



Feeding behavior and mobility of carabid beetles in response to perceived risk of predation *

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Abstract. Carabid beetles are common inhabitants of agricultural fields where they encounter a variety of food options - including prey and weed seeds. The feeding behaviors of carabids are often influenced by the physical and chemical traits of prey and seed species, as such traits determine prey or seed species that are suitable for consumption. However, some carabid species may prey upon other carabids, complicating their role as beneficial insects due to consumptive (direct) and non-consumptive (indirect) intra-guild predation effects. The non-consumptive effects of intra-guild predation are expected to influence prey and seed foraging behaviors of carabids because those behaviors are likely to be adapted as a function of duration and intensity of predation risk. In this study, we wanted to explore the non-consumptive effects of the carabid intra-guild predator *Pterosticus melanarius* on mobility and feeding behavior of two carabid omnivores: *Harpalus amputatus* and *Amara* spp. Choice and no-choice feeding arenas coupled with a video system were used to study the responses of carabid beetles to the odor cues of *P. melanarius*. Odor cues left by *P. melanarius* caused *H. amputatus* to reduce its activity when canola seeds (*Brassica napus*) were offered in the feeding arenas. In contrast, *P. melanarius* cues did not cause *H. amputatus* to alter its mobility when freeze-killed fruit flies were offered in the feeding arenas, although this species did increase consumption of fruit flies under these cues. *Amara* spp. offered canola seeds increased their mobility and relative seed preferences when exposed to the odor cues of *P. melanarius*. Overall, our work shows carabid species do alter aspects of their foraging behavior under intra-guild predation risks, but this is unlikely to reduce their contributions to seed or prey biocontrol.

INTRODUCTION

Animals foraging under predation risk often meet their energy demands by dividing their foraging efforts between food acquisition and predator avoidance (Lima & Dill, 1990; Searle et al., 2008). This often leads animals to modify their foraging activity, feeding decisions, foraging strategies, or habitat use depending on the presence, duration, and intensity of predation risk (Lima & Dill, 1990; Wilder & Rypstra, 2004; Brodin et al., 2006). In other words, the time that foragers allocate to foraging versus anti-predator behaviors should differ depending on perceived risk of predation in the environment (Searle et al., 2008). The behavioral changes made under predation risk often give rise to a vigilance-foraging trade-off because food acquisition and predator avoidance are mutually exclusive activities, and animals need to balance these two activities depending on their situation (Brown et al., 1999; Scharf, 2016). Thus, animals need to assess the level of risk in the environment and decide when and where it is relatively safe to

forage based on several factors such as body size (Preisser & Orrock, 2012), hunger level (Scharf, 2016), chemical defenses (Kaplan & Thaler, 2010), hunting or foraging mode (Preisser et al., 2017), and the quantity and quality of available hiding sites (Finke & Denno, 2002; Donelan et al., 2017). This allows the forager to reduce the probability of being eaten either by avoiding risky habitats altogether, or by increasing its vigilance (and thus compromising its foraging efficiency) when foraging occurs in a risky habitat (Brown et al., 1999; Pitt, 1999).

Changes in foraging behavior in response to predator-indicating cues are among the non-consumptive (i.e. indirect) effects of predator-prey interactions (Pessarrodona et al., 2019). The non-consumptive effects of predation are often strong and play essential roles in determining the strength and dynamics of feeding interactions in predator-prey food webs (Hermann & Landis, 2007; Pessarrodona et al., 2019). It is thus important to study how the non-consumptive effects of predation may affect the foraging

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efficiency of predators and parasitoids in agroecosystems as intraguild predation is a common phenomenon in agroecosystems (Snyder & Ives, 2001; Prasad & Snyder, 2006). Intraguild predation is often considered a disruptive force in predator-prey systems because intraguild predators can kill other predators (consumptive effects) or negatively impact their foraging efficiency (non-consumptive effects), which would potentially limit their biocontrol effectiveness against pest species (Prasad & Snyder, 2006; Davey et al., 2013). Despite this, the actual impact of non-consumptive effects of intraguild predators on the foraging ecology of prey or seed predators is not always negative, and is likely to differ depending on the species under study (Hermann & Landis, 2017; Charalabidis et al., 2017, 2019). Therefore, further research is needed to explore how those non-consumptive effects may impact the strength and dynamics of predator-prey and predator-seed interactions in agroecosystems.

Carabid beetles (Coleoptera: Carabidae) have long been considered beneficial predators in agroecosystems as they can feed on numerous species of prey and weed seeds (Lövei & Sunderland, 1996; Suenaga & Hamamura, 1998; Winder et al., 2001; Symondson et al., 2002a; Kulkarni et al., 2015a, 2016; Ali & Willenborg, 2021). However, the contribution of carabids to biological weed suppression is not always predictable based solely on the relationship between carabid abundance and weed seed consumption (Saska et al., 2008; Davis & Raghu, 2010; Petit et al., 2014; De Heij et al., 2022). This may be due to the complexity of feeding habits of carabid predators (Ali & Willenborg, 2021), since most carabids in the agroecosystem are omnivorous feeders able to consume both prey and weed seeds (Toft & Bilde, 2002; Zalewski et al., 2016; Ferrante et al., 2017; Kulkarni et al., 2017). Seed foraging in omnivorous carabids (i.e. seed searching and seed choice) is often influenced by numerous ecological factors such as environmental conditions, food availability, nutritional needs, and learning and experience (Symondson et al., 2002b; De Heij & Willenborg, 2020; Ali & Willenborg, 2021). Carabid seed foraging is also sensitive to predation risks imposed by intra-guild predators, which are likely to further complicate the ecological factors influencing the strength and dynamics of carabid-seed interactions in agroecosystems through consumptive and non-consumptive effects (Blubaugh et al., 2017; Charalabidis et al., 2017).

