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Effect of inter-individual variabilities and intraguild interferences on the foraging strategies of seed-eating carabid species

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Abstract

Making a choice requires, implicitly, an investment of time in one behaviour at the expense of an investment in another. Being choosy would increase the risk of losing many food item opportunities to competitors, and is directly in conflict with other essential tasks such as predator avoidance. Individuals are thus expected to adjust their level of choosiness in response to the competition and predation context. The available foraging theory and the empirical ecology of carabids would suggest that competition and predation interference induces changes in the foraging behaviour of carabid individuals. Carabids typically operate within communities in which competition and predatory interference interactions occur and are ever present; there are high levels of intraguild interference. A better understanding of how risks of these two interference interactions modify individual decision making for prey would therefore help to improve the biocontrol of weeds by communities of carabids. This thesis focused on how changes in level of choosiness occur when individual carabids forage under intraguild interference. Using laboratory experiments, done at various spatio-temporal scales, we demonstrate that the decision-making processes of foraging carabids might differ between contexts, between species and between individuals. Our focal species, the granivore *Harpalus affinis*, was found to reduce its level of choosiness while foraging under intraguild interference. In doing so *H. affinis* individuals increased their overall rate of seed acceptance. This change in choosiness was dependant on the intensity of the risk, the seed species offered in test and the sex of individuals. We found no link between individual levels of choosiness and either immunity or personality traits. When tested under similar conditions, individuals of the omnivorous carabid *Poecilus cupreus* did not change their level of choosiness for seeds. These findings would help explain the high variability in seed predation rates observed between studies conducted in-field, and the differences observed between laboratory studies and fields measurements in carabids. Globally, this thesis has confirmed that a deeper understanding of the decision making process of carabids seed-eating species is requires to evaluate their choice of prey and assess their relevance as biological control agents in the wild.

Keywords: Carabids, predation risk, competition risk, immunity defense, personality, behavioural flexibility, foraging strategy, behaviour.

Résumé

Faire un choix n'est pas juste un évènement spontané. La recherche d'une ressource alimentaire, par exemple, implique un investissement temporel et est donc en conflit avec d'autres activités essentielles telles que la vigilance pour les prédateurs. Ainsi être sélectif augmente le risque de se faire attaquer par un prédateur. Par ailleurs, être sélectif implique aussi de rejeter beaucoup de potentielles options avant de finalement en accepter une et donc accepter une perte non négligeable d'opportunités en présence de potentiels compétiteurs. Pour ces raisons, une réduction du niveau de sélectivité est attendue chez un individu exposé à une situation de forte compétition ou à un fort risque de prédation. Les carabes évoluent au sein de communautés composées, pour la plupart, d'un nombre important de potentiels compétiteurs et prédateurs. Les connaissances actuelles en écologie comportementale et en écologie prévoient que le comportement d'approvisionnement alimentaire des coléoptères carabiques devrait varier en fonction des niveaux de risques de compétition et de prédation qu'ils rencontrent et donc de la composition des communautés dans lesquelles ils se trouvent. Dans cette thèse, nous avons mesuré les changements de sélectivité alimentaire de deux espèces de carabes en présence de signaux de prédateurs ou de compétiteurs. A l'aide d'expériences de laboratoire effectuées à différentes échelles spatio-temporelle, nous avons réussi à montrer que la sélectivité alimentaire d'un carabe granivore *Harpalus affinis* peut varier en fonction du contexte dans lequel il cherche sa nourriture et être diminuée en présence de prédateurs. Par ailleurs le sexe des individus, l'espèce de graine qui leur est proposée et l'intensité du risque auquel ils sont confrontés semblent aussi avoir un effet sur la variation de sélectivité des individus. Aucun lien n'a cependant été trouvé entre le statut immunitaire ou la personnalité des individus et leur niveau de sélectivité alimentaire. Testé dans des conditions similaires, le carabe omnivore *Poecilus cupreus*, quant à lui, ne fait pas varier sa sélectivité pour les ressources testées. S'ils sont extrapolables ces résultats pourraient servir à expliquer la grande variabilité des taux de prédation de graines au champ par les carabes rapportés dans les différentes études. Ces résultats pourraient permettre aussi d'expliquer la difficulté d'extrapolation existante entre les taux de prédation de graines mesurés en laboratoire et les résultats obtenus au champ. Globalement, cette thèse confirme qu'une meilleure compréhension du processus de prise de décision chez les carabes est essentielle pour évaluer leur efficacité en tant que potentiels auxiliaires de cultures.

