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# Sex-specific foraging response to interspecific interactions in carabid beetles

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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 ( $18 \pm 1$  °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

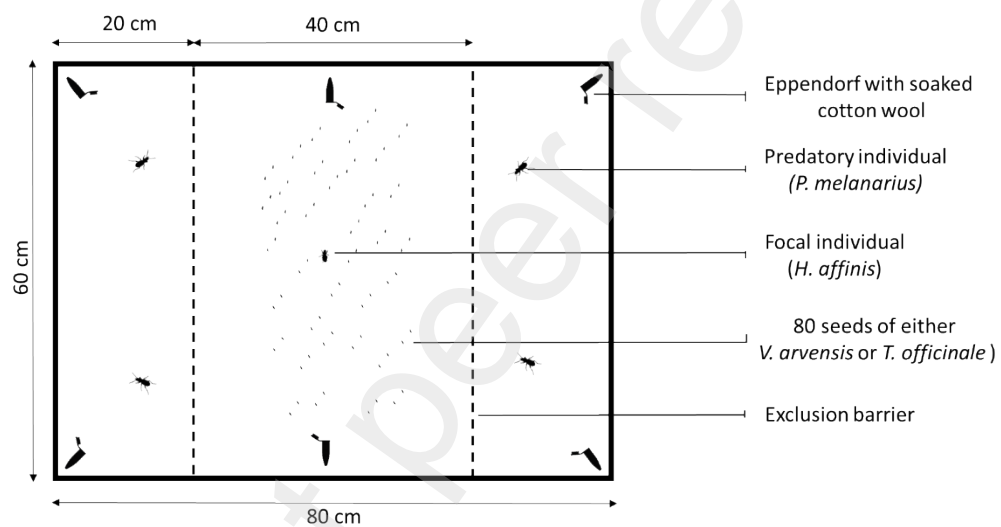
131 A total of 119 individuals of *H. affinis* (60 females and 59 males) were tested under four  
132 different treatments:

- 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/m<sup>2</sup>) is still lower than the reported seeds shed by  
165 weeds in field studies: 3700-24 200 seeds/m<sup>2</sup> for *T. officinale* (Honek et al., 2005) and  
166 approximately 20 000 seeds/m<sup>2</sup> 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.

<b>Control</b>											
	<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	<b>P = 0.001</b>	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	<b>P &lt; 0.001</b>	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	<b>P &lt; 0.001</b>	F = 0.08	df=1,56	P = 0.77	F = 0.62	df=1,55	P = 0.43
<b>Presence of <i>P. melanarius</i></b>											
	<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	<b>P =0.004</b>	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	<b>P &lt;0.001</b>	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	<b>P &lt; 0.001</b>	F = 0.007	df=1,57	P = 0.93	F = 2.07	df=1,56	P = 0.16

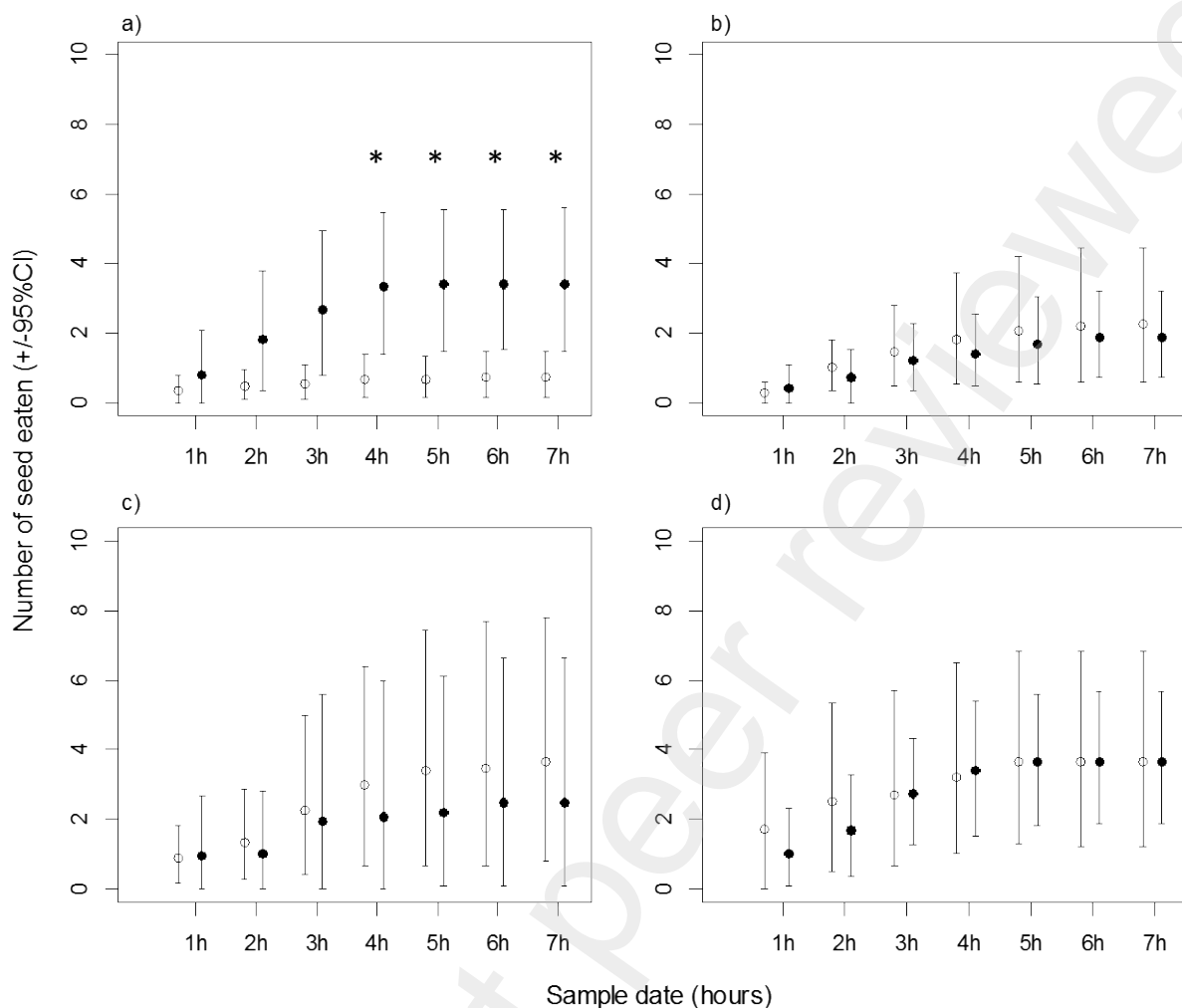
230 **3.2. Effect of the presence or absence of *P. melanarius* on seed consumption**