Intra-guild predators can exert their non-consumptive effects on carabid foraging behaviors via visual, auditory, mechanical, and/or chemical cues (Dicke & Grostal, 2001; Hermann & Thaler, 2014, 2021). For example, the carabid seed predator *Harpalus pensylvanicus* DeGeer has been found to reduce its activity and increase its seed consumption by almost 45% when exposed to predation cues from mice (Blubaugh et al., 2017). Similarly, the carabid *Harpalus affinis* Fabricius has been reported to reduce its seed choosiness and increase its seed consumption in the presence of residual chemical cues from the carnivorous carabid *Pterostichus melanarius* Illiger (Charalabidis et al., 2017, 2019). These studies suggest that carabids would be

likely to contribute more to weed seed loss under greater intra-guild predation risk. However, the carabid *Poecilus cupreus* (L.) showed no change in seed choosiness and no increase in seed consumption when exposed to the chemical cues of *P. melanarius* (Charalabidis et al., 2019). Thus, the non-consumptive effects of intra-guild predators on the intensity and dynamics of carabid weed seed predation remain uncertain, but are likely to differ depending on the landscape of fear (probability and intensity of predation) in the habitat, as well as the species composition of carabid communities (Searle et al., 2008; Charalabidis et al., 2019).

The feeding behavior of carabids under predation risk (or fear) has not been well-studied, especially as it pertains to seed feeding. To understand how this affects the feeding behavior of carabids, further research is needed. Here we explored the feeding behavior of *Harpalus amputatus* Say and *Amara* spp. exposed to cues from *P. melanarius*, a species known to exhibit carnivorous behaviors. In the first experiment, seed preference by *H. amputatus* and *Amara* spp. carabids was assessed when they were exposed to a caged *P. melanarius* or its residual odor cues in multiple-choice feeding arenas. Second, we explored carabid movement and consumption of seeds or sessile prey items when exposed to odor cues of *P. melanarius*. We hypothesized that cues left by *P. melanarius* would cause the carabid species under study to (a) change their movement patterns and (b) to increase their feeding on food items such as weed seeds and freeze-killed fruit flies. This hypothesis was informed by the ‘stress feeding’ concept introduced by Blubaugh et al. (2017), which suggested that intra-guild predation risk can lead an animal to forage preferably for low-risk, sessile food items. We included weed seeds and freeze-killed fruit flies to represent sessile food items present in the agroecosystems with the objective of determining if an increase in the consumption of these food items would be observed for both types of prey (seeds and fruit flies).

2. MATERIALS AND METHODS

2.1. Carabids

Carabids (Coleoptera: Carabidae) were collected using dry pitfall traps during the spring and summer of 2019 and 2021, with the experiments being conducted in each of those years. All carabids were caught in conventionally farmed crop fields at the Kernen Crop Research Farm near Saskatoon, SK, Canada (52°09'10.3"N, 106°32'41.5"W). Within 24 h of collection, beetles were separated by genus and placed in different plastic housing boxes (28 cm × 16 cm) with some wet paper towel and 2.5 cm of moist sand. Approximately 30 beetles of mixed sex were placed in each box. Boxes were placed in a growth chamber at 19 ± 1°C and a 14L:10D cycle (Charalabidis et al., 2017, 2019). Humidity could not be controlled in the growth chamber, but the sand in the boxes was regularly moistened. Beetles were fed every 2–3 days with canola (*Brassica napus* L.) and bluegrass (*Poa pratensis* L.) seeds. Carabids were observed mating, burrowing, and feeding on both food items provided.

Approximately 54 h before the start of experimentation, *H. amputatus* (~11 mm mean body length) and *Amara* spp. were placed in individual petri dishes with moist tissue paper and were then deprived of food. This starvation period ensured beetles were motivated to feed during the experiments (Blubaugh et al., 2017;

Charalabidis et al., 2017, 2019; Yarwood et al., 2021), and also minimized the effects of any learned food preferences prior to experimentation (Glinwood et al., 2011). After each experiment, beetles were euthanized by freezing, their length was measured, and their sex and species identity were confirmed using the keys of Lindroth (1969) and Bousquet (2010). *Amara* spp. individuals belonged to the *lunicollis* group (Lindroth, 1969) and consisted of *Amara farcta* LeConte (~9 mm mean body length) and *Amara littoralis* Mannerheim (~8 mm mean body length), although we note that *A. littoralis* is very hard to distinguish from *A. impuncticollis* Say without dissection (Lindroth, 1969; Rivers et al., 2017). Voucher specimens of all carabid species used in the experiments were deposited at the Weed Ecology and Biocontrol Laboratory, University of Saskatchewan.

Pterostichus melanarius (~20 mm mean body length) was used to create residual chemical cues (Guy et al., 2008) that would serve as the predator cues in the experiments. This carabid species is relatively large, and features complex feeding habits (Zalewski et al., 2016). It has been reported to feed on seeds (Kulkarni et al., 2017), aphids (Winder et al., 2001), and snails (Symondson et al., 2002a). It also scavenges facultatively on dead prey if it is available (Foltan et al., 2005; Ferrante et al., 2017). *Pterostichus melanarius* has also been shown to prey on other carabids, thereby reducing their biocontrol potential (Currie et al., 1996; Snyder & Wise, 1999; Snyder & Ives, 2001). All carabid species used in this study were collected from the same site, which indicated that they were likely to interact directly or indirectly depending on their activity period (diurnal or nocturnal). Based on that, we determined that the three species would make a suitable model for studying the non-consumptive (indirect) effects of intraguild predation using the odor residues of *Pterostichus melanarius*, as odor cues of this predator would likely be encountered in the field by both diurnal and nocturnal species. Odor cues from *P. melanarius* have been used in previous studies similar to ours, and have been shown to induce anti-predator behavioral responses in *H. affinis* (Charalabidis et al., 2017, 2019).

Pterostichus melanarius beetles were housed in mixed sex groups as described above with one exception; they were maintained on the lab bench and not in the growth chamber to avoid these beetles becoming habituated to the odor of *P. melanarius*. *P. melanarius* individuals were fed every 2–3 days with pieces of mealworm larvae *Tenebrio molitor* L. (Coleoptera: Tenebrionidae), canola seeds, and freeze-killed fruit flies *Drosophila melanogaster* Meigen (Diptera: Drosophilidae). Uneaten food was removed weekly. *P. melanarius* were also observed mating, burrowing, and feeding on all food items provided. *P. melanarius* individuals were marked with a dot of nail polish to identify their sex for quicker handling during experimentation (Shearin et al., 2008). There was no indication that the nail polish affected their behavior since chemical cues were expected to mediate self / non-self recognition in carabids (Guy et al., 2008; Rok & Renner, 2018).

