smith, Dauer, & Fox, 2007;
67 O'Rourke, Heggenstaller, Liebman, & Rice, 2006; Petit, Trichard, Biju-Duval, McLaughlin,
68 & Bohan, 2017), suggesting that granivore and obligate omnivore species might contribute
69 relatively equally to weed regulation and that predator interference is of limited importance.
70 Other studies have highlighted the major role of granivore abundance (Diekötter, Wamser,

71 Dörner, Wolters, & Birkhofer, 2016; Trichard, Alignier, Biju-Duval, & Petit, 2013) or,
72 conversely, of obligate omnivore abundance (Bohan et al., 2011; Jonason, Smith, Bengtsson,
73 & Birkhofer, 2013). There is also field evidence that carabid species richness and/or diversity
74 can be better predictors of seed predation rates than carabid abundances (Gaines & Gratton,
75 2010; Jonason et al., 2013; Trichard et al., 2013), suggesting that there could be some level of
76 complementarity between carabid species in weed regulation. These apparent contradictory
77 findings might result from context-dependency, being determined by the composition of the
78 carabid communities and the focal weed prey species. If we are to manage arable systems to
79 promote weed regulation through changes in carabid communities, it appears necessary to
80 clarify the relative contribution of granivore and obligate omnivore species to seed predation.
81 In controlled conditions, two key specific aspects may affect weed seed acceptance by a
82 carabid species. First, one can hypothesise that an obligate omnivore species has a metabolic
83 physiology that is not well adapted to the consumption and digestion of many different
84 species of weed seeds (Lundgren & Lehman, 2010) even if it requires seeds as food to
85 increase its fitness (Kulkarni et al., 2015; Saska & Jarošík, 2001). By contrast, a granivore
86 species, being well-adapted to digesting plant material, might accept a wider range of weed
87 seed species than an obligate omnivore species. Second, several studies indicate that predator
88 interference is common among seed-eating carabid species, as evidenced in several studies
89 using either true individuals (Griffith & Poulson, 1993; Currie et al., 1996) or chemical cues
90 (Charalabidis, Dechaume-Moncharmont, Petit, & Bohan, 2017; Guy, Bohan, Powers, &
91 Reynolds, 2008) to mimic predator interference. This might mean that the effort and time that
92 an individual will invest in foraging for an acceptable feeding item will change according to
93 the perceived intensity and risk of predator interference (Amita, Kawamori, & Matsushima,
94 2010; Davis, Nufio, & Papaj, 2011; Dechaume-Moncharmont, Brom, & Cézilly, 2016;
95 Ibrahim & Huntingford, 1989; Jennions & Petrie, 1997; Metcalfe, Huntingford, & Thorpe,

1987). 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; B. 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 hour and, additionally, counts of seeds consumed and shelter use after 13 hours. 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 *T. officinale* by comparing seed acceptance during 1 hour 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.

117

118 **Materials and Methods**

119

120 *The study system*

121

122 The obligate omnivore, *P. cupreus* (~11-12 mm), and the granivorous *H. affinis* (~9-
123 12 mm), are both medium-sized spring-breeding carabids that are common in arable fields.
124 The four weed species, *Capsella bursa-pastoris* (L.) Medik. (dry weight 0.1 mg, length 0.8
125 mm), *Senecio vulgaris* L. (0.2 mg, 1.75 mm), *Taraxacum officinale* Weber (0.7 mg, 2.67
126 mm), *Viola arvensis* Murray (0.9 mg, 1.36 mm) were collected locally. These weeds are
127 common in farmland and readily consumed by both carabid species, both in field and
128 laboratory conditions (Petit, Boursault, & Bohan, 2014; Trichard, Ricci, Ducourtieux, & Petit,
129 2014). For the experiments using predator and competitor cues, the granivorous
130 *Pseudoophonus rufipes* (De Geer 1774, 11-16 mm) was chosen as the competitor species for
131 both our focal species while *Pterostichus melanarius* (Illiger 1798, 12-19 mm), an obligate
132 omnivore which also preys on other carabids (Currie, Spence, & Niemelä, 1996) was chosen
133 as the predator species.

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

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

148

149 ***General experimental design***

150 We used no-choice tests, where only one seed species was presented to individuals
151 (Dougherty & Shuker, 2014). No-choice tests are widely used in behavioural ecology and
152 assess the absolute acceptance level of a food item (Jennions & Petrie, 1997; Murray,
153 Withers, & Mansfield, 2010; Reinhold & Schielzeth, 2014; Rodríguez & Greenfield, 2003;
154 Rothbart & Hennig, 2012). This method was selected over choice tests (cafeteria tests)
155 because these only provide comparative estimates of acceptance of a food item. The
156 experimental methodology of choice tests can artificially decrease or increase the
157 attractiveness of a given food item, through a contrast effect with other items offered
158 simultaneously (Dougherty & Shuker, 2014; Edward, 2014; Larrinaga, 2010; Murray et al.,
159 2010; Raffa, Havill, & Nordheim, 2002; Underwood, Chapman, & Crowe, 2004).

