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Sex-specific foraging response to interspecific interactions in carabid beetles

Alice Charalabidis ^a, Stéphane A.P. Derocles ^{a,b}, Diana M. Mosquera-Muñoz ^a, Sandrine Petit^a, François-Xavier Dechaume-Moncharmont ^{a,c}, & David A. Bohan ^a

^a Agroécologie, INRAE, Institut Agro, Univ. Bourgogne, Univ. Bourgogne Franche-Comté, F-21000 Dijon, France

^b Univ Rennes, CNRS, ECOBIO [(Ecosystèmes, biodiversité, évolution)] - UMR 6553, F-35000 Rennes, France

^c Univ Lyon, Université Claude Bernard Lyon 1, CNRS, ENTPE, UMR 5023 LEHNA, F-69622, Villeurbanne, France

Author for correspondence:

dr David A Bohan

Email: david.bohan@inrae.fr

Address: INRAe Dijon - Bât. Coste

17 Rue Sully, BP 86510, 21065 Dijon cedex

1 **ABSTRACT**

2 Carabids beetles are considered important biocontrol agents of weeds, but predicting levels of
3 weed seed consumption and regulation is difficult. Olfactory cues from predators or potential
4 competitors alter the selection and consumption of particular food resources by foraging
5 individuals. Whether this change actually leads to changes in consumption levels or simply to
6 changes in consumption kinetics is not yet known. Identifying and understanding the factors
7 that drive the seed foraging behaviour of carabid beetles, in contexts of interspecies interaction,
8 is essential for predicting consumption levels in different carabid communities and hence
9 improve the ecosystem service of weed regulation by carabid beetles.

10 We tested the response of 119 *Harpalus affinis* individuals when foraging for *Viola arvensis*
11 or *Taraxacum officinale* seeds, to encounters with individuals of another carabid species,
12 *Pterostichus melanarius*. Their foraging behaviour (i.e. total consumption, latency to first seed
13 acceptance and space use) was recorded for 72 h and the consumption kinetics were reported
14 in detail for the first 7 h of the experiment for all treatments.

15 While the total number of seeds consumed after 24 hours did not differ when *H. affinis* was
16 in the presence of *P. melanarius*, the kinetics of seed consumption changed significantly. This
17 suggests that looking at the total amount of seeds consumed after a long period of time may be
18 misleading and that more focus on consumption kinetics is needed if we are to understand
19 carabids interest in specific weed species in a specific foraging context. Moreover, only females
20 seemed to react to the presence of *P. melanarius* individuals in our experiment, indicating that
21 the perception of the level of risk may be sex-specific in carabid beetles.

22
23 **KEYWORDS**

24 Interspecific interactions; weed seeds regulation; gender-specific; consumption kinetics;
25 biocontrol

26

28 1. INTRODUCTION

29 Crop damage due to pests causes significant yield reduction in agricultural crops (Marshall
30 et al., 2003). Weeds alone can account for up to 30% of yield losses (Oerke, 2006). Weed seed
31 feeding carabid beetles can consume a substantial amount of weed seeds in the field (Frank et
32 al., 2011; Honek et al., 2003; Menalled et al., 2007; Saska et al., 2008; Thiele, 1977; Ward et
33 al., 2014) and are the primary consumers of weed seeds among invertebrates (Honek et al.,
34 2003). Their polyphagous diet (Kromp, 1999; Lovei and Sunderland, 1996; Thiele, 1977) and
35 potential regulation effect on pest species have led to the interest of carabid beetles as biocontrol
36 agents for agricultural weeds (De Heij et al., 2022; Fischer et al., 2021; Kulkarni et al., 2015a;
37 Schumacher et al., 2020). Although the estimation of weed seed predation in field conditions
38 have been linked to the abundance of carabids (Bohan et al., 2011), the consumption levels
39 reported in field studies are highly variable, making it difficult to draw conclusions about the
40 effectiveness of weed seed regulation (Davis and Raghu, 2010; Petit et al., 2014; Saska et al.,
41 2008; Westerman et al., 2003). Variation in predation rates may be explained in part by
42 differences in the feeding preferences of carabid beetles for certain seed species, as
43 demonstrated in laboratory choice tests (Honek et al., 2011, 2007, 2006, 2003; Petit et al., 2014;
44 Saska et al., 2019). Trophic relationships between specific carabid and weed species are only
45 partially documented (Saska et al., 2019), and the preferences identified from laboratory choice
46 tests rarely match the observed choices of carabids in the field (Petit et al., 2014). An
47 understanding of those factors that drive carabid beetles to accept or reject a seed in the field is
48 necessary to improve the operational utility of the ecosystem service of weed regulation by
49 carabid beetles.

50 Farmland communities are composed of granivore, omnivore and predatory species, each
51 of which can be cannibalistic, inter-specific predators and competitors (Currie et al., 1996;
52 McKemey et al., 2003). Interspecific interference is widespread and its impact on foraging
53 behaviours and of the broader ecological consequences of interference has rarely been
54 examined (Carbonne et al., 2019; Charalabidis et al., 2019, 2017; De Heij et al., 2022; Guy et
55 al., 2008). Carabid beetles may adjust their foraging behaviour according to the biotic context
56 (Blubaugh et al., 2017; Charalabidis et al., 2017), with olfactory cues from potential predators
57 and competitors affecting the level of consumption of foraging individuals, modifying both the
58 selection and consumption of food resources (Blubaugh et al., 2017; Carbonne et al., 2019;
59 Charalabidis et al., 2019, 2017; Sivy et al., 2011; Wyatt Hoback et al., 2001). Carabid beetles
60 have been shown, in laboratory experiments, to increase their seed consumption when foraging

61 under stress, for example (Blubaugh et al., 2017; Charalabidis et al., 2017). These results
62 suggest that the foraging behavior of an individual carabid beetle, and thus the level of
63 consumption of observed weed species, is shaped by the composition of the carabid community.
64 It could therefore be hypothesised that some communities would result in increased seed
65 consumption while others would result in reduced seed consumption. Another option, rarely
66 considered, is that total consumption does not change with community composition, but only
67 the consumption levels of individuals. The total number of seeds that an individual can consume
68 could be set by a maximum consumption threshold and thus only the kinetics of consumption
69 would be expected to change (Mols, 1988). The kinetics of seed consumption would also have
70 an impact on weed control: more rapid seed consumption would decrease the number of seeds
71 in a plot that are able to enter the seed bank, for example. Furthermore, as carabid species do
72 not seem to respond in the same way to stress cues (Charalabidis et al., 2019), their consumption
73 kinetics will differ potentially affecting their species-specific contribution to weed seed
74 regulation. A better understanding of how such changes in foraging behaviour occur, would
75 deliver a predictive explanation of the observed trophic links between carabid and weed species,
76 within farmland communities, and their associated seed consumption levels.