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* ( $\chi^2$   
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:  $\chi^2= 0.05$ ,  $df=1$ ,  $P= 0.82$ ).

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#### 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

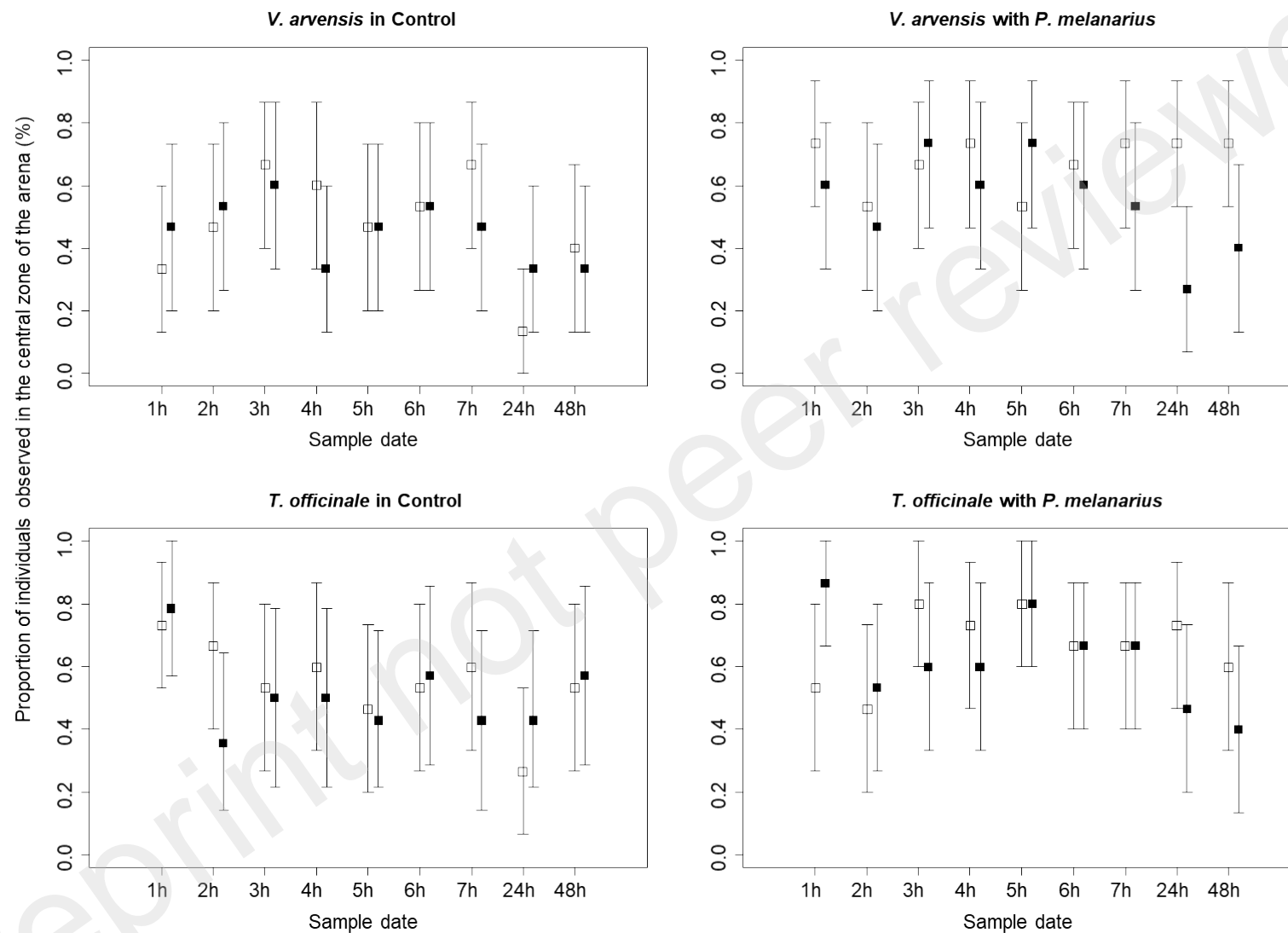
**Table A1:** Mean cumulative number (bootstrapped +/- 95% CI) of seed consumed by both sexes of *H. affinis* in each of the four treatments and at each sample date

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	<b>P= 0.03</b>	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	<b>P= 0.03</b>	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	<b>P= 0.03</b>	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	<b>P= 0.03</b>	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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Preprint not peer reviewed



**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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