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

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## HIGHLIGHTS

- Effects of interspecies interactions on foraging biocontrol agents are underexamined.
- We tested whether interspecific interactions alter consumption levels or dynamics.
- Interspecies interactions impact carabids' consumption dynamics rather than levels.
- Interspecific interactions induce a higher response in females than in males.

## ARTICLE INFO

## ABSTRACT

Carabids beetles are considered important biocontrol agents of weeds, but predicting levels of weed seed consumption and regulation is difficult. Olfactory cues from predators or potential competitors alter the selection and consumption of particular food resources by foraging individuals. Whether this leads to changes in consumption levels or simply to changes in the rate at which consumption takes place over time is not yet known. Identifying and understanding the factors that drive the seed foraging behaviour of carabid beetles, in the context of interspecific interaction, is essential for predicting consumption levels in different carabid communities and hence improve the ecosystem service of weed regulation by carabid beetles.

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

Even though the total number of seeds consumed after 24 h did not differ, the dynamic of seed consumption by *H. affinis* changed significantly in the presence of *P. melanarius*. The attraction of individuals to the seeds diminished over time, indicating a probable state of satiety being reached. This suggests that looking at the total number of seeds consumed after a long period of time may be misleading and that a greater focus on of the temporal dynamics of consumption is needed if we are to understand carabids interest in specific weed species in a specific foraging context. We found that only females seemed to react to the presence of *P. melanarius* individuals, indicating that the perception of the level of risk may be sex-specific in carabid beetles.

## 1. Introduction

Crop damage due to pests causes significant yield reduction in agricultural crops (Marshall et al., 2003). Weeds alone can account for up to 30 % of yield losses (Oerke, 2006). Weed seed feeding carabid beetles can consume a substantial amount of weed seeds in the field (Thiele, 1977; Honek et al., 2003; Menalled et al., 2007; Saska et al., 2008; Frank et al., 2011; Ward et al., 2014) and are the primary invertebrate consumers of weed seeds (Honek et al., 2003). Their polyphagous diet (Thiele, 1977; Lovei and Sunderland, 1996; Kromp, 1999) and

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potential regulation effect on pest species have led to interest in carabid beetles as biocontrol agents for agricultural weeds (Kulkarni et al., 2015a; Schumacher et al., 2020; Fischer et al., 2021; De Heij et al., 2022). Although the estimation of weed seed predation in field conditions has been linked to the abundance of carabids (Bohan et al., 2011), the consumption levels reported in field studies are highly variable, making it difficult to draw conclusions about the effectiveness of weed seed regulation (Westerman et al., 2003; Saska et al., 2008; Davis and Raghu, 2010; Petit et al., 2014).Variation in consumption levels may be explained in part by differences in the feeding preferences of carabid beetles for certain seed species, as demonstrated in laboratory choice tests (Honek et al., 2003, 2006, 2007, 2011; Petit et al., 2014; Saska et al., 2019). Trophic relationships between specific carabid and weed species are only partially documented (Saska et al., 2019), and the preferences identified from laboratory choice tests rarely match the observed choices of carabids in the field (Honek et al., 2003; Petit et al., 2014). An understanding of those factors that drive carabid beetles to accept or reject a seed in the field is necessary to improve the operational utility of weed regulation by carabid beetles.

Farmland communities are composed of granivore, omnivore and predatory species, each of which can be cannibalistic, inter-specific predators and competitors (Currie et al., 1996; McKemey et al., 2003). Interspecific interactions are widespread, and their impact on foraging behaviour and the wider ecological consequences of interactions has rarely been examined (Guy et al., 2008; Charalabidis et al., 2017, 2019; Carbonne et al., 2019; De Heij et al., 2022). Carabid beetles may adjust their foraging behaviour according to the biotic context (Blubaugh et al., 2017; Charalabidis et al., 2017), with olfactory cues from potential predators and competitors affecting the level of consumption of foraging individuals, modifying both the selection and consumption of food resources (Wyatt Hoback et al., 2001; Sivy et al., 2011; Blubaugh et al., 2017; Charalabidis et al., 2017, 2019; Carbonne et al., 2019). For example, carabid beetles have been shown, in laboratory experiments, to increase their seed consumption when foraging under stress (Blubaugh et al., 2017; Charalabidis et al., 2017). These results suggest that the foraging behavior of an individual carabid beetle, and thus the level of consumption of observed weed species, is shaped by the composition of both the carabid and weed communities. It could therefore be hypothesised that some carabid communities would result in overall increased seed consumption while others would result in overall reduced seed consumption. An often overlooked alternative is that the total consumption remains unchanged irrespective of the carabid community composition. The only factor that varies is the rate at which consumption takes place over time. The total number of seeds that an individual can consume could be set by a maximum consumption threshold, as carabids individuals apparently avoid filling their abdomen completely if they have enough reserves stored (Mols, 1988), and thus only the temporal dynamic of consumption (i.e. the rate at which consumption takes place over time) would be expected to change (Honek et al., 2003). Solely focusing on maximum consumption levels can lead to a poor understanding of the foraging behavior of individuals and, consequently, result in erroneous predictions regarding the potential ecosystem services provided by a particular community of carabids. It could be hypothesized, therefore, that some carabid communities would provide increased seed consumption while others may have reduced seed consumption. Furthermore, as carabid species do not seem to respond in the same way to stress cues (Charalabidis et al., 2019), their temporal dynamic of consumption will differ potentially affecting their species-specific contribution to weed seed regulation. A better understanding of how such changes in foraging behaviour occur, would deliver a predictive explanation of the observed trophic links between carabid and weed species, within farmland communities, and their associated seed consumption levels.