Mot clés : Carabes, prédation, compétition, immunité, personnalité animale, flexibilité comportementale, stratégie d'approvisionnement

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First Chapter

General introduction

1. The implicit costs of choosing

Making a choice implicitly requires investment of time in one behaviour at the expense of a simultaneous investment in another (Baum, 2010). Should I decide to spend some time shopping, I have to sacrifice a party with friends in the same moment. Thus, making a choice should be thought of as an allocation of time between behaviours, rather than just as a small scale switching between two activities (Baum, 2010). This same problem is encountered by foraging individuals. One of the first decisions that an individual foraging or seeking for a mate in the wild would have to make is deciding when to stop searching. As resources can vary markedly in their availability and quality across time and space, and considering that these variations are often erratic (Fawcett et al., 2014), choices have to be made between almost limitless alternatives. When should an individual stop looking and how long should it spend assessing each resource before choosing?

Individuals foraging in the wild compete for resources with other individuals also dealing with the same problems, such as eating and finding a mate often enough to increase fitness. Discarding an encountered resource implies running the risk that the resource becomes unavailable because the competitors use it. Moreover, the time invested assessing the quality of the resource increases the opportunity costs should the resource finally be rejected (Etienne et al., 2014). Individuals that encounter a resource should therefore try to optimize as much as possible the time they invest assessing its quality before consuming it or not. This is especially true when the time spent in assessing the relative quality of this resource could have concurrent energy costs. Bees, for example, invest time flying in front of flowers before deciding on which flower to pollinate. Flying is an energetically costly behaviour and spending too much time assessing the quality of an item may be more detrimental than accepting some wrongly assessed resources (Burns, 2005). Making a quick choice, when alternatives are not hazardous would, in this case be a better option since it would both reduce the energy invested in flying and potential opportunity costs (Etienne et al., 2014). It is therefore important to understand the impact of an error on individual fitness, in a given context, when looking at individual choice (Hammerstein and Stevens, 2012).

Investing too much time searching for a good resource or alternatively discarding too many resources is costly (Burns, 2005; Etienne et al., 2014). However, stopping at the first randomly encountered item is also often not a good strategy, particularly where resources are hazardous such as flower harbouring predators or prey that are poisonous. Not investing enough time assessing the quality of a potentially hazardous prey item and ending up using a dangerous item could thus result in a relatively higher cost, as it could lead to injuries or death, than the initial cost of just investing more time on resource assessment (Wang et al., 2013). In the presence of flowers harbouring ambush predators, bees spend a longer time assessing alternative flowers before deciding on which to use (Wang et al., 2013). Indeed, the more the prey is hazardous, the longer time that should be invested in assessing prey quality before making a choice on whether to use it or not (Chittka et al., 2009). Thus, beyond the requirement to make choices fast in the response to opportunity costs, there is a requirement for accuracy. This results in a trade-off between being fast and being accurate, which is commonly referred to as a *speed-accuracy trade-off* (Chittka et al., 2009; David et al., 2014).The amount of time invested before making a decision might thus be expected to reflect the difficulty and the value (in terms of fitness outcome) of the choice (Hammerstein and Stevens, 2012). Where bees are exposed to normal flowers in mixture either with flowers harbouring predators or distasteful flowers containing quinine for example, the bees increase their assessment time before making a choice (Wang et al., 2013).

Once a choice is made, switching to another encountered resource can also be detrimental under competition interference. Gammarid amphipods engage in long-lasting precopulatory mate guarding behaviours. Males are thus expected to choose and guard the best females possible. However, when they have initiated an amplexus with a female, they do not switch to a better female (Galipaud et al., 2015). This choice is best explained as a risk of losing both alternatives and ending up with nothing. An individual leaving a good enough female in order to try to pair with a better one runs the risk of losing both, particularly in presence of larger competitors. One way to reduce the time spent before making a choice would be to rank the alternatives and make choices based on this ranking. However, an active ranking of alternatives is cognitively challenging and requires the assessment of the relative advantages offered by each option. Alternatively, individual foragers might have innate or learned preferences for some resources that impact their choice (Jennions and Petrie, 1997).

2. Feeding preferences and individual levels of choosiness

Food preferences have been reported for a wide variety of predators (Rapport and Turner, 1970). Feeding preferences might arise as a consequence of nutritional requirements, morphology and availability of the prey (Xia et al., 2012). Sexual preferences are also expected to increase fitness. Female red groined toadlets, *Uperoleia larvigata*, prefer to mate with males that are 70% of their own body-weight. Heavier males would increase the risk of drowning and lighter males might not have enough sperm. Females have therefore established a threshold for mate acceptance that leads to higher fitness, which determines both their mating preference (Robertson, 1990) and allows females to rank males based on a qualitative factor (Dechaume-Moncharmont et al., 2013). Preferences have been extensively studied in mating behaviour and it has been proposed that females preferences have shaped the evolution of male secondary sexual traits (Wagner, 1998).