Residual predator odor cues were created by randomly placing one (weed seed choice experiments) or five (3 females, 2 males – behavioral experiments) *P. melanarius* beetles into the experimental arena 24 h prior to experiment initiation. This is in line with the timeframe used to create predation cues in other experiments (Storm & Lima, 2008; Charalabidis et al., 2017). However, we used sand instead of filter paper as it resembles a more natural substrate for carabids and tended to hold weed seeds better in place. *P. melanarius* beetles were randomly selected for the experiments and were used multiple times to create the predator cues.

2.2. Weed seed choice experiments

In this experiment we offered seeds of six common weed species; dandelion (*Taraxacum officinale* Wigg., ~50 mg/100 seeds (weight of 100 seeds without pappus – seeds presented with pappus), ~3.33 mm length by ~0.89 mm width), foxtail (*Setaria viridis* L., ~140 mg/100 seeds, ~2.39 mm length by ~1.35 mm width), kochia (*Bassia scoparia* Scott, ~72 mg/100 seeds, ~1.63 mm length by ~0.91 mm width), stinkweed (*Thlaspi arvense* L., ~90 mg/100 seeds, ~1.92 mm length by ~1.34 mm width), wild mustard (*Sinapis arvensis* L., 229 mg/100 seeds, ~1.56 mm length), and wild buckwheat (*Fallopia convolvulus* Löve, ~645 mg/100 seeds, ~3.27 mm length). These weed species represented common weed species in the fields from which the carabids were collected (Leeson & Beckie, 2014).

We used modified multiple choice seed feeding arenas to assess whether carabid food choices changed when exposed to predator cues (arena design is shown in Fig. 1). The experimental arena was made from a large Petri dish (14.5 cm diameter) in which a smaller petri dish (9 cm) was secured with a piece of double-sided tape. The bottom of the arena was filled with a thin layer of sifted and moistened sand (Quikrete® play sand – washed, screened, and heat sterilized by manufacturer). The arenas were used in four treatment groups: residual odor, caged predator, residual odor and caged predator, and control. In the residual odor treatment, a *P. melanarius* beetle was left to roam the outer ring for 24 h without feeding and was removed immediately before seeds were placed in the arena. In the caged predator treatment, a *P. melanarius* beetle was placed in the inner ring immediately prior to the start of the experiment. In the residual odor and caged predator treatment a *P. melanarius* was placed in the outer ring for 24 h (without feeding), after which it was moved to the inner circle. The control arenas had no contact with *P. melanarius* and as such, were devoid of predator cues.

The outer ring was divided into six equal sections (no actual physical divisions were present) in which a group of ten seeds of one weed species was placed, with five seeds placed along

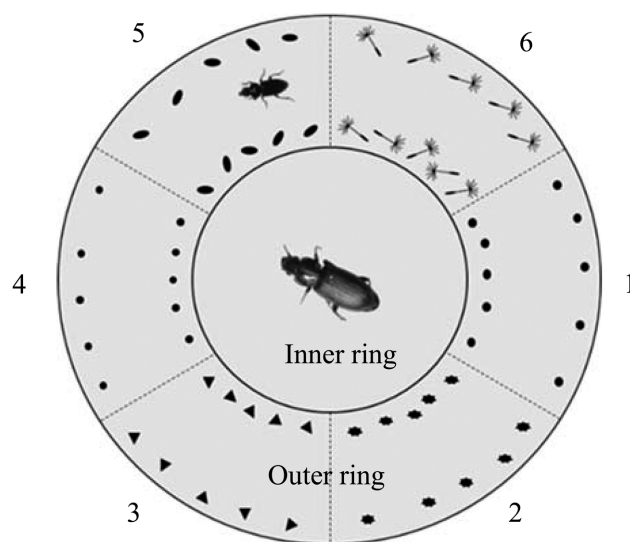


Fig. 1. Cafeteria multiple choice seed feeding bioassays were conducted in Petri dishes. Dotted lines indicate the 6 equal parts in which the seeds were presented, but do not represent actual barriers. The arena was divided into an outer arena (14.5 cm across) and inner arena (9 cm across). The outer ring was further divided into six sections (1 through 6) and 10 seeds of one weed species were offered per each section.

the outer edge and five seeds along the inner edge of the arena section (Fig. 1). Because carabids tend to be thigmotactic – they follow edges – (Plotkin, 1979), this design helped to ensure that beetles encountered the seeds. The order in which the six weed species were placed was randomized in each arena. One beetle was placed in the outer ring of the arena in each replicate ($n = 8$ replicates per treatment for each carabid). The experiments were run in the dark for 15 h because most carabids are thought to be nocturnal (Lővei & Sunderland, 1996). At the end of the experiment, beetles were removed and the number of remaining seeds of each weed species in the Petri dish was counted. The sex ratio was variable across treatments as the number of males and females in the catches fluctuated over time, precluding the use of an even sex ratio across treatment groups.

2.3. Behavioral experiments

We performed behavioral assays to evaluate the behavioral responses of *Amara* spp. and *H. amputatus* to the presence of residual odor cues left by *P. melanarius*. The odor cues were mainly derived from the faeces released on the sifted sand and pygidial gland secretions as the insects were manipulated by the hand and not fed during cue collection. The pygidial glands of *P. melanarius*, *Harpalus* spp. and *Amara* spp. secrete species-specific defensive chemicals, and these differences in defensive chemicals among species are expected to enable carabids to distinguish “self” from “non-self” odors (Rok & Renner, 2018; Giglio et al., 2021). During these assays, activity and position of the beetles in the presence and absence of cues were recorded and tracked with the EthoVision® software system (Noldus, Lessburg, VA, USA). EthoVision® is often used for studying the behavior of rodents (rats and mice), but it also has been used for studying the behavior of various insects, including fruit flies, aphids, and carabid beetles (Noldus et al., 2002; Harrison & Gallandt, 2012). Our behavioral assays were performed in a custom-designed “video box” that minimized the disturbance and glare from laboratory equipment lights during the experiment. Experiments were performed in the dark, with only an infrared security lamp placed in the video box to provide illumination for the camera. Previous work has used red light for behavioral studies with nocturnal insects as it was thought to be invisible to insects, although this has been disproven for the carabid *P. melanarius* (Allema et al., 2012). The video box consisted of a chipboard construction on a lab bench in which the camera hung and in which the arenas could be placed (Fig. 2). Within the video box, six experimental arenas were established. Each arena consisted of a 27 cm by 12 cm hard plastic food prepping container with rounded edges. The bottoms of the arenas were covered with a 2.5 cm layer of moistened, sifted sand, and arenas were covered with unperforated Clingfilm® to preserve moisture and avoid odor interference between arenas.