77 Foragers can choose where to forage and whether to avoid areas of potential interspecific
78 interference (Guy et al., 2008). How foragers react to encounters would improve our
79 explanation of weed seed removal. Past experiments on the effect of signals from predators or
80 competitors on foraging behaviour of carabid beetles have focused only on olfactory chemical
81 signals, and have not provided safe areas, or refugia, where signals are absent. Given that an
82 encounter with a predator induces a more acute perception of risk than indirect signals alone
83 (Tapia-Lewin and Pardo, 2014), we expect that individuals exposed to potential predators will
84 express more intense behavioural changes than those previously observed with chemical signals
85 (Blubaugh et al., 2017; Charalabidis et al., 2019, 2017). This could result in more widespread
86 flight behaviours, for example, and thus potentially lead to lower consumption levels. However,
87 compensatory feeding has already been observed in insects, whereby consumption increases to
88 compensate for previously induced reductions in food availability (Hawlena and Schmitz, 2010;
89 Thaler et al., 2012). Because immobile seeds are easy prey items to acquire, requiring less active
90 foraging than mobile prey and lower transportation costs, seeds might be consumed as a 'stress
91 food' by carabids (Blubaugh et al., 2017). This could lead to increased consumption levels by
92 stressed individuals for the duration of the experiment.

93 To understand whether interspecies interference impacts carabid foraging behaviour, we
94 investigated the change in interest of *Harpalus affinis* (Schrank, 1781) to seeds of two weed

95 species, *Viola arvensis* Murray, 1770 and *Taraxacum officinale* F.H. Wigg., 1780, during
96 potential encounters with *Pterostichus melanarius* (Illiger, 1798) individuals. *H. affinis* is an
97 abundant carabid beetles and are able to adapt their foraging strategy to the olfactory context
98 (Charalabidis et al., 2019, 2017). Individuals of *P. melanarius* were chosen to provide the risk
99 cues because they are voracious predators of live prey (Currie et al., 1996; Foltan, 2004;
100 Hatteland et al., 2010; Kromp, 1999; McKemey et al., 2003), are found with *H. affinis* in
101 European farmland communities and their olfactory cues have been documented to change the
102 foraging behaviour of *H. affinis* (Charalabidis et al., 2019, 2017). The latency time to first
103 acceptance of a seed, consumption levels as well as consumption kinetics were taken as metrics
104 of individual foraging behaviour. Space use by focal individuals was also assessed to measure
105 the response to the presence of *P. melanarius* and the propensity to flee from potential
106 predators.

107

108 2. METHODS

109 2.1. Study systems

110 Both species of carabids used in test were collected using pitfalls traps at the INRAe
111 Experimental Farm (Dijon, France; 47°14'11.4" N 05°05'53.4" E) between April and June
112 2017. Carabids were identified following Jeannel (1942). Individuals were maintained in plastic
113 boxes segregated by species (34 x 19 x 11 cm for *H. affinis* and 80 x 55,9 x 15,5 cm for *P.*
114 *melanarius*) in a climate-controlled chamber (18 ± 1 °C, 60% humidity, 14:10h light:dark
115 cycle). Species were held in different boxes to prevent interspecific predation (Currie et al.,
116 1996) and in different climat chambers to prevent exposure to any interspecific chemical cues
117 for at least two weeks prior to the test. The boxes were filled with soil and moistened paper
118 tissue. Water was provided *ad libitum* in Eppendorf tubes sealed with cotton wool. *H. affinis*
119 individuals were fed with seeds in an equal mixture of four weed species: *V. arvensis* (0.9mg,
120 1.36mm), *T. officinale* (0.7 mg, 2.67mm), *Senecio vulgaris* L. (0.2 mg, 1.75 mm), *Capsella*
121 *bursa-pastoris* (L.) Medik. (0.1 mg, 0.8mm). These four species were chosen because they
122 were common in the field where the individuals were trapped and are known to be readily
123 consumed by this species (Petit et al., 2014; Trichard et al., 2014). The *P. melanarius*
124 individuals were fed with a combination of frozen mealworms, *Tenebrio molitor*, and pre-
125 moistened dry cat food (Charalabidis et al., 2019).

126 Individual *H. affinis* were isolated in round plastic containers (9 cm diameter) 62 hours prior
127 to the experiments and deprived of food to standardize their feeding history. The bottom of each
128 petri dish was covered with a clean, moist filter paper, providing the individual forager with
129 shelter and water, *ad libitum*.

130 2.2. Behavioural experiment

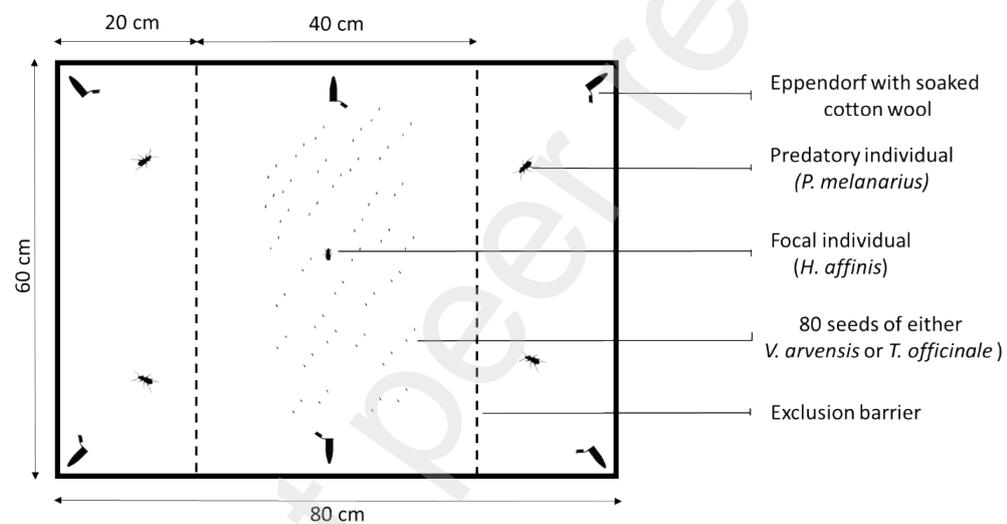
131 A total of 119 individuals of *H. affinis* (60 females and 59 males) were tested under four
132 different treatments:

- 133 - Treatment 1 (T1): *H. affinis* (15 females and 15 males) foraging alone on *V. arvensis* seeds
- 134 - Treatment 2 (T2): *H. affinis* (15 females and 14 males) foraging alone on *T. officinale* seeds
- 135 - Treatment 3 (T3): *H. affinis* (15 females and 15 males) foraging on *V. arvensis* seeds in the
136 presence of *P. melanarius*
- 137 - Treatment 4 (T4): *H. affinis* (15 females and 15 males) foraging on *T. officinale* seeds in
138 the presence of *P. melanarius*