Foragers can choose where to forage and whether to avoid areas of potential interspecific interactions (Guy et al., 2008). Past experiments on the effect of signals from predators or competitors on foraging behaviour of carabid beetles have focused mainly on olfactory chemical cues rather than direct interactions through encounters, and have often not provided areas where signals are absent (Charalabidis et al., 2017, 2019; De Heij et al., 2023). Given that an encounter with a predator induces a more acute perception of risk than indirect signals alone (Tapia-Lewin and Pardo, 2014), we expect that individuals exposed to potential predators will express more intense behavioural changes compared with chemicals cues alone (Blubaugh et al., 2017; Charalabidis et al., 2017, 2019; De Heij et al., 2023). This could result in more widespread flight behaviours, for example, and thus potentially lead to lower levels of seed consumption. However, compensatory feeding has already been observed in insects, whereby consumption increases to compensate for previously induced reductions in food availability (Hawlena and Schmitz, 2010; Thaler et al., 2012; Blubaugh et al., 2017; De Heij et al., 2023). Because immobile seeds are easy prey items to acquire, requiring less active foraging than mobile prey and lower transportation costs, seeds might be consumed as a 'stress food' by carabids (Blubaugh et al., 2017). This could lead to increased consumption levels by stressed individuals for the duration of the experiment.

To examine the impact of interspecies interactions on carabid foraging behaviour, we investigated how the interest of *Harpalus affinis* (Schrank) in seeds from two weed species, *Viola arvensis* Murray, and *Taraxacum officinale* F.H. Wigg., changed over time during potential encounters with individuals of *Pterostichus melanarius* (Illiger). To investigate the impact of areas free of interspecific signals on the consumption levels of individuals, safe zones were also provided in the test arenas (Blubaugh et al., 2017).

*H. affinis* is an abundant carabid beetle able to adapt its foraging strategy to the olfactory context (i.e. to the presence/absence of olfactory cues from potential predators or competitors) (Charalabidis et al., 2017, 2019). Individuals of *P. melanarius* were chosen to provide the risk cues because they are voracious predators of live prey (Currie et al., 1996; Kromp, 1999; McKemey et al., 2003; Foltan, 2004; Hatteland et al., 2010), are found with *H. affinis* in European farmland communities and their olfactory cues have been documented to change the foraging behaviour of *H. affinis* (Charalabidis et al., 2017, 2019). The latency time to first seed acceptance, total consumption levels, and the temporal dynamics of consumption were taken as metrics of individual foraging behaviour. The positions of the focal individuals within the arena were recorded hourly to explore the relationship between their likelihood of being observed more frequently in a specific zone and the presence or absence of *P. melanarius* in the arena, thereby examining *H. affinis* individual's inclination to flee and remain in safe areas when *P. melanarius* was present.

## 2. Methods

### 2.1. Study systems

Both species of carabids used in the study were collected using pitfall traps at the INRAe Experimental Farm (Dijon, France; 47°14′11.4″ N 05°05′53.4″ E) between April and June 2017. Carabids were identified to species following Jeannel (1942) and maintained in plastic boxes segregated by species (34 × 19 × 11 cm for *H. affinis* and 80 × 55,9 × 15,5 cm for *P. melanarius*) in a climate-controlled chamber (18 ± 1 °C, 60 % humidity, 14:10 h light:dark cycle). Species were held in different boxes to prevent interspecific predation (Currie et al., 1996) and in different climate chambers to prevent exposure to any interspecific chemical cues for at least two weeks prior to the test. The boxes were filled with soil and moistened paper tissue. Water was provided *ad libitum* in Eppendorf tubes sealed with cotton wool. *H. affinis* individuals were fed with seeds in an equal mixture of four weed species: *V. arvensis* (0.9 mg, 1.36 mm), *T. officinale* (0.7 mg, 2.67 mm), *Senecio vulgaris* L. (0.2 mg, 1.75 mm), *Capsella bursa-pastoris* (L.) Medik. (0.1 mg, 0.8 mm). These four species were chosen because they were common in the field
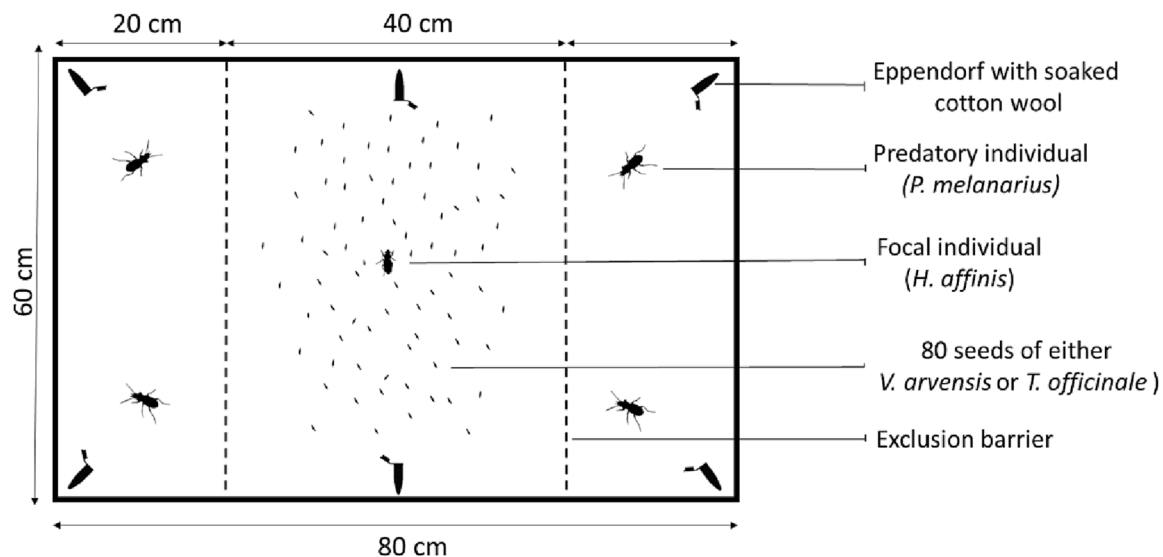
**Fig. 1.** Schematic diagram of the test arena. The arena was divided in three areas using plastic 'exclusion' barriers to exclude *P. melanarius* from the central area. The plastic barriers were drilled with holes of 4 mm in order to allow free movement of *H. affinis* individuals into the right and left areas but prevent *P. melanarius* from accessing the central area. 80 seeds of either *T. officinale* or *V. arvensis* were placed and spaced out in the central area. This representation is approximately to scale: carabids measure ~1 cm and seed ~2.5 mm in length.