Fixing a threshold of acceptance could therefore help to reduce the time spent looking for acceptable resources as it would provide an objective metric of comparison to the prospecting individual. However, given that preferences might induce a greater interest for a particular resource type, a population composed of individuals with the same preferences would create a situation of competition. As a consequence, selection may favour alternative preference phenotypes or plasticity in preferences within a population, and individuals having preferences that differ from the population average might be at an advantage (Wagner, 1998). Preferences have been observed to vary between individuals and species (Bell et al., 2014). In the case of the red groined toadlets females, for example, females differ in their preferences based on their own relative weight (Dechaume-Moncharmont et al., 2013; Robertson, 1990).

Preference might also be shaped by factors such as sampling behaviour and environmental conditions, and might therefore vary through time or context (Bell et al., 2014). How alternative resources are encountered, such as the number of options encountered simultaneously (Peterson and Renaud, 1989; Raffa et al., 2002), could also impact individual preference. If an individual usually has a slight preference for option (A), rather than option (B) when encountered jointly, the occurrence of a third option (C) might, in some cases, cause a switch in the relative preference for (A) to a preference for (B) (Fawcett et al., 2014; Larrinaga, 2010). This effect is commonly described as the “decoy effect”. When buying a TV, for example, people enter the shop with a relatively clear picture of what they want to buy and of their budget. If sticking to his budget is what matters most for the prospective buyer, when exposed to two models, one that fits the requirements (A) and a second model that has slightly more options but is much more expensive (B), then choice would more often be for option (A). However, if a third model (C) is introduced, which has a specification in between option (A) and (B) but at a more expensive price than (B), then prospective buyers might leave with model (B) instead of (A) believing that it was their preferred choice all along. Choice (B) would have been an irrational choice, however, as the buyer would invest more money than initially planned in order to pay for extra TV options that were previously considered superfluous (Fawcett et al., 2014). The choice made would therefore not be based on an absolute assessment of the available options but rather on a simple comparison of all of them (Bateson and Healy, 2005; Lea and Ryan, 2015). Low quality males of the guppy, *Poecilia reticulata*, were observed benefiting from staying close to a male of lower quality as females made their choices comparatively rather than objectively (Gasparini et al., 2013). Observed preferences are also not necessarily transitive and might depend on how prey are encountered (Arbuthnott et al., 2017; Dechaume-Moncharmont et al., 2013; Kirkpatrick et al., 2006) . If (A) is encountered with (B), (A) might be preferred to (B). Yet, if (C) is preferred to (B), it does not mean that (C) would be preferred to (A). Relative preference might also be impacted by the composition of prey groups that are compared (Fawcett et al., 2014; Murray et al., 2010). The order and timing in which prey are encountered may also impact preference. A prey item encountered after a long fasting period would be preferred when encountered subsequently, even if paired with a prey of a relatively higher quality (Fawcett et al., 2014).

Choices made by an individual among a high diversity of alternative resources might not always reflect its preference (Underwood et al., 2004; Wagner, 1998). Choice and preference are often confounded when preference is evaluated using choice tests (Box 1). Consequently, it is important to clearly disentangle these two notions, as choice can be affected by factors independent of preference (Jennions and Petrie, 1997; Liszka and Underwood, 1990; Stallings, 2010). One prey item might be chosen over another because it is easier to catch and eat rather than because it is preferred (Stallings, 2010). The availability and ease of capture of a prey sometimes supplants preference (Rapport and Turner, 1970). Predators have been observed choosing prey based on their relative abundance rather than on preference for a specific trait (Jaworski et al., 2013). When the densities of a preferred or previously more abundant prey is low, a predator may switch to consume a different species (Hall-Scharf and Stallings, 2014), because spending too much time searching for a preferred prey, that might not exist in a patch, could lead the forager to starve. Choice can also be shaped by the relative risk posed by the prey or by the amount of energy that needs to be invested in prey capture (Eubanks and Denno, 2000; Kislalioglu and Gibson, 1976; Xia et al., 2012).

BOX 1: Comparison between choice and no-choice paradigm

Designing a choice experiment allowing to infer the underlying preference and decision rule used by an animal is not a trivial task. Many studies tried to address this problem and thoughtfully discussed the issues raised by two of the most commonly used experimental designs, either choice or no-choice paradigm. If no full consensus was reached between these studies, most of them still agreed on the fact that both protocols provide helpful insights, although from different nature.