139 Tests were conducted in plastic trays of 80 x 60 x 15 cm divided in three compartments by
140 plastic exclusion barriers: two external compartments of 20 cm width respectively referred as
141 “right area” and “left area” and an internal compartment of 40 cm width (Fig. 1) referred as
142 “central zone”. Based on preliminary measurements made on *H. affinis* individuals, holes of 4
143 mm in diameter, made in the barriers every 2 cm, would allow only *H. affinis* to pass freely
144 through the barriers and have access to all three areas (*i.e.* right, left and central area). The larger
145 individuals of *P. melanarius* would be prevented by the size of the 4 mm holes from moving
146 between the areas (Fig. 1). The plastic trays were filled with a thin layer of washed river sand
147 (1.5 Kg per tray), that had been passed through a 400 µm sieve before use. The sand was used
148 to more closely represent the porous substrates of field soils on which the carabids were caught.
149 The thin layer of sand limited the amount of seeds lost due to burial. Six Eppendorf tubes filled
150 with water and sealed with cotton wool were placed (two in each area, *i.e.* 6 per tray), to provide
151 an *ad libitum* water supply for all the carabids. The trays were sprayed with water twice a day
152 (morning and late afternoon) to prevent the sand from drying out and to keep the seeds moist.
153 This has been shown to improve the palatability and detectability of seeds by carabid beetles
154 (Law and Gallagher, 2015). After each experiment, the sand was sieved (500 µm gauge) to
155 retrieve the uneaten seeds. To eliminate potential olfactory cues left by the carabids, the sand
156 was washed using a sieve of 315 µm, dried in an oven at 110°C for 48 hours and sieved again
157 to eliminate sand clumps before re-use. The cotton wool was changed and Eppendorf tubes,

158 plastic trays and plastic barriers were cleaned using 70% ethanol before and after each
159 experiment.

160 A total of 80 seeds of the tested weed species, either *V. arvensis* or *T. officinale* according
161 to the treatment, were randomly distributed in the central area of the tray (Fig. 1). This number
162 of seeds was obtained from a pre-experiment assessment made in order to provide individuals
163 with sufficient seeds to avoid total seed depletion during the experiment. Despite this, the seed
164 density used in our experiment (i.e. 333 seeds/m²) is still lower than the reported seeds shed by
165 weeds in field studies: 3700-24 200 seeds/m² for *T. officinale* (Honek et al., 2005) and
166 approximately 20 000 seeds/m² for *V. arvensis* (Gerowitt and Bodendörfer, 1998).



167

168 **Figure 1: Schematic diagram of the test arena.** The arena was divided in three areas using
169 plastic 'exclusion' barriers to exclude *P. melanarius* from the central area. The plastic barriers
170 were drilled with holes of 4mm in order to allow free movement of *H. affinis* individuals into
171 the right and left areas but prevent *P. melanarius* from accessing the central area. 80 seeds of
172 either *T. officinale* or *V. arvensis* were placed and spaced out in the central area. This
173 representation is approximately to scale: carabids measure ~1 cm and seed ~2.5 mm in length

174 For T3 and T4, two *P. melanarius* individuals were placed in the two outside areas of the
175 tray (i.e. right and left areas) from where they were excluded from accessing the seeds located
176 in the central area (Fig. 1), giving a total of 4 *P. melanarius* per tray. The number of *P.*
177 *melanarius* used in the test was based on the work of Guy et al., (2008), who demonstrated that
178 perception of conspecifics by carabid individuals does not increase above a threshold of four
179 individuals. Temperature and humidity were recorded and treatments were randomized to avoid
180 any effects of the position of trays in the room.

181 For each tray, the experiment started as soon as an individual of *H. affinis* was released in
182 one of the external compartments of the arena. This starting location was chosen to increase the

183 chance that each individual would encounter *P. melanarius* at least once during the experiment.
184 A release directly into the central area, where the seeds are located, might have led individuals
185 to the *H. affinis* neglecting the external compartments and thus potentially never encountering
186 *P. melanarius* individuals.

187 The impact of *P. melanarius* individuals on the foraging behaviour of *H. affinis* individuals
188 was first assessed by examining the latency of individuals to first seed acceptance as an
189 indicator of their context-dependent interest in eating seeds (Charalabidis et al., 2017). To
190 estimate the effect on seed consumption by individuals, the total number of seeds consumed by
191 each individual was recorded every hour for the first 7 hours in order to get a fine-grained view
192 of consumption dynamics during the first few hours after the seed encounter. Subsequent
193 measurements were taken at 24, 48 and 72 hours. On each sampling date, the number of *H.*
194 *affinis* that had not yet consumed seeds was recorded. To measure the effect of *P. melanarius*
195 on the relative use of the space in the arena by *H. affinis* (referred to hereafter as "space use"),
196 their position, either in the central zone or in the right and left zones was noted every hour for
197 the first 7 hours (Fig.1) and then at 24 and 48 hours. The proportion of time individuals were
198 recorded in each area was then used as a proxy for space use.

199 All combinations of treatments (i.e. T1, T2, T3 and T4) were tested simultaneously each
200 week in order to avoid any effect of the date. Each *H. affinis* was randomly assigned to a
201 treatment, and tested alone and only once. Males and females were tested separately to avoid
202 confounding olfactory cues in the test room that might induce mating related behaviours that
203 are distinct from foraging. This was done by one sex being tested in one week and the other sex
204 the next week, in sequence.

205 **2.3. Statistical Analysis**

206 All statistical analyses were done in R 3.1.3 (R Core Team, 2017). Total seed
207 consumption for each treatment and sampling date was analysed using a generalized linear
208 model, assuming a negative binomial distribution for the data from the first 7 hours of testing
209 and a normal distribution for the remaining time steps (i.e., 24, 48, and 72 hours). Latencies of
210 the first seed acceptance in the four treatments were compared by means of the Cox proportional
211 hazard models (Dechaume Moncharmont et al., 2003) in the 'cox.ph' function from the package
212 'survival' (Therneau, 2015). For each Cox regression model fit, the proportional hazards
213 assumption was assessed using the 'cox.zph' function. Space use by individual foragers was
214 modelled as a generalized linear model assuming a binomial distribution. For all parametric
215 analysis a full model including the effects of the weed species, sex of individuals, and their

216 interactions was compared sequentially to nested sub-models with and without a given covariate
217 using stepwise backward elimination of non-significant variables and interaction terms.