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

165

166 ***Acceptance of weed seeds without olfactory disturbance***

167

168 *Experimental setting*

169

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

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

182

183 *Statistical analysis*

184 The proportion of individuals eating and/or using a shelter (i.e shelter usage) were
185 modelled with generalized linear models using a binomial distribution. If the seed species
186 effect was significant, the difference between seed species was analysed using exact Fisher's
187 test for the null hypothesis of odds-ratio OR=1 based on the 'twoby2' function from 'Epi'
188 package (Carstensen et al., 2017). Latency to first seed acceptance was analysed using Cox
189 proportional hazard models in the 'cox.ph' function from the 'survival' package (Therneau,
190 2015) and effect size indices and the corresponding 95% confidence intervals reported to
191 allow meta-analysis or comparisons in future studies (Lakens, 2013; Nakagawa & Cuthill,
192 2007). The measure of effect size for all latencies was the hazard ratio estimated as the
193 exponential of the regression coefficient, $\exp(\beta)$, of the Cox model (Dechaume
194 Moncharmont, Decourtye, Hennequet-Hantier, Pons, & Pham-Delègue, 2003). The total

195 number of seeds consumed was analysed using beta regressions with the function ‘betareg’
196 from the ‘betareg’ package (Cribari-Neto & Zeileis, 2010). If the weed species effect was
197 significant, differences between specific pairs of weeds were tested using *post-hoc* multiple
198 comparisons with Tukey adjustment. Data were analysed in R version 3.3.2 (R Development
199 Core Team, 2016).

200

201 *Effect of predator and competitor cues on seed acceptance*

202

203 *Experimental setting*

204 The experiment was conducted on *P. cupreus* and results were compared with those obtained
205 for *H. affinis*, reported in Charalabidis et al. (2017). Using the method of Armsworth et al.
206 (2005), predators and competitors were simulated with chemical cues. It has been shown that
207 walking carabids leave olfactory cues along their path of movement and that these cues can
208 induce behavioural change in carabids and in their prey (Armsworth, Bohan, Powers, Glen, &
209 Symondson, 2005; Charalabidis et al., 2017; Guy et al., 2008). This method was preferred
210 over the use of actual competitors or predators which would have not allowed to separate the
211 weed seed consumption of the focal individual from that of the competitor or predator.
212 Moreover, mating-related behaviours, which might have occurred in the intraspecific competition
213 treatment, or predatory interactions, which might have occurred in the predation treatment, would
214 have distracted individuals from foraging.

215 Predator and competitor cues were simulated by placing in the arena a white filter paper
216 impregnated with non-volatile cuticular carabid hydrocarbon chemical cues using the method
217 of Armsworth et al., (2005). To produce an appropriate level of stimulus on the filter paper
218 (Guy et al., 2008), 20 carabids (10 females and 10 males) were released to walk over the
219 papers for 24h (Armsworth et al., 2005). Chemical cues from either *H. affinis* or *P. cupreus*,

220 or *P. rufipes* or *P. melanarius* were used to simulate respectively intraspecific competition,
221 interspecific competition and intraguild predation. For the control treatment clean test papers,
222 with no carabid chemical cues, were used.

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

226 As experiments were conducted during the reproductive season of carabids, cues left by
227 conspecifics on the impregnated paper of the intraspecific competition treatment could also be
228 perceived as sexual olfactory cues and could induce mating-related behaviours and distract
229 individuals from foraging. In order to disentangle the behaviours due to perceived food
230 competitors from those due to perceived sexual competitors, we treated interspecific
231 competition as a control for these potential sexual olfactory interactions. Test individuals
232 were placed under a plastic pot at the centre of the arena for 8 min prior to the start of each
233 replicate test, the pot was then removed and the test individuals were observed and filmed for
234 one hour using a monochrome video camera (Imaging Source DMK 31AU03) suspended over
235 the arena. A total of 287 *P. cupreus* individuals were split into four treatment groups: control,
236 intraspecific competition, interspecific competition and predation. Results were compared to
237 those obtained with 290 *H. affinis* individuals split into similar groups and reported in
238 Charalabidis et al. (2017). The numbers of males and females tested in each treatment are
239 presented in Table 2.

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

244 Information Technology, Wageningen, The Netherlands) as the number of 1 x 1 cm cells of
245 the arena visited at least once.

246

247 *Statistical analyses*

248

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

255

256

257 **Results**

258 *Acceptance of weed seeds without olfactory disturbance*

259

260 Estimates for the variables recorded during the first hour of the experiment are
261 presented in Table 1. Potential sex effects and of interactions between sex and weed species
262 are presented in the appendices (see Appendix A: Table 1) and are mentioned in the text
263 where the results are significant.