In these behavioral experiments, three different food-beetle combinations were examined with and without the presence of predator cues. The food-beetle combinations were: *Amara* spp. paired with canola seed (total $n = 51$ replicates), *H. amputatus* paired with canola seed (total $n = 74$ replicates), and *H. amputatus* paired with freeze-killed fruit flies (total $n = 71$ replicates). Canola seeds were used as the seed source in this study because they are often highly palatable to carabid predators (Kulkarni et al., 2015b, 2016), so the impact of unpalatable seeds on feeding behavior could be avoided. To create odor cues and avoid beetle dehydration, each arena was moistened once during the 24-h period that the five *P. melanarius* beetles remained in the arenas. *P. melanarius* beetles were observed exploring the entire arena. Any excrement from *P. melanarius* was left in the arenas, adding to the odor cues. An uneven sex ratio of *P. melanarius* was used due to the female-skewed catch during the early sum-

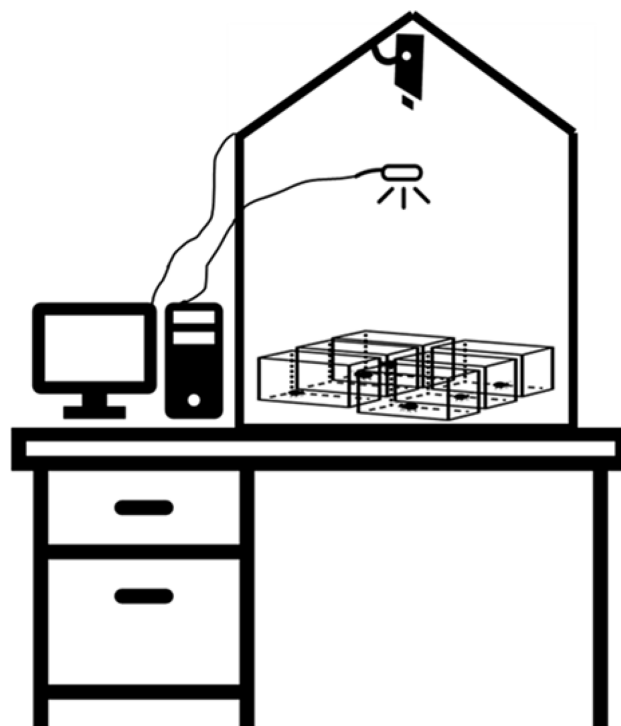


Fig. 2. Schematic representation of the setup for the behavioral experiment. Six beetles were monitored with a camera at the same time and their movements were logged with the EthoVision® software. Trails were run over night, an infrared security lamp provided illumination for the camera. The front of the video box was closed with a large sheet of paper after a trial was set up.

mer, but this sex ratio was maintained continually for consistency across the experimental replicates. *P. melanarius* beetles were removed immediately before the start of the experiment, after which 20 water-imbibed canola seeds or freeze-killed fruit flies were randomly scattered in each arena. Imbibed seeds were used because they are often more acceptable to carabids than dry seeds (Kulkarni et al., 2016). Following this, a single beetle of either *Amara* spp. or *Harpalus amputatus* was placed in each arena, and arenas were closed off with Clingfilm®. Preparation of the experimental setup was completed within an hour, and since the experimental setup allowed for simultaneous observation of six arenas, the experiment began after all arenas containing beetles had been placed in the video box and the software had correctly identified the location of all six beetles. In each experiment, the same treatment (predator cues or no predator cues) was applied across the six arenas being simultaneously observed to avoid predator cues interfering with the control trails. Once the experiment commenced, the activity and position of the beetles were recorded and tracked with EthoVision® software (Noldus et al., 2001) for 14 h \pm 30 min during the night, at a temperature of $\sim 20^{\circ}\text{C}$. After each behavioral assay, all arenas were thoroughly washed with dish soap and ample water, dried, and cleaned with 70% alcohol. Two sets of arenas were used, one for odor trials and one for control trials, and these were not intermixed in case any residual odors were left in the arenas.

3. STATISTICAL ANALYSES

The R Package Version 4.0.3 (R Development Team, 2021) was used for all data analyses. Data normality was checked using the Shapiro-Wilk normality test in the R package *rstatix* (Kasambara, 2021), and figures were created using the R package *ggplot2* (Wickham, 2016). Data for *H. amputatus* and *Amara* spp.

were analyzed separately, but data for *Amara* spp. carabids were pooled together due to low catches and difficulty in confirming species identity (Lindroth, 1969).

3.1. Weed seed choice experiments

The consumption of the different seeds under different predator cue treatments (4 treatments) was analyzed with a permutational multivariate analysis of variance (PERMANOVA). PERMANOVA does not require normally distributed data, allows for within-group variance, and is insensitive to zero-inflated data (Legendre & Anderson, 1999; Anderson, 2017). PERMANOVA analyses were performed using function *capscale* from the *Vegan* package (Oksanen et al., 2018), with p-values adjusted for false discovery rate (because analysis was based on pairwise comparisons between treatments and control). The best distance metric for the data was the Chord dissimilarity distance, as determined with function *rankindex* in the R package *Vegan*. The Chord dissimilarity distance is determined by scaling separately each beetle vector and then calculating the Euclidean distance (literal distances) on the chord-transformed (standardized) data by object (per beetle, in this case) (Legendre & Gallagher, 2001). By using the Chord distances, the focus of the analysis is shifted from differences in absolute seed consumption to relative seed preferences. Treatment and sex of the beetles were used as explanatory variables in the model to test if feeding behavior would differ among males and females. Because the offered seeds differed in size, the analysis was performed with the consumed seed weight per species (calculated by multiplying the number of seeds consumed with the average seed weight per species) as the response matrix. Post-hoc pairwise analysis of significant differences between the seed consumption in each treatment were conducted with function *pairwise.factorfit* in package *RVaideMemoire* (Hervé, 2021), with p-values adjusted for false discovery rate. Relative seed consumption per treatment are displayed in an ordination graph with 95% confidence ellipses using function *ordiellipse* in package *Vegan* (Oksanen et al., 2018).