In multiple choice tests, individuals can freely compare and choose between at least two (but frequently more) alternative items offered simultaneously. Choices (i.e. total amount of each prey type consumed or amount of time spent with a given mate) of the tested individuals are, then, ranked and compared in order to assess individuals feeding or mating preferences (Underwood et al., 2004). This type of test is particularly relevant to assess relative preference among available resource presented simultaneously (Driesche and Murray, 2004). Consequently, the results of these tests are strongly dependent on the combination of alternatives offered (Bruzzone and Corley, 2011; Larrinaga, 2010). For instance, the focal animal evaluate the relative values of each items (comparative choice) and not the absolute value of each item independently (Gasparini et al., 2013). One resource can appear less desirable when presented with another one than when presented alone (Bruzzone and Corley, 2011; Dougherty and Shuker, 2015; Edward, 2014; Fawcett et al., 2014; Murray et al., 2010; Peterson and Renaud, 1989). Overlooking of a resource in a choice test configuration might not mean that this resource would not be used in another context (Driesche and Murray, 2004). Individuals could also focus on prey that are more abundant (Jaworski et al., 2013; Stallings, 2010; Symondson et al., 2000) or easier to handle rather than on their absolute preference (Jennions and Petrie, 1997; Liszka and Underwood, 1990). As the value of the resource simultaneously offered in multiple choice test would not be perceived independently by the focal individual, care must be taken when interpreting the data (Bruzzone and Corley, 2011; Larrinaga, 2010; Peterson and Renaud, 1989; Raffa et al., 2002; Roa, 1992; Stallings, 2010). In addition the experimental design chosen to present the alternative items (in pair or in bigger group with several potential alternatives presented) might also impact the results (Peterson and Renaud, 1989).

BOX 1 (CONT.)

For example, if preferences are deducted from the total amount of items consumed during the test duration or on stomach contents, preference might be confused with handling time (i.e. capture, manipulation and ingestion) (Fairweather and Underwood, 1983; Hall-Scharf and Stallings, 2014; Liszka and Underwood, 1990; Underwood and Clarke, 2005). Moreover, the number of alternatives that an individual might be able to compare simultaneously might be limited and individuals might lose consistency as the number of available options increases (Bruzzone and Corley, 2011; Raffa et al., 2002). Because how alternatives are presented in choice test paradigm might impact the observed results, these tests would more likely illustrate individual's relative preference between all the items proposed during the test than inform on individual reluctance toward an item (Allison and Cardé, 2008; Dougherty and Shuker, 2014; Murray et al., 2010; Raffa et al., 2002).

No-choice tests, for their part, are based on the presentation of only one option (Dougherty and Shuker, 2015), or one type of item (e.g. one species of seed). Number of no-choice tests required to compare alternative options thus depend on the number of options that have to be compared. In such test, the preference is estimated from the probability of acceptance of the item (i.e. total amount of each prey type consumed or latency to first item acceptance) of the tested individuals are then compared between treatments to assess an individual interest for a given resource. Results obtained from these tests often differ from results obtained in multiple choice design (Dougherty and Shuker, 2015). This could first be explained by the independency of results obtained from these test as resource are always presented with no alternatives options (Murray et al., 2010). Moreover, rejection of a food item in a no-choice paradigm is less likely to occur, if the resource can be used, given that the consequence of this rejection would be higher than in choice test where the cost of rejecting one of the option is zero, as there is always at least one other option available (Dougherty and Shuker, 2015; Murray et al., 2010). No-choice tests are thus particularly relevant when assessing the individual absolute motivation to use a given resource (Driesche and Murray, 2004). The strength of no-choice tests is that negative results are very robust and provide convincing evidence that a neglected resource would not likely be used in the wild.

BOX 1 (CONT.)

However, high rate of acceptance under no-choice test could result from the lack of alternative option rather than from a high level of preference for that items. Several authors, thus, point the fact that “preference” could not be tested using no-choice test (Allison and Cardé, 2008; Manly, 1993; Peterson and Renaud, 1989; Xia et al., 2012). Choice will reflect individual willingness to accept or reject rather than its preference for the tested item and could thus inform on difference of attractiveness of different resource tested separately (Larrinaga, 2010; Peterson and Renaud, 1989).

Both these test paradigms thus assess different component of the individual decision making process and use of either of these paradigms would depend on the objective of the study (Driesche and Murray, 2004). Choice tests, as they allow to compare more than two alternatives simultaneously would be adapted to assess individual relative preferences and underlined the “most preferred” option. No-choice tests, conversely, have been suggested to be very suitable in order to measure the amount of energy or effort that an individual would invest into the search for one alternative prey item, over those already encountered (i.e. level of choosiness *sensu* Jennions and Petrie, 1997). Finally choice for one test design over another should be based on the ecology of the species tested (Dougherty and Shuker, 2015; Driesche and Murray, 2004). If individuals are more likely to encounter resource sequentially in their natural environment, no-choice tests would be more realistic than choice tests paradigm in order to understand how individual make choices (Allison and Cardé, 2008; Driesche and Murray, 2004). Conversely, if resource would more likely be encountered simultaneously, use of choice test would be more relevant.