264 For *P. cupreus*, the proportion of individuals consuming seeds differed between weed
265 species ($\chi^2 = 24.41$, $df = 3$, $P < 0.001$) and was lower for *C. bursa-pastoris* than for *S. vulgaris*
266 ($P = 0.016$), *T. officinale* ($P = 0.0042$) and *V. arvensis* ($P = 0.002$) (see Appendix A: Table 2).
267 Individuals accepted their first seed of *C. bursa-pastoris* significantly later than in *S. vulgaris*
268 ($P = 0.0085$), *T. officinale* ($P < 0.001$) and *V. arvensis* ($P < 0.001$) (see Appendix A: Table 3).

269 The amount of seeds consumed differed between weed species during the first hour ($\chi^2 =$
270 11.58, df =3, P = 0.0090, Fig. 1), with more *T. officinale* consumed than *C. bursa-pastoris* (P
271 = 0.013, see Appendix A: Table 4). There was also a significant difference at 13 hours ($\chi^2 =$
272 41.17, df =3, P <0.001, Fig. 1) for pairs of weed species (see Appendix A: Table 4). *T.*
273 *officinale* was consumed more than *C. bursa pastoris* (P < 0.001) and *V. arvensis* (P < 0.001)
274 while *S. vulgaris* was consumed more than *C. bursa-pastoris* (P < 0.001) and *V. arvensis* (P =
275 0.001). Females used the shelter more than males ($\chi^2 = 8.45$, df = 1, P = 0.0036) and shelter
276 usage was not affected by the weed species ($\chi^2= 1.26$, df =3, P = 0.74), with no interaction
277 between weed species and sex of individuals ($\chi^2 = 5.76$, df =3, P = 0.12).

278 For *H. affinis*, the weed species did not affect either the proportion of individuals
279 eating ($\chi^2 = 1.33$, df =3, P = 0.72), the latency to first seed consumption ($\chi^2 = 1.56$, df =3, P =
280 0.67), or the mean amount of seeds consumed in the first hour ($\chi^2 = 0.66$, df =3, P = 0.88, Fig.
281 1) and at 13 hours ($\chi^2 = 4.74$, df =3, P = 0.19, Fig. 1). Females used the shelter more than
282 males ($\chi^2 = 54.12$, df =1, P < 0.001) and shelter usage was not affected by the weed species (χ^2
283 = 2.04, df =3, P = 0.56) with no interaction between weed species and sex of individuals ($\chi^2 =$
284 2.83, df =3, P = 0.42).

285 The two carabid species differed in their seed acceptance for the four weed species in the first
286 hour and at 13 hours. In the first hour, the proportion of individuals of *P. cupreus* that had
287 consumed *S. vulgaris* ($\chi^2 = 7.64$, df =1, P = 0.0057), *V. arvensis* ($\chi^2 = 17.21$, df =1, P < 0.001)
288 and *T. officinale* ($\chi^2 = 23.33$, df =1, P < 0.001) was higher than that of *H. affinis*. The two
289 carabid species differed in their latency to first seed acceptance ($\chi^2 = 48.77$, df =1, P < 0.001)
290 with *P. cupreus* accepting the first seed earlier than *H. affinis* for the four weed species
291 (hazard ratio for *P. cupreus* compared with *H. affinis* = 6.1, 95%CI= [3.52, 10.60], P <
292 0.001). At the end of the experiment, *H. affinis* had consumed more weed seeds than *P.*
293 *cupreus* ($\chi^2 = 17.67$, df =1, P < 0.001), with mean amounts of 14.6 and 11 seeds at 13 hours,

294 respectively. The two carabids also differed in their mean consumption of specific weed seeds
295 ($\chi^2 = 9.08$, $df = 3$, $P = 0.028$). *Harpalus affinis* consumed more seeds of *C. bursa-pastoris* ($\chi^2 =$
296 20.72 , $df = 1$, $P < 0.001$) and *V. arvensis* ($\chi^2 = 12.17$, $df = 1$, $P < 0.001$) than *P. cupreus*.
297 Conversely, *P. cupreus* consumed more seeds of *T. officinale* ($\chi^2 = 16.37$, $df = 1$, $P < 0.001$)
298 than *H. affinis*. The two carabid species did not differ in their mean consumption of *S.*
299 *vulgaris* ($\chi^2 = 0.23$, $df = 1$, $P = 0.63$). *Harpalus affinis* females ($\chi^2 = 156.33$, $df = 1$, $P < 0.001$)
300 and males ($\chi^2 = 71.55$, $df = 1$, $P < 0.001$) used the shelter more often than *P. cupreus*
301 individuals.