3.2. Behavioral experiments

Seed consumption (only canola seeds were offered here) and mobility of carabids exposed to residual predator cues versus control (2 treatments) were analyzed with generalised linear models (GLMs). The consumption of canola seeds (number of seeds consumed) by *Amara* spp. was analysed using a Poisson distribution (count data), while the consumption of canola and flies by *H. amputatus* was analyzed using a negative binomial distribution (over-dispersed count data). The mobility (% time the beetle was moving) and distance traveled (in m) by the beetles was analyzed using GLM models with Gamma distribution. All models were run in R using package *mgcv* included treatment (presence versus absence of predator cues) and sex as explanatory variables.

4. RESULTS

4.1. Weed seed choice experiments

Both *Amara* spp. and *H. amputatus* consumed numerous dandelion seeds (an average consumption of 5 approx. 5 seeds out of 10 seeds offered for each seed species, respectively) within the 15-h duration of the experiment. Wild buckwheat was not consumed at all and was thus excluded from analyses. *Amara* spp. showed different seed consumption rates when exposed to predator cues, based on seed weight consumed per weed species (Table 1). Pairwise comparisons between seed species showed differences in seed consumption rates when *Amara* spp. was

Table 1. Results of weed seed choice experiment modeled with PERMANOVA's. The four treatments in this experiment were: residual odor, caged predator, residual odor & caged predator, and control.

	df	SS	F	p
<i>Amara</i> spp.				
Treatment	3	1.867	1.601	0.038
Sex	1	0.271	0.698	0.697
Residual	26	10.106		
<i>Harpalus amputatus</i>				
Treatment	3	1.468	1.053	0.391
Sex	1	0.549	1.182	0.275
Residual	26	12.078		

Numbers are rounded to 3 decimal points. Significant effects at the $P < 0.05$ level are displayed in bold, and at the 0.1 level underlined.

exposed to predator cues compared with when they were not (Table 2, Fig. 3). *Amara* beetles exposed either to a caged predator or residual odor cues showed no difference in seed consumption rates. However, beetles exposed to both a caged predator and residual odor cues at the same time exhibited relative seed predation that differed from those exposed only to one type of predator cue (Table 2, Fig. 3). *H. amputatus* did not show any difference in seed consumption preferences when exposed to predator cues. Males and females of both *Amara* spp. and *H. amputatus* exhibited no differences in seed consumption rates (Table 1).

4.2. Behavioral experiments

The EthoVision® system can create heatmaps that display residence time at a particular location. In this study, the heatmaps showed that the beetles explored most of their arena, but their movement was concentrated along the edges of the arena, in line with their thigmotactic behavior (Plotkin, 1979). On average the beetles were mobile for about 9.5% of the ~14 h duration of the trail, and during that time they traveled approximately 510 m (on average).

4.3. Consumption, mobility, and distance moved

Amara beetles consumed the same amount of canola seeds regardless of whether or not they were exposed to residual odor cues of *P. melanarius*. Compared with the control, male *Amara* beetles were mobile for a larger percentage (~50%) of the time they spent in the arenas with residual odor cues present. Both male and female *Amara* spp. increased their overall mobility when exposed to residual odor cues, although the increase in the mobility of males was greater than that of females (Fig. 4). Despite

Table 2. Results of pairwise comparison of seed predation per treatment by *Amara* spp., after PERMANOVA analysis.

	Control	Residual odor	Caged predator
Residual odor	0.015		
Caged predator	0.014	0.127	
Residual odor & Caged predator	0.014	<u>0.060</u>	0.014

Significant effects at the $P < 0.05$ level are displayed in bold, and at the 0.1 level underlined.