218 **3. RESULTS**

219 ***3.1. Effect of weed species on seed consumption***

220 From 24 to 72 hours, total seed consumption in controls differed between the two weed
221 species (Table 1). *H. affinis* individuals, of both sexes, consumed more *T. officinale* seeds than
222 *V. arvensis* seeds. There was no effect of sex or interaction between sex and weed species at
223 any of the time points. Similar results were observed in the presence of *P. melanarius* in the
224 trays, with more *T. officinale* seeds consumed than *V. arvensis* seeds after 72 hours. There was
225 also no effect of *H. affinis* sex or interaction between sex and weed species at any of the time
226 points (Table 1).

Table 1: Mean seed consumption (bootstrapped +/- 95%CI) by *H. affinis* individuals (both sexes combined) for seeds of either *V. arvensis* or *T. officinale* in both treatment situation. Significant P-values are in bold.

Control											
	<i>T. officinale</i>	<i>V. arvensis</i>	Effect of seed species			Effect of sex			Sex and seed species interactions		
1h	1.27, [0.38, 2.41]	0.30, [0.10, 0.57]	$\chi^2= 3.09$	df=1	P = 0.078	$\chi^2= 0.15$	df=1	P = 0.70	$\chi^2= 0.37$	df=1	P = 0.55
2h	1.89, [0.69, 3.48]	0.73, [0.33, 1.23]	$\chi^2=2.89$	df=1	P = 0.089	$\chi^2= 1.48$	df=1	P = 0.22	$\chi^2= 0.14$	df=1	P = 0.91
3h	2.48, [0.96, 4.45]	1.00, [0.40, 1.77]	$\chi^2= 2.86$	df=1	P = 0.09	$\chi^2= 1.48$	df=1	P = 0.22	$\chi^2= 0.52$	df=1	P = 0.47
4h	3.10, [1.31, 5.34]	1.23, [0.50, 2.27]	$\chi^2= 3.15$	df=1	P = 0.076	$\chi^2= 0.80$	df=1	P = 0.37	$\chi^2= 0.70$	df=1	P = 0.40
5h	3.52, [1.48, 6.00]	1.37, [0.53, 2.53]	$\chi^2= 3.29$	df=1	P = 0.070	$\chi^2= 0.97$	df=1	P = 0.32	$\chi^2= 0.89$	df=1	P = 0.35
6h	3.55, [1.52, 6.07]	1.47, [0.57, 2.70]	$\chi^2= 2.89$	df=1	P = 0.089	$\chi^2= 0.89$	df=1	P = 0.34	$\chi^2= 0.86$	df=1	P = 0.35
7h	3.65, [1.65, 6.31]	1.50, [0.60, 2.70]	$\chi^2= 3.13$	df=1	P = 0.077	$\chi^2= 0.89$	df=1	P = 0.34	$\chi^2= 1.08$	df=1	P = 0.30
24h	21.3, [16.3, 26.5]	11.3, [3.03, 13.6]	F =11.9	df=1,56	P = 0.001	F = 1.19	df=1,56	P = 0.27	F = 2.05	df=1,55	P = 0.15
48h	34.5, [28.5, 40.6]	19.2, [16.2, 22.2]	F =19.25	df=1,56	P < 0.001	F = 0.118	df=1,56	P = 0.73	F = 0.79	df=1,55	P = 0.38
72h	48 [41.6, 54.0]	28.7, [25.8, 31.6]	F =26.02	df=1,56	P < 0.001	F = 0.08	df=1,56	P = 0.77	F = 0.62	df=1,55	P = 0.43
Presence of <i>P. melanarius</i>											
	<i>T. officinale</i>	<i>V. arvensis</i>	Effect of seed species			Effect of sex			Sex and seed species interactions		
1h	0.97, [0.13, 2.10]	0.6, [0.10, 1.33]	$\chi^2= 3.13$	df=1	P = 0.077	$\chi^2= 0.10$	df=1	P = 0.74	$\chi^2= 0.18$	df=1	P = 0.67
2h	1.33, [0.37, 2.57]	1.27, [0.43, 2.33]	$\chi^2= 0.02$	df=1	P =0.88	$\chi^2= 0.058$	df=1	P = 0.81	$\chi^2= 0.91$	df=1	P = 0.34
3h	2.33, [0.80, 4.47]	1.93, [0.83, 3.17]	$\chi^2= 0.15$	df=1	P =0.69	$\chi^2= 0.12$	df=1	P = 0.72	$\chi^2= 0.93$	df=1	P = 0.34
4h	2.73, [1.00,5.00]	2.37, [1.23,3.67]	$\chi^2= 0.12$	df=1	P =0.72	$\chi^2= 0.09$	df=1	P = 0.75	$\chi^2= 1.64$	df=1	P = 0.20
5h	2.93, [1.20, 5.27]	2.53, [1.37, 3.87]	$\chi^2= 0.12$	df=1	P =0.72	$\chi^2= 0.038$	df=1	P = 0.85	$\chi^2= 1.73$	df=1	P = 0.19
6h	3.07, [1.30, 5.37]	2.63, [1.47, 4.00]	$\chi^2= 0.14$	df=1	P =0.71	$\chi^2= 0.043$	df=1	P = 0.84	$\chi^2= 1.22$	df=1	P = 0.27
7h	3.07, [1.33, 5.40]	2.63, [1.49, 3.97]	$\chi^2= 0.14$	df=1	P =0.71	$\chi^2= 0.043$	df=1	P = 0.84	$\chi^2= 1.22$	df=1	P = 0.27
24h	18.67, [15.4, 21.9]	12.77, [10.7, 14.8]	F = 8.93	df=1,57	P =0.004	F = 2.57	df=1,57	P = 0.11	F = 1.80	df=1,56	P = 0.18
48h	32.87, [27.6, 38.1]	21.10, [18.0, 24.0]	F =13.52	df=1,57	P <0.001	F = 1.34	df=1,57	P = 0.25	F = 1.25	df=1,56	P = 0.27
72h	46.8 [39.8, 53.4]	28.7 [24.0, 33.1]	F =17.88	df=1,57	P < 0.001	F = 0.007	df=1,57	P = 0.93	F = 2.07	df=1,56	P = 0.16