The time individuals invest searching for a preferred item might vary. The effort that an individual is willing to put into the search for one alternative prey item, over those already encountered, is termed “choosiness” in the behavioural literature (Jennions and Petrie, 1997). Individuals discarding more available resources or spending more time in assessment of resources before acceptance are then defined as being choosier than an individual accepting a resource more rapidly. Being choosy therefore implies greater tolerance to opportunity costs than the non-choosy individuals (Dechaume-Moncharmont et al., 2016; Etienne et al., 2014). Choosiness can thus be considered as the amount of time an individual would invest before accepting a resource or as the number of resources overlooked before acceptance, and is often evaluated in no-choice experimental designs (Box 1).

3. Variation of choosiness

Being choosy is time consuming. Some investment of energy and time assessing resources prior to making a choice (i.e. choosiness) may be required in order to reduce the risk of accepting poor quality resources, being ambushed by cryptic predators and even succumbing to poisonous prey. This energy and time invested in being accurate will no longer be available to other essential, yet time consuming tasks such as antipredator avoidance (Sih, 1980). Resource acquisition, such as foraging and the search for mates, and predation avoidance are commonly considered as two conflicting tasks (Beauchamp, 2008; Milinski and Heller, 1978; Sih, 1980; Underwood, 1982; Wang et al., 2013) or as mutually exclusive behaviours (Lima and Dill, 1990; Nonacs and Blumstein, 2010). Cognitively challenging tasks such as foraging or mate sampling are performed at the expense of anti-predator behaviour. In essence, animals face a trade-off in which they have to balance "the value of life to the value of food/mate" (Caraco, 1979; Higginson et al., 2012). Given the immediate and lethal outcome of predation, behaviours linked to predator avoidance have been considered as the task of greatest priority when the risk of predation is high (Lima and Dill, 1990). Levels of choosiness should therefore be adjusted, conditional on the risk context of predation in which individuals forage or seek mates (Leaver and Daly, 2003). Most of the studies looking at variation of choosiness under predation risk have shown an increase in the level of individual choosiness in the foraging context (Ibrahim and Huntingford, 1989; Leaver and Daly, 2003; Lima and Valone, 1986). In order to reduce the time spent exposed to predators, individuals can decide to consume only prey that are more quickly eaten (Mikheev and Wanzenböck, 2010) or to focus on prey that can be transported to a safe burrow, with an energetic value that would compensate for the transport (Lima and Valone, 1986). However, being choosier would imply a reduction in the number of prey accepted and an individual's total energetic input, which can in some situations be highly detrimental.

While reductions in choosiness have been extensively studied in mate choice, where opportunity costs can be important (Atwell and Wagner, 2015; Davis and Leary, 2015; Etienne et al., 2014; Hedrick and Dill, 1993; Lima and Dill, 1990), they have been observed in foraging studies less often (Blubaugh et al., 2017; Leaver and Daly, 2003; Metcalfe et al., 1987a, 1987b; Perea et al., 2011; Wang et al., 2013). A reduction in choosiness can be beneficial, however, where the consumption of resources, irrespective of their quality, assure a non-zero energetic input while potentially freeing up time for predation avoidance behaviours. However, reductions in choosiness also have some drawbacks. The resources that an individual may encounter, at any particular location or on any given date, will not be identical. Resources can vary in quality and amount, availability and in the time required for consumption. An individual might then invest a substantial part of its time consuming low quality resources and, therefore, not fulfil its needs. This would suggest that reducing or increasing choosiness is not an optimal solution in every situation. Individuals might be able to modulate or adjust their investment in the evaluation of resources and thereby modify their choosiness without changing their preference. This would allow a forager to find the optimum in "the value of life to the value of food/mate" trade-off (Higginson et al., 2012) and maximise their fitness to the extent possible in any given situation. Their variation in choosiness should thus be adjusted to the intensity of the predation risk (Abrams, 1994).

Another situation where choosiness might vary is under the risk of competition. With an increasing number of competitors, individual foragers would face an increasing risk of opportunity costs. Indeed, several studies have demonstrated that competition can decrease choosiness (Davis et al., 2011; Dechaume-Moncharmont et al., 2016) either for sexual partners (Dubois and Belzile, 2012; Etienne et al., 2014) or for food resources (Amita et al., 2010; David et al., 2014). In an environment where predation and competition risks require predation avoidance and opportunity cost reduction behaviours, both types of risk might be expected to influence individual levels of choosiness. However, factors intrinsic to the individuals themselves may also lead to systematic variation in levels of choosiness.