where the individuals were trapped and are known to be readily consumed by this species (Petit et al., 2014; Trichard et al., 2014). Seeds used for feeding were purchased from Herbiseed ® (Twyford, Great Britain, https://www.herbiseed.com) in 2014 and kept in the laboratory collection. The *P. melanarius* individuals were fed with a combination of frozen mealworms, *Tenebrio molitor*, and pre-moistened dry cat food (Charalabidis et al., 2019). Individual *H. affinis* were isolated in round plastic containers (9 cm diameter) 62 h prior to the experiments and deprived of food to standardize their feeding history. The bottom of each petri dish was covered with a clean, moist filter paper, providing the individual forager with shelter and water, *ad libitum*.

### 2.2. Behavioural experiment

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

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

Tests were conducted in plastic trays of 80 × 60 × 15 cm divided in three compartments by plastic exclusion barriers: two external compartments of 20 cm width respectively referred as "right area" and "left area" and an internal compartment of 40 cm width (Fig. 1) referred as "central zone". Based on preliminary measurements made on *H. affinis* individuals, holes of 4 mm in diameter, made in the barriers every 2 cm, would allow only *H. affinis* to pass freely through the barriers and have access to all three areas (i.e. right, left and central area). The larger individuals of *P. melanarius* would be prevented by the size of the 4 mm holes from moving between the areas (Fig. 1). The plastic trays were filled with a thin layer of washed river sand (1.5 Kg per tray), that had been passed through a 400 μm sieve before use. The sand was used to more closely represent the porous substrates of field soils on which the carabids were caught. The thin layer of sand limited the amount of seeds

lost due to burial. Six Eppendorf tubes filled with water and sealed with cotton wool were placed (two in each area, i.e. 6 per tray), to provide an *ad libitum* water supply for all the carabids. The trays were sprayed with water twice a day (morning and late afternoon) to prevent the sand from drying out and to keep the seeds moist. This has been shown to improve the palatability and detectability of seeds by carabid beetles (Law and Gallagher, 2015). After each replication of the experiment, the sand was sieved (500 μm gauge) to retrieve the uneaten seeds. The residual chemical persistence of *P. melanarius* olfactory cues has been found to decrease with time (Guy et al., 2008) thus, the impact of the odor on the behavior of other individuals should be significantly less if they were exposed to a 2-day-old odor (Guy et al., 2008). Since sand is more porous than paper, we expect that the preservation of odors on this support is inferior to that on paper. In any case, to ensure that we had removed potential olfactory cues left by carabid beetles, the sand was washed using a sieve of 315 μm, dried in an oven at 110 °C for 48 h and sieved again to eliminate sand clumps before re-use. The cotton wool was changed and Eppendorf tubes, plastic trays and plastic barriers were cleaned using 70 % ethanol before and after each experiment.

A total of 80 seeds of the tested weed species, either *V. arvensis* or *T. officinale* according to the treatment, were randomly distributed in the central area of the tray (Fig. 1).

The number of seeds used was obtained from a pre-experiment assessment made in order to provide individuals with sufficient seeds to avoid total seed depletion during the experiment. Despite this, the seed density used in our experiment (i.e. 333 seeds/m$^2$) is still lower than the reported seeds shed by weeds in field studies: 3700–24 200 seeds/m$^2$ for *T. officinale* (Honek et al., 2005) and approximately 20 000 seeds/m$^2$ for *V. arvensis* (Gerowitt and Bodendörfer, 1998). Seeds of *V. arvensis* and *T. officinale* used in the experiment were purchased in 2017 just prior to the start of the experiment from Arbiotech (Arbiotech, Saint-Gilles, France: lcs@arbiotech.com). Seeds had a thousand-kernel-weight of 0.60 g for *V. arvensis* and 0.47 g for *T. officinale*.