302

303 ***Effect of predator and competitor cues on seed acceptance***

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

307 For *P. cupreus*, irrespective of treatment, the proportion of males consuming seeds
308 was higher than that of females ($\chi^2 = 4.1$, $df = 1$, $P = 0.04$). Females accepted their first seed
309 later ($\chi^2 = 8.09$, $df = 1$, $P = 0.004$), consumed seeds faster ($\chi^2 = 7.8$, $df = 1$, $P = 0.005$) and had
310 a higher space use ($F_{1,285} = 4.33$, $P = 0.038$) than males. Treatment had no significant effect
311 on the proportion of individuals consuming seeds ($\chi^2 = 3.91$, $df = 3$, $P = 0.27$), the latency to
312 first seed acceptance ($\chi^2 = 1.99$, $df = 3$, $P = 0.57$, Fig. 2A), the mean amount of seeds
313 consumed ($\chi^2 = 5.10$, $df = 6$, $P = 0.53$, Fig. 2B), seed handling time ($\chi^2 = 3.46$, $df = 3$, $P =$
314 0.32) and space use ($F_{1,283} = 0.73$, $P = 0.53$).

315 For comparison, identical analyses conducted on *H. affinis* and reported in
316 Charalabidis et al. (2017) were as follows. Irrespective of treatment, *H. affinis* females

317 consumed more seeds than males ($\chi^2 = 16.45$, $df = 1$, $P < 0.001$). A treatment effect was
318 observed on the proportion of individuals consuming weeds ($\chi^2 = 10.62$, $df = 3$, $P = 0.014$),
319 the latency to first seed consumption ($\chi^2 = 12.6$, $df = 3$, $P < 0.001$, Fig. 2A), the total number
320 of seeds consumed ($\chi^2 = 17.22$, $df = 6$, $P = 0.0085$, Fig. 2B). More individuals consumed weed
321 seeds with predator cues than in the control ($P = 0.0025$, odds-ratio = 2.94, 95%CI = [1.49,
322 5.79]). Latency was lower with predator cues than in the other treatments (control: $P < 0.001$,
323 hazard ratio = 2.22, 95%CI = [1.38, 3.56]; intraspecific competition: $P = 0.032$, hazard ratio =
324 1.59, 95%CI = [1.02, 2.47]; interspecific competition: $P = 0.020$, hazard ratio = 1.67, 95%CI
325 = [1.08, 2.57], Fig. 2A). *H. affinis* consumed more seeds with predator cues than in the other
326 treatments (control $P = 0.030$; intraspecific competition $P = 0.031$; interspecific competition P
327 = 0.019 (Fig. 2B)) with a sex effect ($\chi^2 = 6.58$, $df = 2$, $P = 0.037$), but no interaction between
328 sex and treatment ($\chi^2 = 1.47$, $df = 6$, $P = 0.96$). Handling time did not vary with treatment ($\chi^2 =$
329 1.40, $df = 3$, $P = 0.71$). Space use differed between treatments ($F_{3,257} = 3.95$, $P = 0.0088$) and
330 was higher under interspecific competition than under intraspecific competition ($F_{3,257} =$
331 3.36, $P = 0.019$).

332 There was an effect of carabid species and treatment on the proportion of individuals
333 consuming seeds ($\chi^2 = 8.82$, $df = 3$, $P = 0.032$). More individuals of *P. cupreus* consumed
334 seeds in the control ($\chi^2 = 24.44$, $df = 1$, $P < 0.001$), intraspecific competition ($\chi^2 = 4.45$, $df = 1$,
335 $P = 0.035$) and interspecific competition treatments than *H. affinis* ($\chi^2 = 15.77$, $df = 1$, P
336 < 0.001). There was no significant difference in seed consumption by the two carabid species
337 under predation ($\chi^2 = 1.31$, $df = 1$, $P = 0.25$). Latency to first seed acceptance differed between
338 the two carabid species ($\chi^2 = 8.14$, $df = 3$, $P = 0.043$). *P. cupreus* started consuming seeds
339 earlier than *H. affinis* in all four treatments (control: $\chi^2 = 28.76$, $df = 1$, $P < 0.001$; intraspecific
340 competition: $\chi^2 = 4.51$, $df = 1$, $P = 0.034$; interspecific competition: $\chi^2 = 22.66$, $df = 1$, $P <$
341 0.001 and predation: $\chi^2 = 4.51$, $df = 1$, $P = 0.034$). Moreover, across treatments *P. cupreus*

342 individuals spent more time handling seeds of *T. officinale* than individuals of *H. affinis* ($\chi^2_1 =$
343 33.60, $df = 1$, $P < 0.001$, results for the control: $\chi^2 = 8.46$, $df = 1$, $P = 0.0036$; predation: $\chi^2 =$
344 12.60, $df = 1$, $P < 0.001$; intraspecific competition: $\chi^2 = 7.65$, $df = 1$, $P = 0.0057$; interspecific
345 competition: $\chi^2 = 4.45$, $df = 1$, $P = 0.035$). There was no interaction between carabid species
346 and treatment ($\chi^2 = 2.26$, $df = 3$, $P = 0.52$). The proportion of space used did not differ
347 between the two carabid species ($F_{1,543} = 3.06$, $P = 0.08$). There was no interaction between
348 carabid species and treatment ($F_{3,540} = 0.51$, $P = 0.67$).