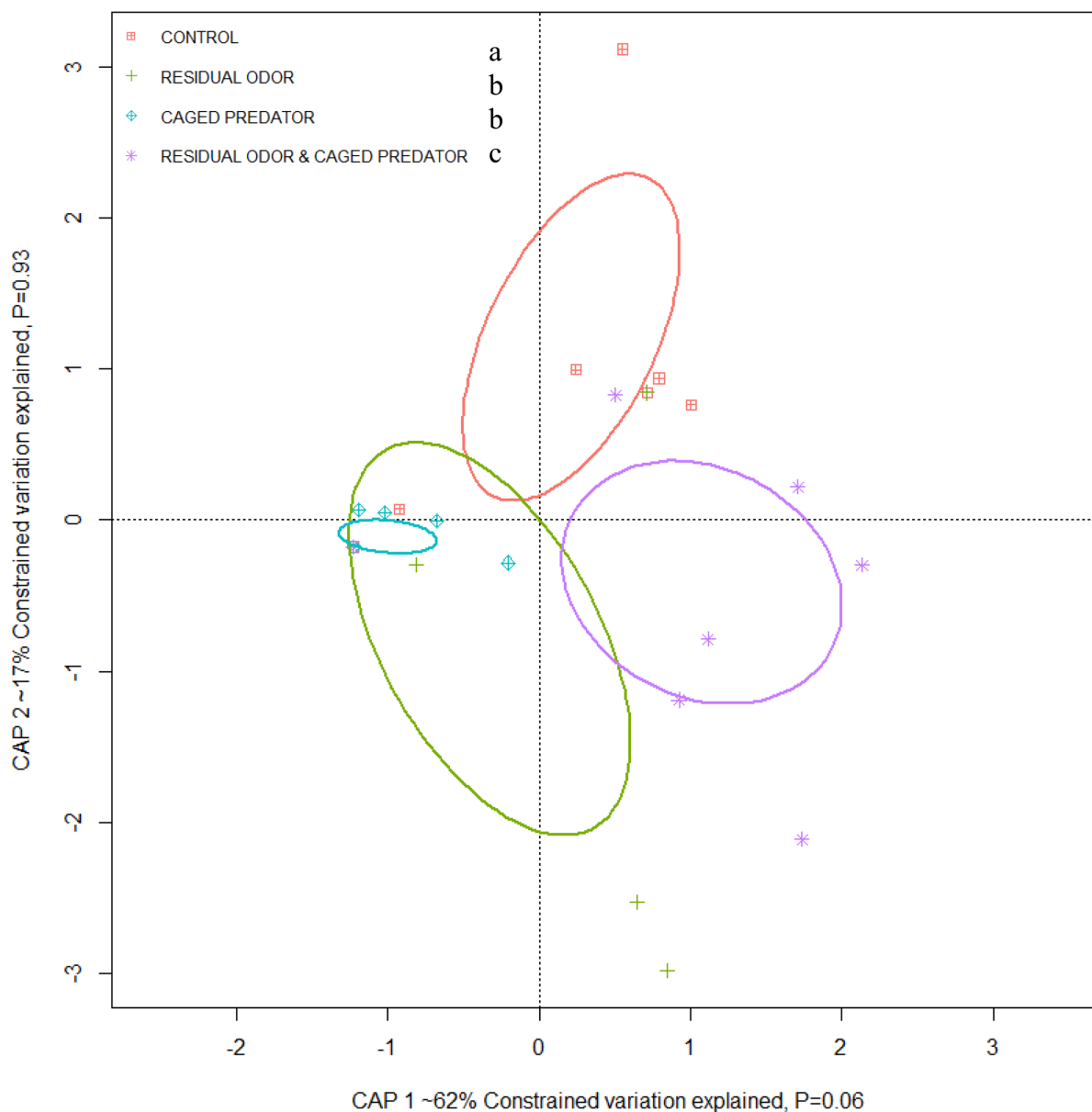


Fig. 3. Constrained ordination graph of the weed seed predation (by weight) by *Amara* spp. based on PERMANOVA model (Table 1). Different letters behind legend indicate significant ($p < 0.1$) differences between treatments (Table 2). $n = 8$ per treatment.

the change in mobility, the distance *Amara* spp. covered did not significantly change when exposed to residual odor cues (Table 3, Fig. 4).

Harpalus amputatus beetles exhibited differences between the sexes both in seed consumption and mobility. Male *H. amputatus* consumed more canola seeds than females, but were less mobile and covered less distance (Fig. 4). Females exhibited a much greater change (decline) in mobility than did males, although the change in total distance traveled was similar between the sexes (Fig. 4). The consumption and behavior of *H. amputatus* when offered dead flies was very different from that when offered canola seeds. When exposed to predator cues, *H. amputatus* of both sexes consumed significantly more fruit flies, but an overall increase in consumption was not found for canola seeds. The mobility and distance moved by *H. amputatus* was reduced when exposed to predator cues in feeding are-

nas containing canola seeds, but it remained the same in feeding arenas containing flies (Table 3, Fig. 4).

5. DISCUSSION

When animals need to forage in risky habitats, they face a vigilance-foraging trade-off (Ferrari et al., 2009). However, animals need to consume a minimum level of resources to survive a given period (Ferrari et al., 2009). The risk allocation model predicts that prey exposed to prolonged periods of risk should reduce their vigilance to obtain enough resources to survive (Lima & Bednekoff, 1999). Under these conditions, prey can be expected to be less discriminative about their food choices so they can fulfill their energy requirements while also maintaining some level of vigilance (Ferrari et al., 2009). As such, we expected seed-feeding carabids would be less choosy about weed seeds and thus consume more seeds when exposed

Table 3. ANOVA results for feeding and foraging behavior with and without predator cues (Treatment), modeled with GLMs.

		Chisq	Df	P
<i>Amara</i> spp. feeding on <i>Canola</i>				
Consumption	Treatment	0.615	1	0.433
	Sex	0.254	1	0.615
Mobility	Treatment	9.458	1	0.002
	Sex	3.354	1	0.067
Distance moved	Treatment	1.201	1	0.273
	Sex	0.404	1	0.525
<i>H. amputatus</i> feeding on <i>Canola</i>				
Consumption	Treatment	0.359	1	0.549
	Sex	3.343	1	0.068
Mobility	Treatment	3.303	1	0.069
	Sex	18.597	1	<0.001
Distance moved	Treatment	3.855	1	0.050
	Sex	7.127	1	0.007
<i>H. amputatus</i> feeding on flies				
Consumption	Treatment	3.841	1	0.050
	Sex	1.223	1	0.269
Mobility	Treatment	0.179	1	0.672
	Sex	0.093	1	0.760
Distance moved	Treatment	0.001	1	0.973
	Sex	0.043	1	0.836

Numbers are rounded to 3 decimal points. Significant effects at the $P < 0.05$ level are displayed in bold, and at the 0.1 level underlined.

to predator cues, in line with the findings of Charalabidis et al. (2017). This was not the case in our study, however, as we did not observe an increase seed consumption under predation risk. Instead, both *Amara* spp. and *H. amputatus* did not consume fewer seeds when exposed to predator cues, and this was consistent across both experiments. For *Amara* spp. we found that the relative seed preference was different for beetles exposed to predator cues compared to unexposed ones. Furthermore, the relative seed preference for beetles exposed to both residual odor cues and a caged predator differed from that of beetles exposed to only one type of predator cue. Based on this, it could be hypothesized that *Amara* spp. beetles would rely on both chemical and visual or tactile (vibrational) cues when assessing the level of predation risk in their environments. By contrast, *H. amputatus* did not show differences in relative seed preference when exposed to different predator cues. This may be an artifact of the experimental design, which may have presented the seeds too close together (i.e. high seed density) to elicit a response in this more mobile beetle. Alternatively, *T. officinale* seeds were so highly preferable to carabids that perhaps the beetles consumed it irrespective of the predation risk. *T. officinale* seeds are known to be easily consumed by carabids (Charalabidis et al., 2019), and this may have led to a higher consumption of *T. officinale* seeds across the treatment groups.