For T3 and T4, two randomly chosen *P. melanarius* individuals were placed in the two outside areas of the tray (i.e. right and left areas) from where they were excluded from accessing the seeds located in the central area (Fig. 1), giving a total of 4 *P. melanarius* per tray. The number of *P. melanarius* used in the test was based on the work of Guy et al., (2008), who demonstrated that perception of conspecifics by carabid individuals does not increase above a threshold of four individuals. Since Guy et al.
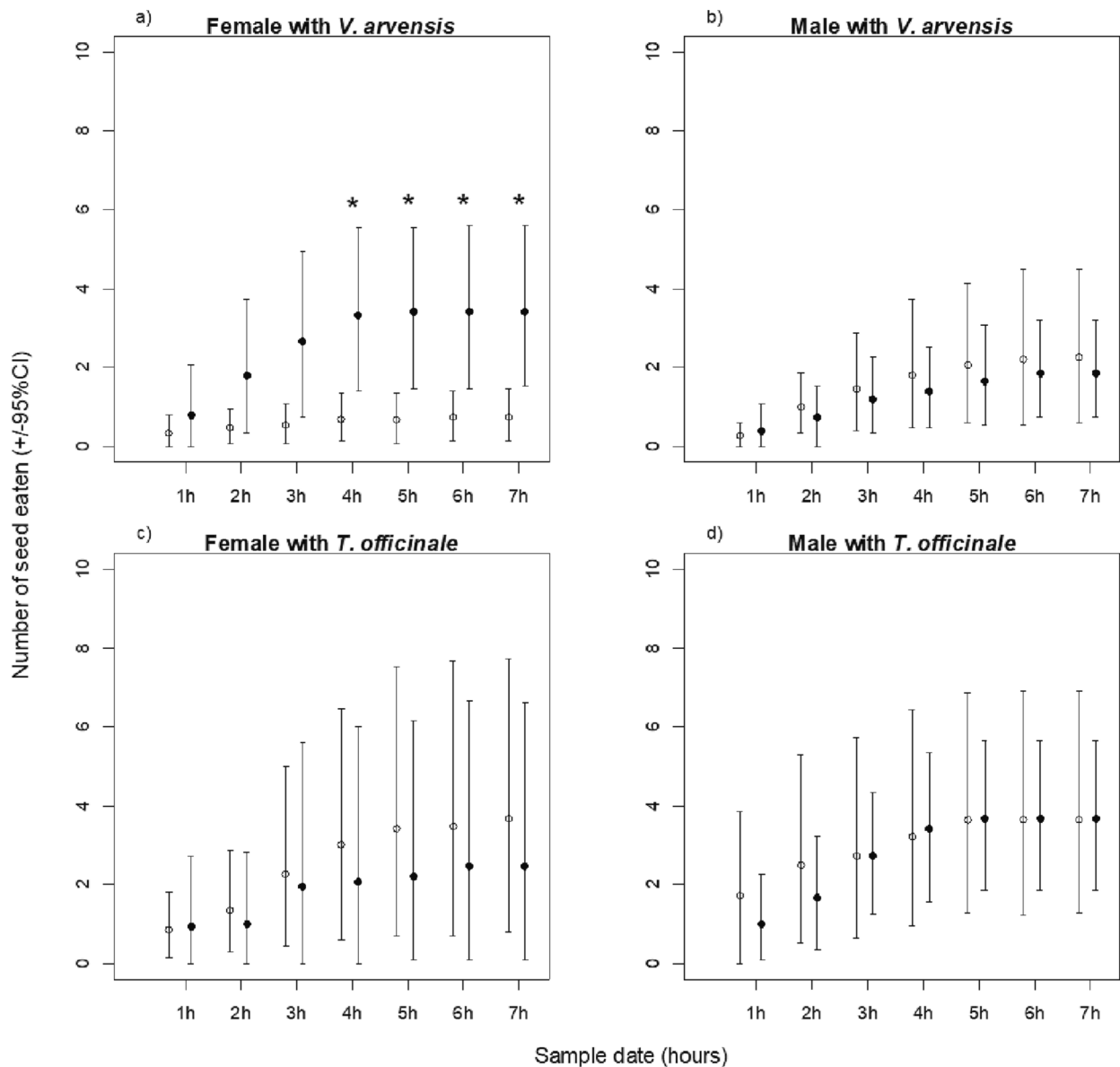
**Fig. 2.** Cumulative number of seed eaten (boostrapped +/− 95 %CI) during 7 h in absence of *P. melanarius* (○) or in presence of *P. melanarius* (●) for a) females with seeds of *V. arvensis*, b) males with seeds of *V. arvensis*, c) females with seeds of *T. officinale*, d) males with seeds of *T. officinale*.