As the behaviour leading to the highest fitness (i.e "the optimal behavioural option") would have been selected through evolution, one might hypothesise that decision consistency would be observed between all individuals of a given population. All individuals should make similar decision in a given situation. However, differences in between individuals in their behaviour and decision making occur frequently, even in the same situation. The existence of differences in the decisions adopted by individuals could initially be explained by the relative cost of remembering all decision types and all linked solutions. Similarity in the decisions adopted by individuals would imply that the individual should be able to accurately choose the "correct decision to make", among all the potentialities of any given situation. This is commonly referred to as the "tool box problem". The question then becomes "Which tool would be the best to unlock a given situation"? It is now acknowledged that differences in decision making exists between individuals. These differences might, for example, sometimes serve as a way to reduce competition. When offered a resource some individuals would always accept it earlier than others (Hammerstein and Stevens, 2012). These consistent differences in individual levels of choosiness would allow the coexistence of more individuals. Differences in behaviour among individuals could also be a good way, evolutionarily, to reduce predation risk. If all individuals behaved consistently, it would be relatively easy for a predator to predict all decisions made by these prey. In contrast, the same predator would have much lower success against a species where the behaviour or reactions of individuals differ with the situation. The study of these consistent behavioural differences, between the individuals of a given population, is referred to as the study of “behavioural syndromes” or “personality” (Hammerstein and Stevens, 2012; Reale et al., 2010). The “bold-shy” personality axis has received particular attention in respect of foraging behaviour. Bolder individuals are less neophobic and have higher rates of exploration than shy individuals. Thus, the foraging success and the choosiness of bold individuals should be consistently higher than shy individuals (Toscano et al., 2016; Wolf and Weissing, 2012). However, in being exposed to more potentially dangerous places, bold individuals should also be exposed to greater risk of predation. These personality traits, which shape individual behaviour and decision making, should therefore be taken into account when trying to disentangle the process of decision making in a given species and to understand observed noise/variation in foraging patterns.

Variation in individual choosiness might also arise from factors such as individual differences in physiological needs. As the level of hunger of a foraging individual increases, for example, the level of risk that it might be willing to accept will also increase, leading hungry individuals to invest more energy in foraging or spend more time foraging in risky habitats (Cartar, 1991; Croy and Hughes, 1991; Godin and Crossman, 1994). Thus, individuals having different energetic requirements might also have different levels of choosiness.

How individuals make a choice for a particular prey item is therefore a difficult question to answer as it varies with the situation and the individual’s traits. Decision making has become a staple subject of behavioual ecology, particularly for understanding mating behaviour, with a robust framework of theory and empirical support. I believe that it is now time to transfer this behavioural understanding to explain the trophic interactions that underlie, but are often ignored, in Community and Network Ecology. Given that the choice of individual predator might differ between contexts and between individuals, a better understanding of how predators make prey choices would, for example, help to improve the predictability of pest control in agriculture. Predators used as biocontrol agents typically operate within communities in which competition and predatory interference occur and are ever present and in which the quality of resources can vary dramatically. Gaining a better understanding of how the choosiness of biocontrol agents vary in different contexts could thus help to identify agricultural management guidelines that would increase the efficiency and reliability of biocontrol agents.

4. A growing interest for the use of biocontrol agents in agricultural fields

4.1. Agronomy general context

The post-second world war need to provide enough food for a growing population culminated in the green revolution of the 1960s, which drove significant structural changes in agriculture, world-wide. Characterized by a specialization and intensification of cropping, an increase of the area of arable land used, coupled to an increase in mechanization, irrigation and the use of chemical inputs (Matson et al., 1997), the green revolution doubled the world production of food between 1965 and 1995 (Mann, 1999).

Pest damage is one of the predominant causes of yield reduction in agricultural crops (Marshall et al., 2003), and weeds alone can account for up to 30% of yield loss (Oerke, 2006). One of the main measures to increase yield was thus the regulation and control of pest populations. The most common method for pest regulation is the use of pesticides which have been highly successful in terms of production. However, it has since been shown that pesticides also have negative environmental impacts (*e.g.* increased nitrate and pesticide emissions in the soil and in water (Moss, 2008)), raise public health concerns (*e.g.* presence of pesticides and heavy metals residues in food (Nasreddine and Parent-Massin, 2002)) and lead to biodiversity loss (Bommarco et al., 2011; Gaba et al., 2014; Stoate et al., 2009)). Moreover, overreliance on chemicals to control weeds has led to the emergence of resistance to herbicides making the current agricultural systems ever more fragile (Chauvel et al., 2001; Heap, 2014). Conventional weed management operations also require considerable monetary resources (Kulkarni et al., 2015b).

4.2. Alternatives to the use of pesticides products

In order to reduce the use of pesticides by 50% within 10 years, the Ministry of Agriculture and Fisheries of France (2015) designed a regulatory framework, the “Ecophyto plan” as a part of a EU-wide movement that seeks to reduce the use of pesticides and encourage alternative agricultural management practices by Member States. The world market for food requires, however, that agricultural production is maintained at a certain level. Reliable and effective alternative solutions must therefore be put in place in order to compensate for the future fall in pesticides use. These alternatives include biological control (Butault et al., 2010); which is defined by the Organization for Biological Control – West Palearctic Regional Section (IOBC-WPRS) as “the use of living organisms to prevent or reduce damage caused by pests”(Ferron, 1999). The core idea of biological control is that to achieve a substantial reduction of a pest species, bringing it below ecological or economic thresholds (Suty, 2010), it is necessary to take advantage of the mechanisms of natural regulation of populations to promote interactions such as pest predation, parasitism or competition (Ferron, 1999).