349

350 **Discussion**

351

352 *Seed acceptance for four weed species*

353 *Poecilus cupreus* and *H. affinis* differed in their relative acceptance for the four weed
354 species, with subsequent differences in seed diet breadth. *Poecilus cupreus* exhibited a high
355 level of seed acceptance for *T. officinale* and *S. vulgaris* seeds. Individuals accepted seeds
356 earlier and ate more seeds, and a higher total proportion of individuals consumed seeds. This
357 high acceptance by *P. cupreus* for *T. officinale* and *S. vulgaris* might be explained by their
358 ease of consumption. Conversely, the other two weed species were less accepted. We
359 observed that *P. cupreus* individuals had difficulties handling seeds of *V. arvensis* and often
360 lost these seeds; as a result, the initial interest of *P. cupreus* in *V. arvensis* declined
361 dramatically after the first hour of the experiment, i.e. these seeds were subsequently
362 discarded. The same behaviour was observed for seeds of *C. bursa-pastoris*. Ease of
363 consumption could be explained by an allometric compatibility between the size of the
364 mandibles of the carabid and the size of the seed species (Honěk, Martinkova, Saska, &
365 Pekar, 2007). *P. cupreus* individuals might be too large (in comparison to *H. affinis*) to
366 consume *V. arvensis* but can handle well seeds of *T. officinale* that are twice as long as those

367 of *V. arvensis* for the same weight. The lack of interest of *P. cupreus* individuals in seeds of
368 *V. arvensis* might also be explained by the lower digestibility of *V. arvensis* seeds
369 (Hengeveld, 1987; Lundgren & Lehman, 2010; Schmid, Lehman, Brözel, & Lundgren, 2014).

370 In contrast, the granivore *H. affinis* consumed all seed species similarly, with equal
371 levels of seed acceptance. *Harpalini* species have been described as unspecialized feeders of
372 seeds (Acorn & Ball, 1991; Forsythe, 1983; Kulkarni et al., 2015; Zetto Brandmayr, Giglio,
373 Marano, & Brandmayr, 1998) and *Harpalus sp.* have evolved broad mandibles with massive
374 adductors that are able to readily crush seeds (Paarmann, Faust, Arndt, Lühtrath, & Rohe,
375 2006; Zetto Brandmayr et al., 1998). The greater ability of *H. affinis* to consume seeds, as
376 compared to *P. cupreus*, is illustrated by a markedly different handling time for *T. officinale*,
377 a weed otherwise preferred by *P. cupreus*. While *P. cupreus* consumed more seeds of *T.*
378 *officinale* in total than *H. affinis* did, *P. cupreus* individuals had longer handling times for
379 seeds of this weed. The ability of *H. affinis* individuals to feed on several species of seeds,
380 regardless of their shape or size, is a benefit for a granivore, which subsists predominantly on
381 seeds (Kamenova, Leroux, Polin, & Plantegenest, 2017) and requires these food items
382 throughout its period of activity. Discarding seeds might result in strong opportunity costs
383 (Stephens, 2008) either because of competition (Dechaume-Moncharmont et al., 2016) or
384 because uneaten seeds enter the seed bank and become unavailable. Our study also showed
385 that *H. affinis* was much slower at commencing the consumption of weed seeds than *P.*
386 *cupreus*. During the first five hours of the first experiment, *P. cupreus* accepted their first seed
387 earlier and ate significantly more seeds than *H. affinis*, irrespective of the weed species, and a
388 similar pattern was observed in the control treatment of the predator cue experiment. This
389 apparent lower initial interest for seeds by *H. affinis* is unlikely to be due to the weed species
390 offered, as these weed species have been found to be ‘preferred’ by *H. affinis* in multiple
391 choice-test studies (Honěk, Martinkova, & Saska, 2011; Honěk et al., 2007; Honěk, Saska, &

392 Martinkova, 2006; Petit et al., 2014; Saska, Martinkova, & Honěk, 2010). Rather, the pattern
393 might simply result from a lower activity in *H. affinis* than in *P. cupreus* (Thiele, 1977).
394 Smaller species, such as *H. affinis* have been found to be less active than larger species like *P.*
395 *cupreus* (Greenslade, 1964; A. Lang, 2000; Luff, 1975). We also observed that most *H. affinis*
396 individuals sought shelter and hid during the first experiment, with subsequently less time to
397 forage actively for seeds.