**Table 1**
Proportion of occurrence in the outer areas during the first seven hours of test across treatments (bootstrapped 95 %CI) according to the sex of *H. affinis*.

|  | *V. arvensis* in control (T1) | *T. officinale* in control (T2) | *V. arvensis* with *P. melanarius* (T3) | *T. officinale* with *P. melanarius* (T4) |
|---|---|---|---|---|
| Males | 0.55[0.40, 0.69] | 0.49[0.32, 0.66] | 0.45[0.32,0.59] | 0.38[0.28, 0.47] |
| Females | 0.53[0.4, 0.64] | 0.45[0.29, 0.63] | 0.32[0.21, 0.44] | 0.33[0.24, 0.44] |

(2008) also showed that the sex of the beetles used did not impact the perception of individuals, the sex of *P. melanarius* individuals was not considered. Temperature and humidity were recorded and treatments were randomized to avoid any effects of the position of trays in the room. The experiments were conducted under natural light conditions for multiple days, exposing the individuals to a day-night cycle that aligns with their natural nycthemeral rhythm. The experiment began during the daytime on the first day.

For each tray, the experiment started as soon as an individual of *H. affinis* was released in one of the external compartments of the arena. This starting location was chosen to increase the chance that each individual would encounter *P. melanarius* at least once during the experiment. A release directly into the central area, where the seeds are located, might have led individuals to the *H. affinis* neglecting the external compartments and thereby never encountering *P. melanarius* individuals.

The impact of *P. melanarius* individuals on the foraging behaviour of *H. affinis* individuals was first assessed by examining the latency of individuals to first seed acceptance (i.e. the time interval between the start of the experiment and the first record of a seed consumed by an individual) as an indicator of their context-dependent interest in eating seeds (Charalabidis et al., 2017). To estimate the effect on seed consumption by individuals, the total number of seeds consumed by each individual was recorded every hour for the first 7 h in order to get a fine-
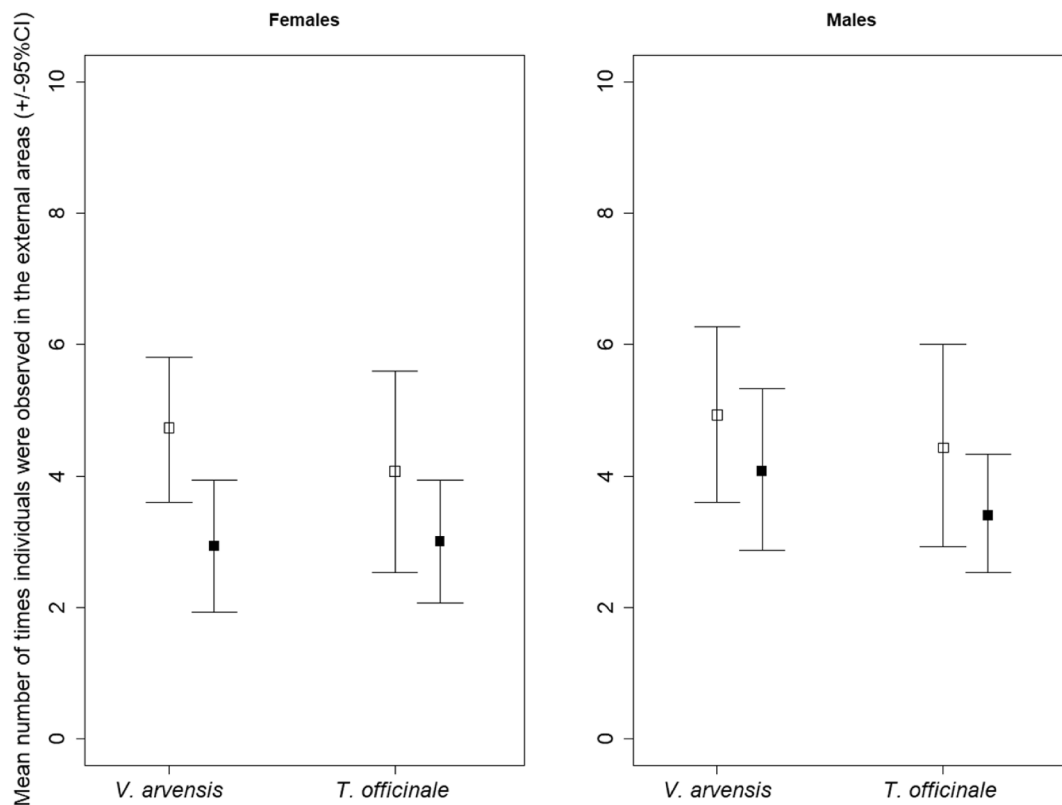
**Fig. A1.** Mean number of times individuals were recorded in the external areas of the arenas across treatments (absence of *P. melanarius* (□) and presence of *P. melanarius* (■)) and weed species (bootstrapped 95 %CI).

grained view of consumption dynamics during the first few hours after the seed encounter. Subsequent measurements were taken at 24, 48 and 72 h. On each sampling date, the number of *H. affinis* that had not yet consumed seeds was recorded. To evaluate the influence of *P. melanarius* on the probability of *H. affinis* individuals visiting the left and right sections of the arena, the location of the focal individual in the arena was noted every hour for the first 7 h (Fig. 1). The frequency of individual recordings in each area was subsequently analyzed to investigate the correlation between their higher likelihood of being observed in a specific zone and the presence or absence of *P. melanarius* in the arena.

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

### 2.3. Statistical analysis

All statistical analyses were done in R 4.3.0 (R Core Team, 2023).