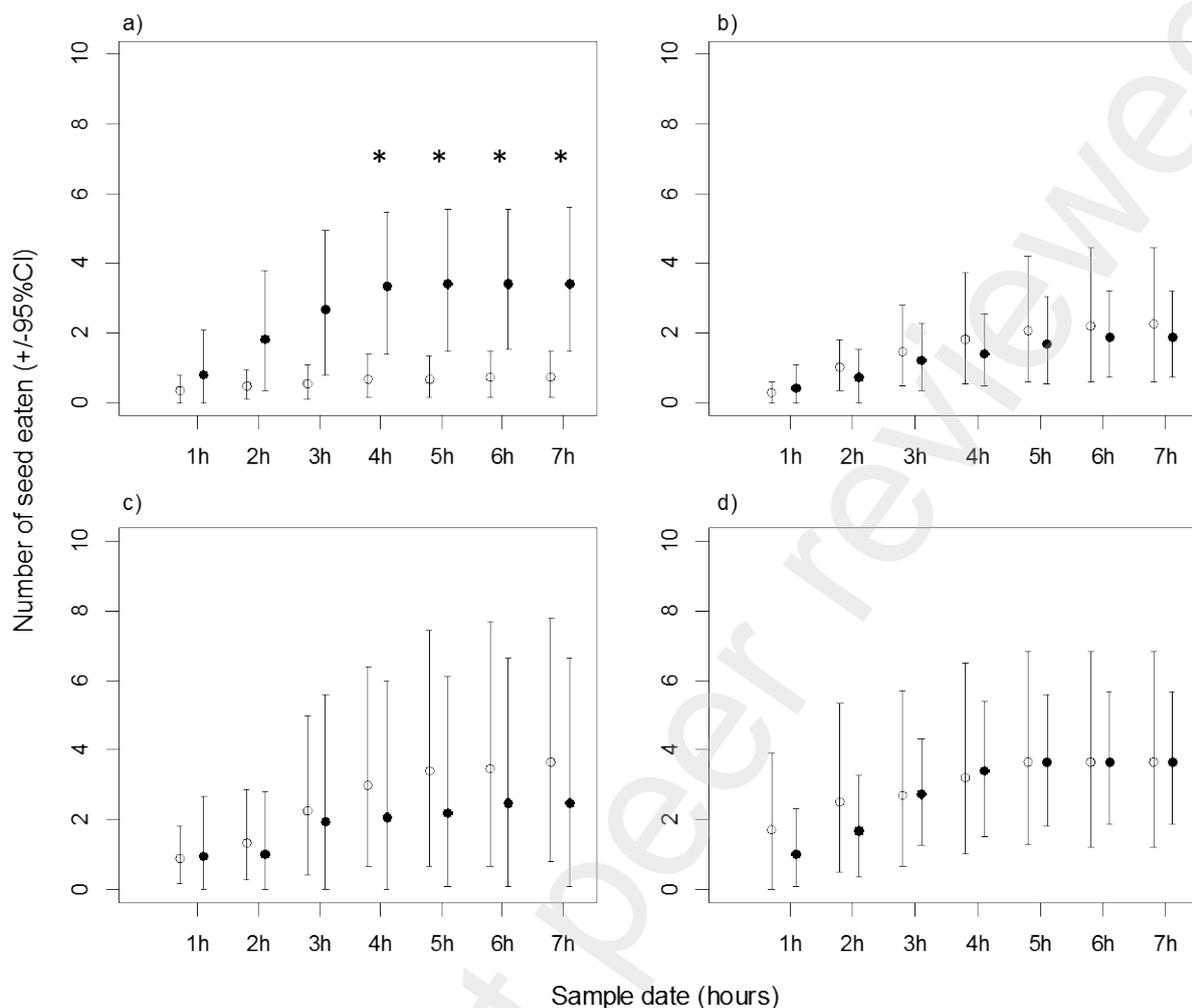
230 **3.2. Effect of the presence or absence of *P. melanarius* on seed consumption**

231 After the first hour of experiment, 20% of individuals, regardless of the treatment, sex or
232 the weed species, had eaten at least one seed. Of these 20% of individuals, 46% had eaten a
233 seed of *V. arvensis* and 54% a seed of *T. officinale*. After 7h of seed exposure this percentage
234 went up to 49% of individuals that had eaten at least one seed (irrespective of the treatment, sex
235 of individuals or the weed species). At the end of test (*i.e.* after 72h) 99% of the individuals had
236 eaten at least one seed.

237 The latency to first seed acceptance did not differ between weed seed species in the
238 control ($\chi^2=0.65$, $df=1$, $P=0.42$), with no effect of sex, ($\chi^2=1.89$, $df=1$, $P=0.17$) or interaction
239 between sex and seed species ($\chi^2=0.47$, $df=1$, $P=0.49$). In the predation treatment, latency to
240 first seed acceptance did not differ between seed species ($\chi^2=0.35$, $df=1$, $P=0.55$) and there
241 was no effect of sex ($\chi^2=3.23$, $df=1$, $P=0.07$) or sex by seed species interaction ($\chi^2=2.60$, $df=1$,
242 $P=0.11$). Latency to first acceptance among females did not differ between treatments for seeds
243 of either *V. arvensis* ($\chi^2=1.58$, $df=1$, $P=0.21$, hazard ratio = [1.61, 95%CI [0.77, 3.36]) or *T.*
244 *officinale* ($\chi^2=1.37$, $df=1$, $P=0.24$, hazard ratio = [0.64, 95%CI [0.30, 1.35]). Latency to first
245 acceptance in males did not differ between the treatments for seeds of either *V. arvensis* (χ^2
246 =0.06, $df=1$, $P=0.79$, hazard ratio = [1.09, 95%CI [0.53, 2.25]) or *T. officinale* ($\chi^2=0.58$, $df=1$,
247 $P=0.44$, hazard ratio = [1.33, 95%CI [0.64, 2.779]).

248 After the first four hours of the trial, *H. affinis* females had consumed cumulatively more
249 *V. arvensis* seeds in the presence of *P. melanarius* than in the control group. (Fig. 2, Table A1).
250 The significant difference in *V. arvensis* seed consumption by females observed early in the
251 trial was no longer significant after 24 hours (Table A1). There was no significant difference
252 between treatments in the number of *T. officinale* seeds eaten by females (Table A1). Seed
253 consumption of *T. officinale* or *V. arvensis* by males did not significantly differ between
254 treatments (Table A1).

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263 **Figure 2: Cumulative number of seed eaten** (bootstrapped +/- 95%CI) during 7 hours in the
 264 control situation (○) or in the predation treatment (●) for a) females with seeds of *V. arvensis*,
 265 b) males with seeds of *V. arvensis*, c) females with seeds of *T. officinale*, d) males with seeds
 266 of *T. officinale*.

267

268 3.3. Space use by individuals

269 In the control condition, the proportion of time foragers were recorded in the central
 270 area of the arena did not differ between seed species ($\chi^2=2.26$, $df=1$, $P = 0.13$). There was no
 271 effect of the sex on space use ($\chi^2= 0.51$, $df=1$, $P = 0.47$) and no sex and seed species interaction
 272 ($\chi^2= 0.04$, $df=1$, $P = 0.84$). In the treatments with *P. melanarius*, there was no effect of seed
 273 species on the number of times an individual was observed in the central area ($\chi^2= 0.65$, $df=1$,
 274 $P = 0.42$). There was, however, a significant effect of sex on space use, with females spending
 275 on average more time in the central area during the 72 h of testing (females 67% of time 95%CI

276 [0.59, 0.74], males 58% of time 95%CI [0.50, 0.67], $\chi^2= 4.20$, $df=1$, $P = 0.04$). There was no
 277 sex and seed species interaction ($\chi^2= 0.89$, $df=1$, $P = 0.34$). This difference in space use by
 278 females was not observed in the first 7 hours of testing and appeared to occur after 24h ($\chi^2=$
 279 0.16827 , $df=1$, $P=0.6817$, Table 2; Fig. A1).