398

399 ***Response to predator and competitive cues***

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

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

434

435 ***Implications of contrasted foraging strategies for weed biocontrol***

436 The present study focused on two carabid species, an obligate omnivore and a granivore and
437 provides evidence that the two species exhibit different seed foraging strategies. Although the
438 two strategies described here cannot be generalised to the trophic guild level, the two carabid
439 species tested here are the two most abundant species and often co-occur within carabid
440 communities sampled regionally. As such, and provided that the strategies we observed in
441 controlled conditions apply in field conditions, one can speculate that the two foraging

442 strategies described here could coexist in arable fields. Although we observed that the two
443 strategies overlap, as shown by the shared high interest of *P. cupreus* and *H. affinis* for
444 dandelion seeds, they would also appear quite complementary in terms of the respective
445 ranges of seed species eaten, and in terms of timing of seed consumption. Future studies
446 characterizing the foraging strategies of granivore and obligate omnivore carabid species
447 should assess whether the two strategies described here are generic and/or if other foraging
448 strategies exist in seed-eating carabid beetles. Gaining such knowledge would enable
449 scientists to test for potential behaviourally-based niche complementarity in seed-eating
450 carabid assemblages and to quantify its effect on seed suppression.

451

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458

459

460 Appendix A. Supplementary data

461 Supplementary data associated with this article can be found, in the online version, at
462 XXXXX."

463

464

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- 698

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

	<i>Poecilus cupreus</i>				<i>Harpalus affinis</i>			
	Males		Females		Males		Females	
<i>T. officinale</i>								
# 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)
<i>S. vulgaris</i>								
# 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)
<i>V. arvensis</i>								
# 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)
<i>C. bursa-pastoris</i>								
# 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)

701

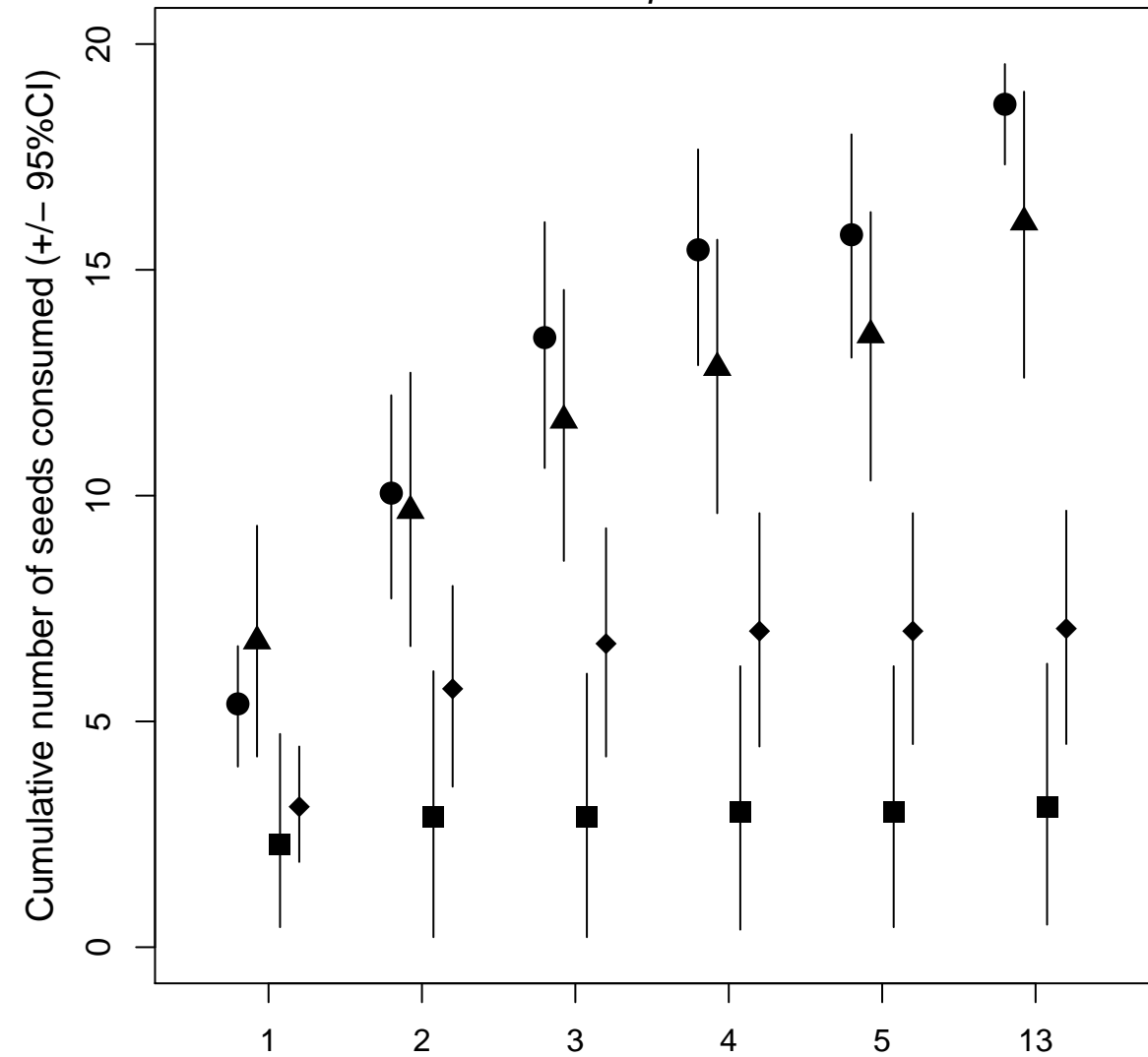
702 **Table 2.** Effect of predator and competitor cues on seed acceptance: Observed mean (and SE) per carabid species and sex for each olfactory cues
 703 treatment. Values for *H. affinis* are derived from Charalabidis et al. (2017)