In order to simplify the models a new variable called 'treatment' was created by merging the "seed species" variable and the "condition" (i.e. presence or absence of *P. melanarius*) variable. Choice was made to merge these two variables as the new variable "treatment" matches the treatment structure (i.e. "T1": foraging alone on *V. arvensis* seeds, "T2": foraging alone on *T. officinale* seeds, "T3": foraging on *V. arvensis* seeds in the presence of *P. melanarius* and "T4": foraging on *T. officinale* seeds in the presence of *P. melanarius*) in which individuals were foraging.

Latencies of the first seed acceptance in the four treatments (i.e. T1, T2, T3 and T4) were compared by means of the Cox proportional hazard models (Dechaume Moncharmont et al., 2003) in the 'cox.ph' function

from the package 'survival' (Therneau and Grambsch, 2000; Therneau, 2023). The full model included as effects the treatment (*i.e* T1, T2, T3 and T4), the sex of the focal individual (i.e. female or male) and their interaction. For each Cox regression model fit, the proportional hazards assumption was assessed using the 'cox.zph' function.

Since data on seed consumption were count data, the dynamic of consumption in the first 7 h of the experiment was modelled as a generalized linear mixed model using a negative binomial distribution family (*Goodness of fit*, $\chi^2 = 0.65$, P = 0.42). The full model included as effects the treatment, the sex of the focal individual, and the sample date (a continuous variable ranging from 1 to 7) and their interactions. We used the individual ID as a random factor to account for repeated measures on the same individual (Zuur et al., 2009).

The frequency at which *H. affinis* individuals were observed in each compartment of the arena during the first seven hours of the experiment, was treated as a series of independent experiments and was modelled as a generalized linear mixed model using a binomial distribution family. Observations made in the central zone were categorized as failures, while observations made in either of the two outer zones (i.e. left and right) were considered successes. The full model included the effect of the treatment, the sex of the focal individual and their interaction. We used the individual ID as a random factor to account for repeated measures on the same individual (Zuur et al., 2009).

To identify the best models based on AIC or BIC (Bolker, 2008), all full models were compared sequentially to nested sub-models with and without a given covariate using stepwise backward elimination of non-significant variables and interaction terms. Differences between nested models were assessed using a likelihood ratio test with the function *lrtest* from the package *lmtest* (Zeileis and Hothorn, 2002). Models assumptions were assessed by checking residuals distribution and homoscedasticity using the package *DHARMa* (Hartig, 2022).

**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 (for the first 7 h of test).

| | Females with *T. officinale* | | | | | Males with *T. officinale* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Without *P. melanarius* | With *P. melanarius* | | | | Without *P. melanarius* | With *P. melanarius* | | | |
| 1 h | 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 |
| 2 h | 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 |
| 3 h | 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 |
| 4 h | 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 |
| 5 h | 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 |
| 6 h | 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 |
| 7 h | 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 |
| 24 h | 24.8, [16.1; 34.1] | 18.93, [13.2; 24.5] | $\chi^2 = 0.68$ | df = 1 | P = 0.41 | 17.5, [14; 21.2] | 18.4, [15.3; 21.6] | $\chi^2 = 0.1360$ | df = 1 | P = 0.71 |
| 48 h | 36.67, [27.3; 45.8] | 32.93, [23.07; 42.5] | $\chi^2 = 3.01$ | df = 1 | P = 0.08 | 32.29, [25.1; 39.4] | 32.8, [28.4; 36.7] | $\chi^2 = 0.013$ | df = 1 | P = 0.91 |
| 72 h | 50, [41.07, 58.6] | 43.93, [31.5; 55.9] | $\chi^2 = 0.35$ | df = 1 | P = 0.55 | 45.85, [37.07; 54.3] | 49.67, [43.7; 55.5] | $\chi^2 = 0.435$ | df = 1 | P = 0.51 |

| | Females with *V. arvensis* | | | | | Males with *V. arvensis* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Without *P. melanarius* | With *P. melanarius* | | | | Without *P. melanarius* | With *P. melanarius* | | | |
| 1 h | 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 |
| 2 h | 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 |
| 3 h | 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 |
| **4 h** | **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 |
| **5 h** | **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 |
| **6 h** | **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 |
| **7 h** | **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 |
| 24 h | 10.87, [7.1; 14.7] | 15.67, [12.5; 18.5] | $\chi^2 = 1.90$ | df = 1 | P = 0.17 | 11.73, [9.4; 14.3] | 9.87, [7.8; 11.8] | $\chi^2 = 1.20$ | df = 1 | P = 0.27 |
| 48 h | 18.27, [13.7; 22.8] | 24.73, [20.07; 28.8] | $\chi^2 = 2.31$ | df = 1 | P = 0.13 | 20.13, [16.3; 24.07] | 17.47, [13.9; 20.7] | $\chi^2 = 0.81$ | df = 1 | P = 0.37 |
| 72 h | 27.73, [23.0; 32.7] | 31.93, [25.5; 37.9] | $\chi^2 = 0.82$ | df = 1 | P = 0.36 | 29.6, [23.9; 35.3] | 25.47, [19.5; 31.6] | $\chi^2 = 0.72$ | df = 1 | P = 0.39 |

## 3. Results

### 3.1. Impact of the treatment and sex of individuals on their latency to first seed acceptance

The latency to first seed acceptance did not differ significantly between the treatments (Cox model, $\chi^2 = 1.27$, df = 3, P = 0.74). There was an effect of the sex of the focal individual with a latency to first acceptance of a seed shorter for males than females (Cox model, $\chi^2 = 5.76$, df = 1, P = 0.016, hazard ratio = 0.63, 95 %IC [0.43, 0.92]). There was no effect of interaction between sex and the treatment (Cox model, $\chi^2 = 3.53$, df = 3, P = 0.32).