In the behavioral experiment using the EthoVision® system we examined both the amount of food consumed in a no-choice setting and the beetles' behavior when exposed to residual odor cues vs. a control setting without predator cues. Here we expected the beetles to reduce their movements but not reduce their consumption, in line with Blubaugh et al. (2017) and Ferrari et al. (2009). *H. amputatus* responded to predator odor cues as expected when

offered canola seeds. Beetles consumed the same amount of canola seeds in both treatments but reduced their mobility and covered less distance when exposed to predator odor cues. This reduction of movement may be a predator avoidance response since reduced movement can diminish the likelihood of being spotted by predators (Lima & Dill, 1990).

Blubaugh and colleagues (2017), after observing an increase in seed predation in response to predator cues, speculated that seeds are a good “stress food” for omnivorous carabids. The idea behind this is that seeds can be a very abundant and easy to find food source that require less foraging than insect prey, thus presenting a ‘safer’ or less risky resource (Blubaugh et al., 2017). Building on this idea, we speculated that the same feeding response could be expected for other abundant sessile food items. Many carabids are opportunistic feeders and will scavenge if an opportunity presents itself (Toft & Bilde, 2002; Lundgren, 2009; Zalewski et al., 2016; Ferrante et al., 2017). Indeed, *H. amputatus* exposed to predator cues consumed more dead fruit flies than in the absence of predator cues, in line with our expectations. The increase in fly consumption by *H. amputatus* when exposed to predator cues is interesting, as no such increase was observed when *H. amputatus* was offered canola seeds. This difference is likely to be explained by the ease of handling (Charalabidis et al., 2017), as the small soft bodied flies were consumed much quicker in laboratory observations. Other mechanisms might underlie these observations, however, but our study design did not allow for any firm conclusions in this regard.

While *H. amputatus* reduced its movement when exposed to predator cues in arenas containing canola, no such difference was observed in arenas containing flies. *Amara* spp., on the other hand, exhibited increased mobility when exposed to predator cues. It is difficult to identify the reason for these differences without further research, but we postulate that either predation risk responses are not equal among carabid species (Wallin & Ekbom, 1988; Charalabidis et al., 2019), or predation risk is influenced by the interactions between beetle species, species mobility, food types available, and the environment (Lima & Dill, 1990). To further explore carabid predation risk responses, aspects like food quality and shelter should be incorporated in future studies. Incorporating shelter quality in studies of non-consumptive predator effects will provide more realistic insight into predation risk effects on carabid beetles as they are often thigmotactic (Plotkin, 1979; Donelan et al., 2017).

Another aspect that could have played a role in the behavior differences between *Amara* spp. and *H. amputatus* is their activity period. Because most carabids are thought to be nocturnal (Lövei & Sunderland, 1996), we performed experiments in the dark. *Harpalus amputatus* and *P. melanarius* are described as being nocturnal, whereas *A. farcta* and *A. littoralis* are described as mostly diurnal (Larochelle & Larivière, 2003). The behavioral experiments in this study indicate that the *Amara* spp. are not completely inactive during the night as the EthoVision® showed they