Beetles of the family *Carabidae*, are often presented as potentially interesting biological control agents (Kromp, 1999; McKemey et al., 2003). Carabids can consume and regulate many species of animal and plant pests in agricultural systems (Holland, 2002; Honek et al., 2007; Kromp, 1999; Symondson et al., 2002). Given their polyphagous diet (Kromp, 1999; Lövei and Sunderland, 1996; Thiele, 1977) and their potential effect on pests species, carabid beetles have received attention as biological control agents for both animal crop pest and weed control (Honek et al., 2003; Kromp, 1999; Kulkarni et al., 2015b).

In the synthesis reports published in the Millennium Ecosystem Assessment, in 2005, ecosystem services were defined as the benefits people obtain from ecosystems. They are classified in four categories: i) provisioning services, ii) regulating services, iii) cultural services and iv) supporting services. Carabid predation is a potential regulating services via the benefits that could be obtained from their natural regulation of pests (Johan Kotze et al., 2011; Kromp, 1999; Lövei and Sunderland, 1996). Significant consumption of crop pests (weeds or animals) by carabids could allow to reduce the impacts on the yields (Bohan et al., 2011; McKemey et al., 2003) and the use of polluting chemicals. Weed seed predation by carabids is now officially recognized as an important ecosystem service in the French National Ecosystem Assessment (EFESE, 2016).

5. Carabids beetles as biological control agents of weeds in arable fields

5.1. Seed of weeds predation by carabids

Ground beetles (Coleoptera: Carabidae) are present and abundant in both natural and man managed habitats (Frank et al., 2011; Kromp, 1999) with approximately 1200 carabid species being recorded in France (Forel and Leplat, 2001) and about 40 000 species world-wide (Dajoz, 2002; Lövei and Sunderland, 1996).

Seed eating carabids beetles can consume a substantial amount of seeds of weeds in the field (Frank et al., 2011; Honek et al., 2003; Menalled et al., 2007; Saska et al., 2008; Thiele, 1977; Ward et al., 2014) and are the main consumers of weed seeds among invertebrates (Honek et al., 2003). Carabids primarily consume seeds at the soil surface (Kulkarni et al., 2015a). These seeds come either from the seed rain of the standing weeds, which are intercepted and consumed prior to entering the seedbank or from the seedbank that is re-exposed by tillage (Honek et al., 2006; Martinkova et al., 2006; Saska et al., 2008). This predation of seeds can kill a large proportion of the seeds produced (Honek et al., 2011, 2009) and hence play a major role in the biocontrol of weeds. It has been estimated that seed-eating ground beetles may consume up to 1000 seeds / m² per day (Honek et al., 2007) and that seed consumption by carabids could help to reduce seed stock of a weed species by 65 to 90% (Honek and Martinkova, 2005). This consumption could impact the demographic repartition of some weed species (Westerman et al., 2005), the amount of seeds entering the seed bank and consequently the change in seedbank size (Bohan et al., 2011). Some species are also capable of removing weed seeds buried in the soil after agricultural operations (Kulkarni et al., 2015a; White et al., 2007).

Carabid mouthparts are typically too small for consuming the larger seeds of domesticated crops (Boursault, 2012). Their peak of activity also does not match the sowing date of crops (Boursault, 2012). Thus, carabids are considered as good candidate agents for the biocontrol of weeds in arable fields as they do not have an antagonistic effect on crop yields by being potential pests in arable fields (Kamenova et al., 2017). Pests can be controlled in two main ways; either by importing natural enemies that destroy pests or by conserving the natural enemies of the pests that are already there or are readily available (Ehler, 1998). The high abundance of carabids in fields could be managed to deliver biocontrol by conservation.

In order to develop effective biological control methods that would use carabids as weed control agents, it is necessary to understand the factors that lead to an efficient and stable seed predation rate. Results achieved in field studies are highly variable, making it difficult to draw conclusions for the potential efficacy of carabid weed seed regulation in real world systems (Davis and Raghu, 2010; Petit et al., 2014; Saska et al., 2008; Westerman et al., 2003). Predation rates of weed seeds can vary from 10% to 80% from one week to the next (Davis and Raghu, 2010; Petit et al., 2014; Saska et al., 2008; Westerman et al., 2003). Predation rates also differ between fields according to their characteristics and their in-field location (Saska et al., 2008; Westerman et al., 2005).

There is, therefore, a need to better understand the origin of this variation in predation rates to improve the potential biocontrol of weeds and, hence, the ecosystem service of weed regulation by carabids.