280 **Table 2: Space use across treatments**, as the proportion of time (bootstrapped 95%CI) in the
 281 central area of the arena, according to the seed species and the sex of *H. affinis*

<i>T. officinale</i>		
	Control	Predation
Males	0.51 [0.34, 0.67]	0.62 [0.53, 0.72]
Females	0.55 [0.38, 0.71]	0.67 [0.56, 0.76]
<i>V. arvensis</i>		
	Control	Predation
Males	0.45 [0.30, 0.60]	0.55 [0.41, 0.68]
Females	0.47 [0.36, 0.60]	0.67 [0.56, 0.78]

282
 283 *H. affinis* individuals of both sexes spent more time in the centre of the arena when
 284 exposed to *P. melanarius* individuals, than in the control treatment (females: $\chi^2 =14.25$, $df=1$,
 285 $P < 0.001$; males: $\chi^2=5.92$, $df=1$, $P= 0.015$). There was no effect of the seed species on space
 286 use (females: $\chi^2 =0.64$, $df=1$, $P = 0.42$; males: $\chi^2=2.29$, $df=1$, $P= 0.13$) and no seed species and
 287 treatment interactions (females: $\chi^2= 0.86$, $df=1$, $P= 0.35$; males: $\chi^2= 0.05$, $df=1$, $P= 0.82$).

288

289 4. DISCUSSION

290 Our results show a significant difference in consumption between *V. arvensis* and *T. officinale*
 291 seeds. *H. affinis* individuals ate more *T. officinale* seeds than *V. arvensis* seeds, regardless of
 292 treatment or sex of the focal individual. However, the dynamics of the consumption of the two
 293 seed species in the first hours of testing, differs between the sexes and between treatments.
 294 During the first seven hours of the trial, *H. affinis* females had a higher predation rate of *V.*
 295 *arvensis* when exposed to *P. melanarius* individuals, when compared to the control. This
 296 difference in consumption does not seem to be explained by a difference in space use in the
 297 presence of *P. melanarius*. Indeed, during the first 7-hour period of the experiment, the number

298 of females observed in the central area where the seeds were located was not different to the
299 control.

300 The higher interest of *H. affinis* individuals for seeds of *T. officinale* is consistent with
301 results previously obtained for this species in laboratory experiments (Carbonne et al., 2019;
302 Charalabidis et al., 2019), although some studies have previously demonstrated the opposite trend
303 (Honek et al., 2007, 2006; Petit et al., 2014). Building an understanding of carabid feeding
304 choice is not straightforward, especially as their decision making and thus observed feeding
305 choices of carabids can be impacted by the experimental design used to test their preferences
306 (Charalabidis et al., 2017; Dougherty and Shuker, 2015; Driesche and Murray, 2004; Murray
307 et al., 2010; Saska et al., 2019). Nevertheless, several studies have examined seed
308 characteristics that may explain the relative preferences of carabid beetles. (Ali and Willenborg,
309 2021; Foffová et al., 2020; Gaba et al., 2019; Honek et al., 2007). It has been recently suggested
310 that the primary sensory mechanism used by carabid beetles to detect and distinguish seeds is
311 olfactory perception and that final choice is determined by surface-derived hydrocarbons (Ali
312 et al., 2022). Thus, foraging in carabid beetles is likely an active process guided by specific
313 sensory information gathered from the environment to assess overall food quality (Ali et al.,
314 2022; Kielty et al., 1996; Law and Gallagher, 2015; Tréfás et al., 2001). Studies have also
315 demonstrated that carabid foraging behavior depends on the surrounding olfactory context and
316 perceived level of risk. (Blubaugh et al., 2017; Charalabidis et al., 2019, 2017). This is
317 illustrated, here, by the differences in foraging behavior of females toward *V. arvensis* seeds
318 when exposed to *P. melanarius* individuals, compared to foraging alone.

319 Although space use by females did not differ between treatments, total *V. arvensis*
320 consumption increased when females foraged in a context of potential encounters with *P.*
321 *melanarius* individuals. This change in interest in *V. arvensis* seeds can be explained as a
322 decrease in the selectivity of females when exposed to what might be perceived as signals of
323 risk. Given that foraging and risk assessment are both cognitively challenging tasks, they are
324 often considered to be in conflict (Beauchamp, 2008; Milinski and Heller, 1978; Sih, 1980;
325 Wang et al., 2013) or to be mutually exclusive behaviors, leading to a vigilance-foraging
326 tradeoff (Lev-ari et al., 2022; Lima and Dill, 1990; Nonacs and Blumstein, 2010). Individuals
327 are thus expected to reduce risk by spending relatively less time in the assessment of the quality
328 of encountered food items (Higginson et al., 2012). Previous results have shown that carabid
329 beetles can adjust their selectivity for food items based on the level of perceived risk
330 (Charalabidis et al., 2019, 2017). Here, however, we found that only females reacted to the

331 presence of *P. melanarius* individuals, with males not changing their foraging behavior or seeds
332 acceptance. From the observed latency to first acceptance of a seed, which did not differ
333 between treatments, sexes or seed species, males appear just as interested in eating as females.
334 After one hour, a similar number of individuals of each sex had eaten at least one seed of the
335 weed species offered to them, regardless of treatment. However, this behaviour seems to change
336 after the first seed encounter, with females eating more *V. arvensis* seeds in the presence of *P.*
337 *melanarius* than males. Sex differences in food consumption levels in carabids have already
338 been observed (Kulkarni et al., 2015a; Saska et al., 2010) and have been explained as an effect
339 of investment by carabid females in the energetically costly process of egg production
340 (Hayward and Gillooly, 2011). Fecundity in female carabids is related to adult diet (Fawki and
341 Toft, 2005; Jorgensen and Toft, 1997; Kulkarni et al., 2015b; Wallin et al., 1992) with the
342 number of eggs produced being related to the amount of food available (Currie et al., 1996;
343 Juliano, 1986; Knapp and Uhnová, 2014; Murdoch, 1966). The seed-based diet of carabids has
344 been shown to affect their survival, overall growth and the subsequent developmental rate of
345 the offspring (Saska, 2005; Saska and Jarošík, 2001). Females also show a higher relative gain
346 in body mass after intensive feeding and a higher relative fat level than males. This may reflect
347 physiological differences between the sexes, which might allow females to increase their mass
348 more than males when food is available, storing energy as lipids, and thereby better manage
349 periods of food shortage (Knapp, 2016; Yarwood et al., 2021). The foraging behaviour of
350 female carabid beetles may therefore differ greatly from that of males, in order to maximize
351 food intake when it is available (Sasakawa, 2010; Szyszko et al., 2004) and to achieve a better
352 body condition than males prior to the overwintering period to maximize reproductive success
353 in the following spring (Baranovská et al., 2014; Knapp and Saska, 2012; Lovei and
354 Sunderland, 1996). In this experiment females may have sacrificed a potential food preference
355 for safety by reducing their level of selectivity for seeds and accepting food of whatever quality
356 in the central part of the arena where safety was perceived to be highest (Altendorf et al., 2001;
357 Blubaugh et al., 2017; Lima and Dill, 1990; Pilakouta, 2009).