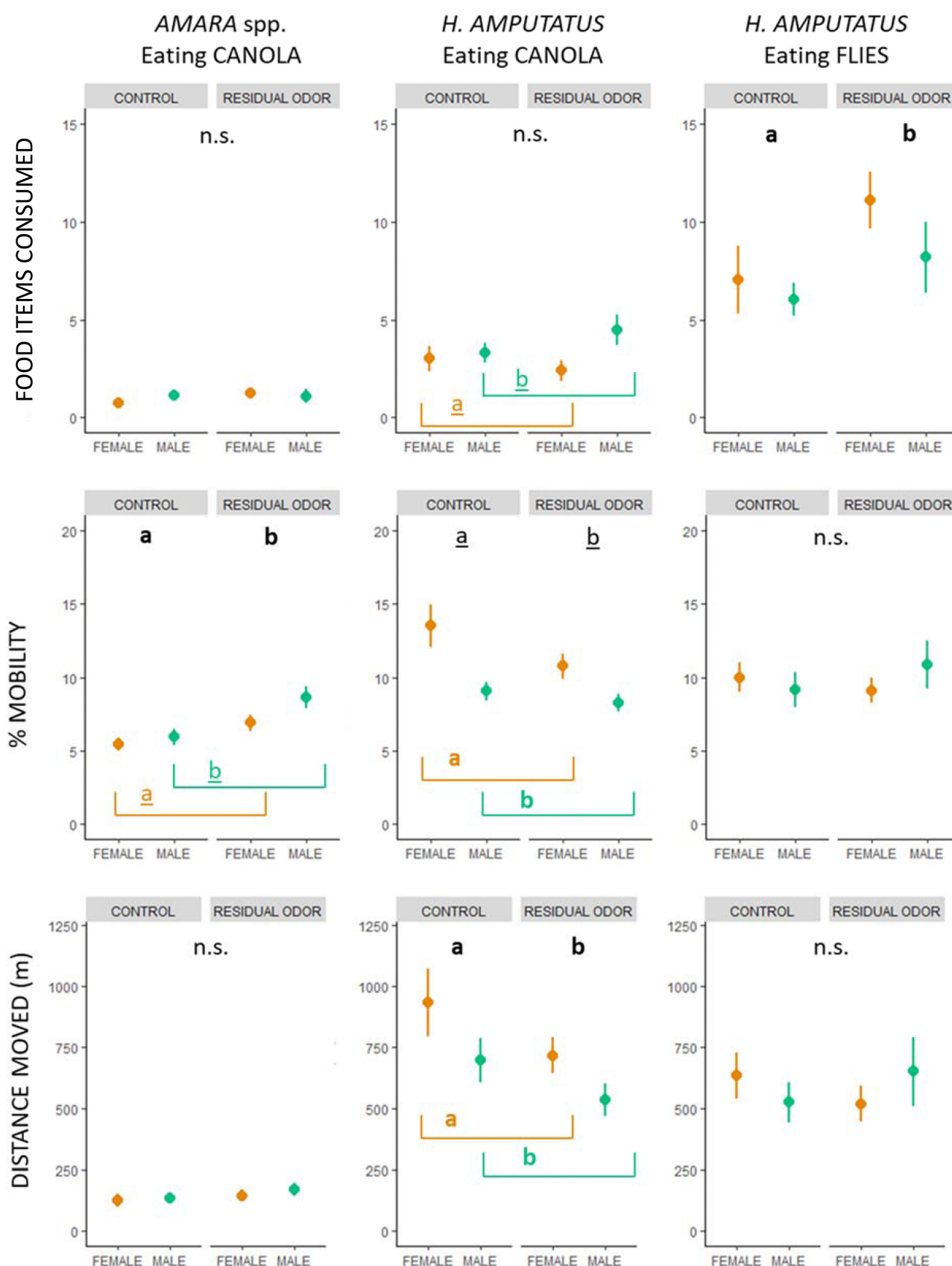


Fig. 4. Seed consumption, percent mobility and distance moved in m (mean \pm standard error of the mean) during ~14 h by *Amara* spp. offered canola seed (left column, $n = 51$), *H. amputatus* offered canola seeds (middle column, $n = 74$), and *H. amputatus* offered freeze-killed fruit flies (right column, $n = 71$), when exposed to residual predator odor cues. Significant differences at the $P < 0.05$ level are displayed in bold, and at the 0.1 level are underlined. Differences between treatments are indicated by different letters at the top of a graph, and between the sexes above the brackets within a graph (Table 5.3).

were mobile between 5% to 10% of the time. *Harpalus amputatus* was mobile up to 15% of the time. Furthermore, while *Amara* spp. never moved over 250 m, *H. amputatus* moved on average between 500 m and 1000 m. The reported differences in the activity period of beetle species likely explains the large difference in activity and distance move between *Amara* spp. and *H. amputatus*.

We found differences in consumption and behavior between the sexes in arenas with canola seeds, particularly for *H. amputatus*. Males of *H. amputatus* consumed more seeds and travelled less distance than females in feeding arenas containing canola seeds. Several differences have been found in the feeding and foraging behavior of male and female carabid beetles (Szyszko et al., 2004; Sasakawa, 2010; Kulkarni et al., 2015b; Yarwood et al., 2021). For example, males and females of *Carabus hortensis* L. have been shown to differ in metabolic rate, behavior, and morphology (Szyszko et al., 2004; Yarwood et al., 2021). Furthermore, female gut capacity is lowered by maturing eggs, allowing females to eat only small amounts of food at a time (Den Boer, 1986). The amount of food that females can consume in a single consumption event influences their activity and exploratory behavior (Den Boer, 1986), which may explain some of the behavioral differences detected between males and females.

Female *H. amputatus* beetles offered canola seeds in our study were significantly more mobile and covered a greater distance than males, and this was consistent across both treatments (control vs. predator odor cues). This is not congruent with the findings of other studies. Hungry males and females have been found to be equally active, but satiated females have been found to be less active than satiated males (Wallin & Ekbohm, 1994; Szyszko et al., 2004). Since *H. amputatus* did not show any difference in behavior between the sexes in feeding arenas containing flies, this would suggest that the nutritional quality or requirements play a role in behavior.

Individual differences in the beetles' behavior may also be explained by their personalities and past experiences. Animal personality can be defined as a consistent response to environmental conditions throughout an individual's lifetime, sometimes also called a behavioral syndrome (Sih et al., 2004). While research on insect personalities is relatively new, several studies have found individual differences in aspects like learning and decision making in insects (Cauchoix et al., 2018; Golab et al., 2021). Within Carabidae, differences in personality between individual beetles have been found for several behavioral traits in *Nebria brevicollis* Fabricius (Labaude et al., 2018; Harris et al., 2020) and *Carabus convexus* Frabricius (Magura et al., 2021). All carabids in the current study were caught on the same farm, but it is possible that individual differences in personality existed among beetles based on their 'home' environment, past experiences with food and predators, or ancestry which could not be tested in our study. Future research would benefit from standardizing these aspects, es-

pecially past predator experiences, which have been found to be significant in other animals (Crane et al., 2017; Des Roches et al., 2021).

Studying indirect predator effects on arthropod foraging behavior can yield valuable information that is useful in better understanding biocontrol services in agroecosystems. However, the indirect intraguild predator effects on carabid biocontrol of weed seeds and pest insects is not well known. Results from carabid biocontrol studies are often interpreted based on the relationship between carabid activity-density and the removal of seeds or insect pests (De Heij et al., 2022). In the current study we have demonstrated that the activity of carabids can be greatly reduced without a corresponding reduction in pest or seed removal, although extrapolation of these laboratory results to field situations should be made with caution. Nevertheless, the results of this study, in addition to those of Blubaugh et al. (2017) and Charalabidis et al. (2017), indicate that perceived predation risk can impact activity and thus, may influence the 'activity' part of the carabid 'activity-density' metric used in field studies. However, further research is needed to verify this hypothesis. If this were shown to be true, it would complicate analyses that aim to correlate activity-density with seed or prey removal. Field studies often report either a poor relationship or no relationship at all between seed predation and carabid activity-density (e.g., Saska et al., 2008; Petit et al., 2014; Bohan et al., 2011; Carbonne et al., 2020). The presence of cues that suggest the presence of predators may be an important factor limiting our ability to properly link activity-density to seed and prey removal under field conditions.

ETHICAL STATEMENT. No ethical approval was required for the experiments described in this study. Insect were handled, housed and eventually euthanized according to the standard protocols used in insect behavioral studies.

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AUTHOR CONTRIBUTIONS. S. de Heij designed the study, identified the beetles, executed the experiments, performed the statistical analysis, and wrote the initial manuscript. C. Willenborg secured funding, helped conceptualize the study, supervised the study, and contributed to the writing and editing of the final manuscript. S. Prager helped in conceptualizing the study and contributed to the writing and editing of the final manuscript. K. Ali contributed to the writing and editing of the final manuscript.

CONFLICT OF INTEREST. The authors declare no conflict of interest.

DATA AVAILABILITY. Datasets analyzed and presented in this study are available from the corresponding author upon request.

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