	<i>Poecilus cupreus</i>				<i>Harpalus affinis</i>			
	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)

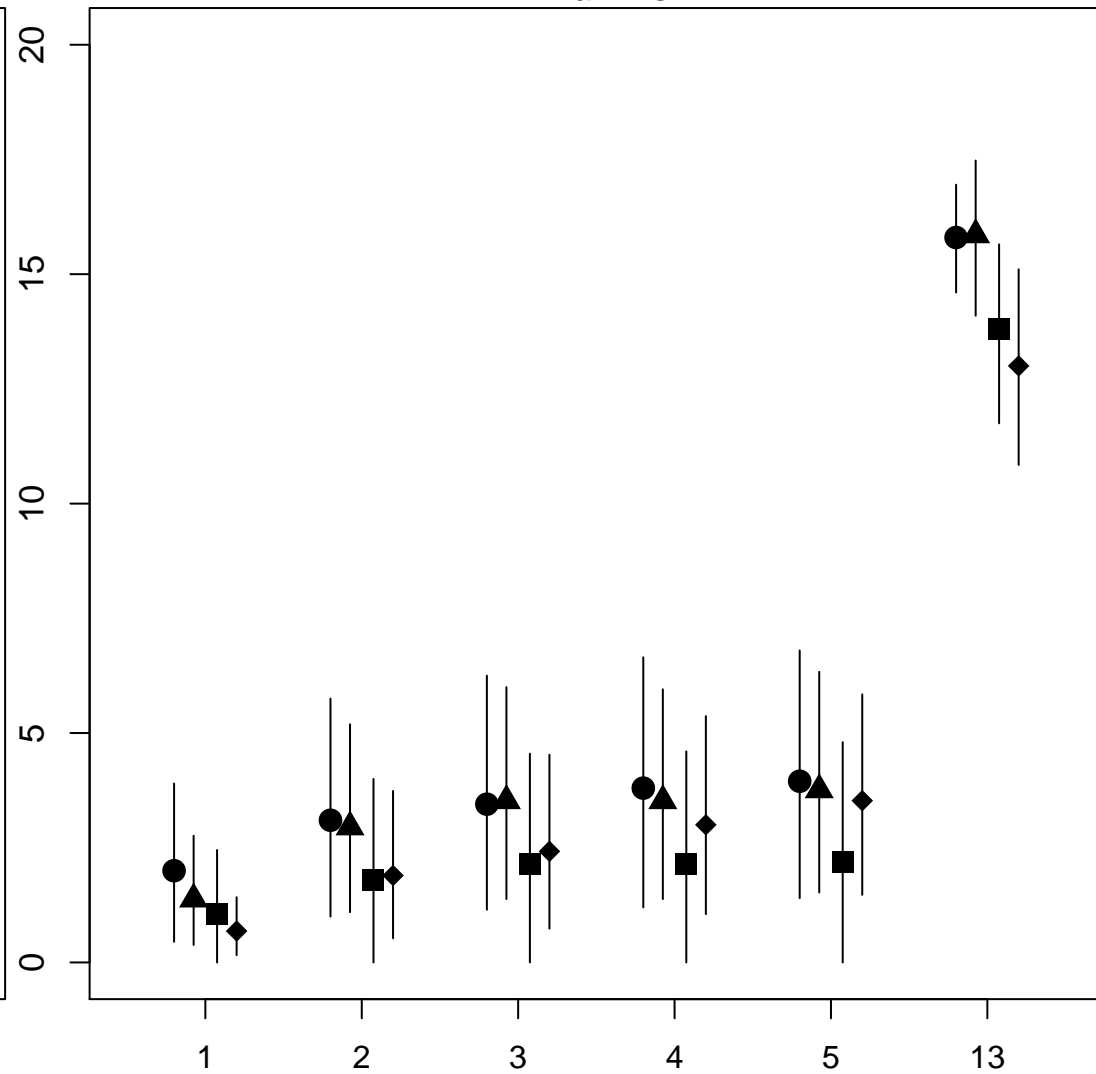
Fig. 1. Cumulative number of seeds consumed (bootstrapped \pm 95%CI) by *P. cupreus* (A) and *H. affinis* (B) individuals at each sample date for seeds of *T. officinale* (●), *S. vulgaris*(▲), *C. bursa-pastoris* (■) and *V. arvensis* (◆).