358 The lack of observed change in feeding behavior of males could be due to differences
359 in their assessment of the level of risk (Tapia-Lewin and Pardo, 2014). Here, foraging *H. affinis*
360 were exposed to live *P. melanarius*, but were also provided with a safe zone (i.e. the central
361 zone of the arena). In previous studies (e.g. Charalabidis et al. 2017, 2019), predation risk was
362 simulated with olfactory cues from *P. melanarius* and a safe zone was not provided. The
363 availability of the safe area in this experiment might therefore have reduced the overall

364 perception of risk (Lima and Bednekoff, 1999; Nersesian et al., 2012; Unck et al., 2009) and
365 consequently the need for males to modify their food choices. The larger body size of females
366 means that their food demand per individual is also greater. In addition, they must spend time
367 searching for suitable egg-laying sites and laying their eggs, and thus have less time available
368 for foraging. Males search for females but may combine this activity with foraging (Bilde and
369 Toft, 1998).

370 The lack of significant differences between treatments and sex for seed consumption
371 after 24 hours could be due to a maximum threshold of seeds that individuals are able to
372 consume before reaching satiety (Mols, 1988). Although the dynamics of consumption during
373 the first 7 hours may vary, a maximum threshold would mean that the average number of seeds
374 consumed after 24 hours is similar in treatments, provided sufficient seeds are available. Future
375 experiments should investigate the 24-hour consumption kinetics in treatments with and
376 without potential risk cues, focusing specifically on consumption levels and satiety thresholds,
377 to explore this expectation.

378 Our results support the expectations that the foraging behaviour of carabid beetles depends on
379 the context in which they forage and that they change their food choices based on potential risks
380 they perceive in their environment (Blubaugh et al., 2017; Carbonne et al., 2019; Charalabidis
381 et al., 2019, 2017). The responses of individuals are less strong when safety patches are
382 available in the environment, however, probably due to a diminished perception of risk
383 provided by the possibility of escape. *H. affinis* females still adapt their foraging behavior when
384 exposed to *P. melanarius* individuals, showing that the perception of the level of risk is
385 probably sex-specific in carabid beetles. An important result here was that while the kinetics of
386 consumption differed the total number of seeds consumed after 24 hours did not vary between
387 treatments. Evaluating the total amount of seed consumed over a long period of time may
388 therefore be misleading, and we suggest that a greater focus on consumption kinetics is
389 necessary if we are to understand the interest of carabid beetles in different combinations of
390 weed species and foraging context, and thus better predict the trophic linkages observed
391 between carabid beetles and weed species, within agricultural communities, and their associated
392 levels of seed consumption.

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APPENDICES

Table A1: Mean cumulative number (bootstrapped +/- 95% CI) of seed consumed by both sexes of *H. affinis* in each of the four treatments and at each sample date

Females with <i>T. officinale</i>						Males with <i>T. officinale</i>				
	Control	Predation				Control	Predation			
1h	0.87, [0.1; 1.8]	0.93, [0.0; 2.7]	$\chi^2 = 0.004$	df=1	P= 0.95	1.71, [0.0; 3.9]	1, [0.7; 2.3]	$\chi^2 = 0.22$	df=1	P= 0.64
2h	1.33, [0.3; 2.9]	1, [0.0; 2.8]	$\chi^2 = 0.09$	df=1	P= 0.76	2.5, [0.4; 5.4]	1.67, [0.3; 3.2]	$\chi^2 = 0.19$	df=1	P= 0.66
3h	2.27, [0.4; 4.9]	1.93, [0.0; 5.6]	$\chi^2 = 0.02$	df=1	P= 0.88	2.71, [0.6; 5.6]	2.73, [1.2; 4.3]	$\chi^2 = 0.0001$	df=1	P= 0.99
4h	3, [0.7; 6.3]	2.07, [0.0; 6.0]	$\chi^2 = 0.11$	df=1	P= 0.74	3.21, [1; 6.5]	3.4, [1.5; 5.4]	$\chi^2 = 0.007$	df=1	P= 0.93
5h	3.4, [0.7; 7.5]	2.2, [0.1; 6.1]	$\chi^2 = 0.17$	df=1	P= 0.68	3.64, [1.2; 6.9]	3.67, [1.9; 5.6]	$\chi^2 = 0.0001$	df=1	P= 0.99
6h	3.47, [0.7; 7.6]	2.47, [0.1; 6.7]	$\chi^2 = 0.10$	df=1	P= 0.74	3.64, [1.3; 7.07]	3.67, [1.8; 5.7]	$\chi^2 = 0.0001$	df=1	P= 0.99
7h	3.67, [0.9; 7.7]	2.47, [0.1; 6.6]	$\chi^2 = 0.17$	df=1	P= 0.68	3.64, [1.2; 6.9]	3.67, [1.9; 5.7]	$\chi^2 = 0.0001$	df=1	P= 0.99
24h	24.8, [16.1; 34.1]	18.93, [13.2; 24.5]	F= 1.09	df=1,28	P= 0.3	17.5, [14; 21.2]	18.4, [15.3; 21.6]	F= 0.13	df=1,28	P= 0.72
48h	36.67, [27.3; 45.8]	32.93, [23.07; 42.5]	F= 0.27	df=1,28	P= 0.60	32.29, [25.1; 39.4]	32.8, [28.4; 36.7]	F= 1.01	df=1,28	P= 0.91
72h	50, [41.07; 58.6]	43.93, [31.5; 55.9]	F= 0.59	df=1,28	P= 0.45	45.85, [37.07; 54.3]	49.67, [43.7; 55.5]	F= 0.48	df=1,28	P= 0.49
Females with <i>V. arvensis</i>						Males with <i>V. arvensis</i>				
	Control	Predation				Control	Predation			
1h	0.33, [0.0; 0.8]	0.80, [0.0; 2.1]	$\chi^2 = 0.61$	df=1	P= 0.43	0.27, [0.0; 0.6]	0.40, [0.0; 1.07]	$\chi^2 = 0.14$	df=1	P= 0.70
2h	0.47, [0.1; 0.9]	1.80, [0.3; 3.8]	$\chi^2 = 2.11$	df=1	P= 0.14	1.00, [0.3; 1.8]	0.73, [0.0; 1.5]	$\chi^2 = 0.14$	df=1	P= 0.70
3h	0.53, [0.1; 1.1]	2.67, [0.7; 4.9]	$\chi^2 = 3.13$	df=1	P= 0.08	1.47, [0.4; 2.8]	1.2, [0.3; 2.3]	$\chi^2 = 0.08$	df=1	P= 0.77
4h	0.67, [0.1; 1.3]	3.33, [1.5; 5.5]	$\chi^2 = 4.86$	df=1	P= 0.03	1.8, [0.5; 3.7]	1.4, [0.5; 2.5]	$\chi^2 = 0.15$	df=1	P= 0.70
5h	0.67, [0.1; 1.3]	3.4, [1.5; 5.6]	$\chi^2 = 4.97$	df=1	P= 0.03	2.07, [0.6; 4.1]	1.67, [0.5; 3.07]	$\chi^2 = 0.11$	df=1	P= 0.74
6h	0.73, [0.1; 1.5]	3.4, [1.5; 5.6]	$\chi^2 = 4.49$	df=1	P= 0.03	2.2, [0.6; 4.5]	1.87, [0.7; 3.2]	$\chi^2 = 0.07$	df=1	P= 0.79
7h	0.73, [0.1; 1.4]	3.4, [1.5; 5.6]	$\chi^2 = 4.49$	df=1	P= 0.03	2.27, [0.6; 4.6]	1.87, [0.7; 3.2]	$\chi^2 = 0.10$	df=1	P= 0.75