### 3.2. Relationship between the probability of seed consumption and the weed species, the presence or absence of P. melanarius, the sex of focal individual and time

After performing backward stepwise selection starting from the full model that include all 3 factors (i.e. treatment, sex of the focal individual and the sample date) and their interactions, a best unique model was identified based on model fit criteria and statistical significance of variables:

$$\log(P_i)\ \beta_0 + \beta_1 treatment_i + \beta_2 sampledate_i + \beta_3 sex_i + \beta_4(sex_i \times treatment_i) + \alpha_i$$

Where $P_i$ is the probability of seed consumption by an individual i; $\alpha_i$ the random intercept for individual i; $\beta_0$ is the estimate for the intercept; $\beta_1, \beta_2, \beta_3$ are the coefficients representing the effects of the corresponding variables; $treatment_i$ represents the treatment variable for individual i; $sampledate_i$ represents the date of sampling for individual i and $sex_i$ represents the sex of the focal individual i. The probability of seed consumption during the first 7 h of test decreased by 30.9 % (95 %CI = [22 %; 39 %]) between successive sampling date ($\chi^2 = 37.44$, df = 1, P < 0.001). Hence, the likelihood of seed consumption decreased over time (Fig. 2). There was no effect of the triple interaction between the treatment, sexes of individuals and sample date ($\chi^2 = 4.52$, df = 3, P = 0.21) nor the interaction between sexes and the sample date ($\chi^2 = 2.18$, df = 1, P = 0.14) or between the treatment and the sample date ($\chi^2 = 5.14$, df = 3, P = 0.16). There was however a significant interaction between the treatment and the sex of individual ($\chi^2 = 10.23$, df = 1, P =

0.017). To assess the relationship between the sex of the focal individual, the treatment and the effect of sampling date on individual consumption, we analysed separately the dataset according to sex and weed species at each sample date (Fig. 2, Table A1). Our results showed that after the first four hours of the trial, *H. affinis* females had consumed cumulatively more *V. arvensis* seeds in the presence of *P. melanarius* than in the control group (Fig. 2, Table A1). Males, however, did not differ in their seed dynamic consumption between treatments (Fig. 2, Table A1).

After 24 h of test, there was no significant difference in the number of *T. officinale* or *V. arvensis* seeds eaten by females or males in presence or absence of *P. melanarius* (Table A1). Seed consumption of *T. officinale* or *V. arvensis* by males did not significantly differ between treatments (Table A1).

### 3.3. Proportion of occurrence of H. affinis individuals in the outer areas of the arena

During the first 7 h of test, the number of times individuals were recorded in the outer areas of the arena did not differ between treatments ($\chi^2 = 5.25$, df = 3, P = 0.15, Table 1, Fig. A1) or between sexes ($\chi^2 = 0.22$, df = 1, P = 0.64). There was no effect of the interaction between the treatment and the sex of individuals ($\chi^2 = 4.56$, df = 3, P = 0.21).

## 4. Discussion

Our results show that the rate of consumption of both seed species decreased during the first seven hours of the test, suggesting a level of satiety reached within this time frame, or at least a temporal decline in individuals' interest in seeds. This is is reinforced by the lack of significant differences between treatments and sex for seed consumption after 24 h, suggesting that individuals might only be able to eat a certain amount of seeds in a given time span before reaching satiety (Honek et al., 2003). This is consistent with previous reports that carabids do not eat more than required if they have enough stored reserves (Mols, 1988). However, it is interesting to note that the consumption dynamics of the two weed species during the first few hours of the trial differed by sex and treatment. During the first seven hours of the trial, *H. affinis* females had a higher consumption rate of *V. arvensis* when exposed to *P. melanarius* individuals, compared to the control (i.e. in absence of *P. melanarius*). Moreover, this difference in consumption does not seem to be explained by the fact that individuals remain only in the central part of the arena, where the seeds were located, when foraging in the presence of *P. melanarius*. Indeed, during the first 7 h of the experiment, the frequency of observation of females in the central zone did not differ from the control. Thus, even if the seed consumption of individuals over a day appears to be limited by a maximum threshold, since differences in consumption levels were no longer visible after 24 h, it is important to note that the dynamics of this consumption, i.e. the speed at which it takes place, may evolve according to potential interspecific interactions. Future experiments looking at consumption levels in carabids in treatments with and without potential interactions should therefore not only look at the total consumption levels but also focus on consumption dynamics over an extended period.

However, even if this change in consumption dynamics with perceived risk is consistent with previous studies (Blubaugh et al., 2017; Charalabidis et al., 2017, 2019; De Heij et al., 2023), we found that only females reacted to the presence of *P. melanarius* individuals, with males not changing their foraging behavior or seeds acceptance in either of the treatments. Differences in foraging or exploratory behavior between male and female carabids have been previously reported (Szyszko et al., 2004; Sasakawa, 2010; Yamashita et al., 2010; Kulkarni et al., 2015b; Charalabidis et al., 2019; Yarwood et al., 2021; De Heij et al., 2023). For instance, in the study by Charalabidis et al., (2019), it was reported that *H. affinis* females took longer to start consuming seeds in a laboratory experiment compared to males. Additionally, females *H. affinis* spent more time hiding during the experiment on average. These findings are consistent with our results, which shows that the latency to first acceptance of seeds is shorter for males compared to females, regardless of the treatment.