Fig. 2. (A) **Mean latency to first seed acceptance** (bootstrapped \pm 95%CI) in each treatment for *H. affinis* (\blacklozenge) and *P. cupreus* (\square), (B) **Mean number of seeds consumed** (bootstrapped \pm 95%CI) by *H. affinis* (\blacklozenge) and *P. cupreus* (\square) 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).

(A) *P. cupreus*

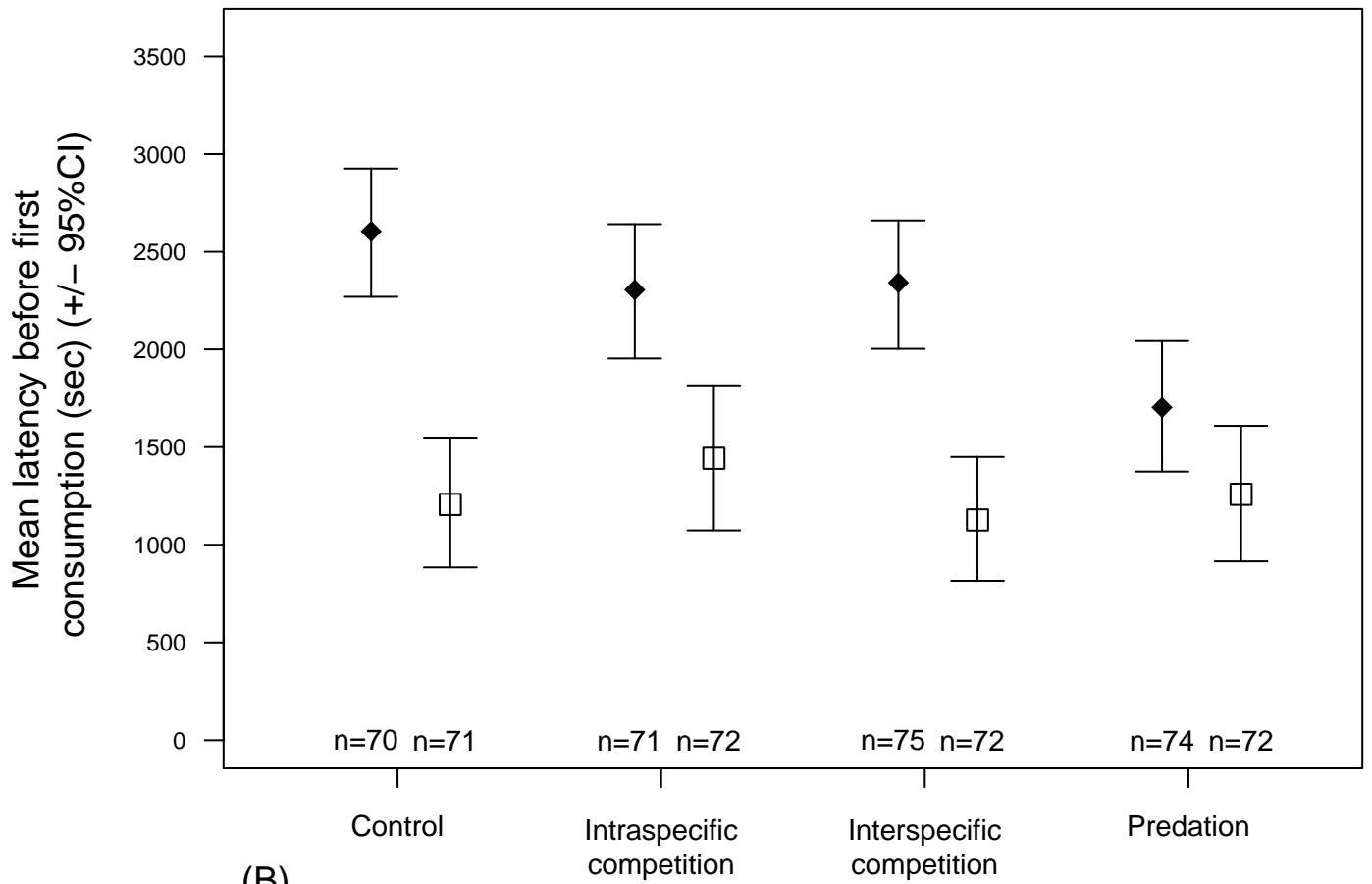


(B) *H. affinis*



Sample hour

(A)



(B)