24h	10.87, [7.1; 14.7]	15.67, [12.5; 18.5]	F= 3.55	df=1,28	P= 0.07	11.73, [9.4; 14.3]	9.87, [7.8; 11.8]	F= 1.21	df=1,28	P= 0.28
48h	18.27, [13.7; 22.8]	24.73, [20.07; 28.8]	F= 3.77	df=1,28	P= 0.06	20.13, [16.3; 24.07]	17.47, [13.9; 20.7]	F= 0.94	df=1,28	P= 0.34
72h	27.73, [23.0; 32.7]	31.93, [25.5; 37.9]	F= 1.02	df=1,28	P= 0.32	29.6, [23.9; 35.3]	25.47, [19.5; 31.6]	F= 0.88	df=1,28	P= 0.36

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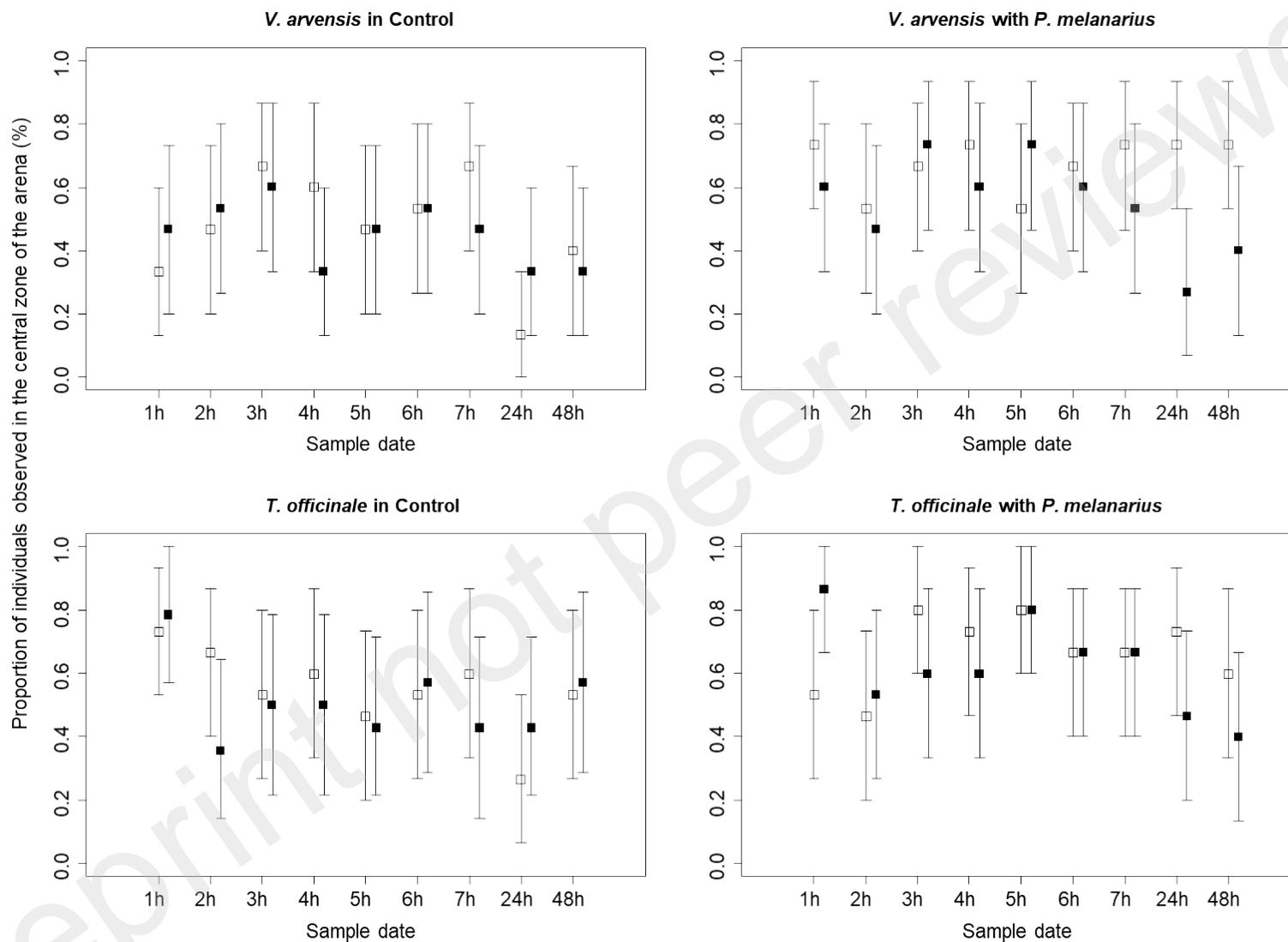


Figure A1: Space use across treatments and weed species, as the proportion of time (bootstrapped 95%CI) females (□) and males (■) *H. affinis* were recorded in the central area of the arena.

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