Female insects also tend to invest more energy in egg production than males invest in sperm production (Hayward and Gillooly, 2011). As a result, females tend to conserve their energy for reproduction (Yarwood et al., 2021), exhibiting reduced activity levels until they become hungry (Wallin and Ekbom, 1994; Szyszko et al., 2004). Males, on the other hand, have the advantage of being able to combine mate finding with foraging, resulting in relatively higher activity levels. Individuals exploring more, by moving over a greater total distance and/or having greater space use are also often more risk prone than less explorative ones (Griffen et al., 2012; Royauté and Pruitt, 2015). Hence, males might be less sensitive to potential stress than female. Also, according to Bateman's principle, male individuals gain fitness by increasing their mating success whilst females increase fitness through longevity because their reproductive effort is much higher (Rolff, 2002; Hayward and Gillooly, 2011). Considering that the availability of a safe zone in this experiment may have reduced individuals' overall perception of risk (Lima and Bednekoff, 1999; Unck et al., 2009; Nersesian et al., 2012), this could explain why only females demonstrated a treatment-dependent change in foraging behavior, and also why this change was only observed on *V. arvensis* seeds and not on *T. officinale* seeds (as previously reported in studies such as Charalabidis et al., 2017, 2019). *V. arvensis* seeds were mostly overlooked by *H. affinis* females in absence of *P. melanarius* and consumption increases with the occurrence of the interspecific interaction. The fecundity of female carabids is influenced by their adult diet (Wallin et al., 1992; Jorgensen and Toft, 1997; Fawki and Toft, 2005; Kulkarni et al., 2015b) where the number of eggs produced is linked to the availability of food (Murdoch, 1966; Juliano, 1986; Currie et al., 1996; Knapp and Uhnavá, 2014). Also the seed-based diet of carabids, as well as the weed species available, has been found to impact their survival, overall growth, and the subsequent developmental rate of their offspring (Saska and Jarošík, 2001; Saska, 2005; Kulkarni et al., 2015b). It is thus possible that, in a less stressful environment, *V. arvensis* was not considered a sufficiently valuable resource to stimulate higher activity in females. Especially as Female gut capacity is lowered by maturing eggs, allowing females to eat only small amounts of food at a time (den Boer, 1986). Foraging and risk assessment are both cognitively challenging tasks and thus are often considered to be in conflict (Milinski and Heller, 1978; Sih, 1980; Beauchamp, 2008; Wang et al., 2013) or to be mutually exclusive behaviors, leading to a vigilance-foraging tradeoff (Lima and Dill, 1990; Nonacs and Blumstein, 2010; Lev-ari et al., 2022). Given that, individuals are thus expected to reduce risk by spending relatively less time in the assessment of the quality of encountered food items (Higginson et al., 2012) and focus on what is easier to catch and eat rather than looking for potential "better" alternatives. Hence, *V. arvensis* seeds may have been utilized by females as compensatory feeding in a more challenging environment (Blubaugh et al., 2017). Our results support the expectations that the foraging behaviour of carabid beetles depends on the context in which they forage and that they change their food choices based on potential risks they perceive in their environment (Blubaugh et al., 2017; Charalabidis et al., 2017, 2019; Carbonne et al., 2019; De Heij et al., 2023). The responses of individuals are reduced when safety areas are available in the environment, however, probably due to a diminished perception of risk provided by the possibility of escape. It is important to acknowledge that despite our meticulous efforts to thoroughly clean the sand, these weaker responses could also be influenced by residual odors that may have persisted, potentially contributing to a less distinct differentiation between the treatments with and without active *P. melanarius* individuals. Nevertheless, *H. affinis* females still adapt their foraging behavior when exposed to *P. melanarius* individuals, showing that the perception of the level of risk is probably sex-specific in carabid beetles.

An important result here is that while the dynamic of consumption differed the total number of seeds consumed after 24 h did not vary between treatments. Evaluating the total amount of seed consumed over a long period of time may therefore be misleading, and we suggest that a greater focus on consumption dynamics is necessary if we are to understand the interest of carabid beetles in different combinations of weed species and foraging context, and thus better predict the trophic linkages observed between carabid beetles and weed species, within agricultural communities, and their associated levels of seed consumption.

## CRediT authorship contribution statement

**Alice Charalabidis:** Supervision, Conceptualization, Methodology, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Stéphane A.P. Derocles:** Supervision, Conceptualization, Methodology, Writing – review & editing, Validation. **Diana M. Mosquera-Muñoz:** Data curation, Investigation, Formal analysis, Writing – review & editing. **Sandrine Petit:** Conceptualization, Funding acquisition, Methodology, Validation, Writing – review & editing. **François-Xavier Dechaume-Moncharmont:** Conceptualization, Methodology, Writing – review & editing, Validation, Formal analysis. **David A. Bohan:** Supervision, Conceptualization, Methodology, Writing – review & editing, Validation, Funding acquisition.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A

See Fig. A1 and Table A1.

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