5.2. Possible source of variation in granivory rates.

5.2.1. Many carabids have a polyphagous diet which could impair their efficiency as biocontrol agents of weeds

Some species of carabids are highly specialist feeders. *Notiophilus biguttatus* can be maintained on a diet exclusively composed of springtails (*Collembola*) (Thiele, 1977), while species from the *Paussini* tribes are myrmecophils (Nagel, 1979). *Epomis* species are specialized for preying upon amphibians (Wizen and Gasith, 2011a, 2011b). However, most species of carabids are polyphagous predators , feeding on both plant and animal prey (R. Hengeveld, 1979a; Kromp, 1999; Lövei and Sunderland, 1996; Thiele, 1977). Significant morphological and behavioural diversity in feeding adaptations exists amongst these polyphagous carabids. While granivory (seed feeding) occurs in many species (R. Hengeveld, 1979a, 1979b; Honek et al., 2003), the relative importance of granivory versus carnivory (i.e plant *vs* animal prey) can differ within and between each carabid species. Depending on the relative importance of seeds in their diet, seed-eating carabid species have been divided into different "trophic guilds" (e.g. specialist granivores that only occasionally feed on animal prey (i.e. opportunistic omnivores) or more generalist predators that are obligate omnivores feeding both on plant and animal prey)(R. Hengeveld, 1979a; Kamenova et al., 2017).

To classify seed-eating species into trophic guilds, there was an initial need to evaluate the feeding panel of carabids, accurately and robustly. Much of the data on carabids diets results from direct observation of carabids predation and on the analysis of guts contents (Šerić Jelaska et al., 2014). Many other methods have since been used to improve our knowledge of carabid diets such as isoenzyme analysis (Paill, 2004, 2000), monoclonal and polyclonal antibodies (McKemey et al., 2003; Symondson et al., 2000) and DNA-based, molecular gut content analysis (King et al., 2010; Šerić Jelaska et al., 2014). While useful in defining what a carabid ate, these techniques do not elaborate the prey choice decision making process that carabids follow. As carabid feeding behaviour might be primarily opportunistic and because carabids can have high diet plasticity (Symondson et al., 2002), characterising the full diet of carabids from the realised, observed diet remains difficult without a better understanding of how foraging decisions are being made.

5.2.2. Relative importance of seeds in the diet of seed-eating carabids

Studies looking at the foraging decisions of seed eating carabid species have been predominantly laboratory based using, for the most part, experiments that conform to the choice-test paradigm (Box 1). These studies show that there are marked differences in the total amount of seeds consumed that appear to depend on the trophic guild of the carabid forager (i.e omnivore *vs* granivore). Granivorous carabids consume more seeds than obligate omnivores with differences between carabid species ranging from 1.28 seeds /day for *Pterostichus melanarius* (Illiger, 1789) individuals, an obligate omnivore that mainly feeds on invertebrate prey (Powell, 2011; Symondson, 2002; Symondson et al., 2000), to 26.35 seeds/day for a similarly sized granivorous species, *Harpalus rufipes* (Petit et al., 2014).

These differences in the amount of seed eaten between carabid species could result from differences in their physiological needs (Kulkarni et al., 2015b). Some carabid species might rely on seeds to eat, while some other species use seeds to ‘top-up’ their fitness (i.e. female fecundity, overall growth, developmental rate and larval survival) (Fawki and Toft, 2005; Kulkarni et al., 2015b; Saska, 2005; Saska and Jarošík, 2001). Differences in total seed predation rates in between seed-eating carabids species could also result from morphological differences (Forsythe, 1983). Granivorous carabids possess robust mandibles (Acorn and Ball, 1991), with adults of the opportunistic omnivore *Amara* and *Harpalus* genera, for example, having broad mandibles to crush hard seeds (Forsythe, 1983; Zetto Brandmayr et al., 1998). Differences in the importance of seeds in the diet of seed-eating species can also be explained by an inability of individuals to effectively digest all seed species (R. Hengeveld, 1979c; Lundgren and Lehman, 2010; Schmid et al., 2014). Lundgren and Lehman (2010) showed that the presence of endosymbiont communities in the gut of carabids could have a role in facilitating the digestion of seed material. If this endosymbiont community is altered, by the use of antibiotics for example, the consumption of seeds by carabid individuals decreases or is even stopped (Schmid et al., 2014). Given that communities of the endosymbionts likely differ between carabids species (Lundgren et al., 2007), one can speculate that some species are better at eating and digesting seeds than others (partly reviewed in Kulkarni et al., 2015). Physiological and morphological differences between species might therefore explain the observed differences in seed consumption between seed-eating species (Acorn and Ball, 1991; Forsythe, 1983; Honek et al., 2011; Kulkarni et al., 2015b; Lundgren and Lehman, 2010).

Seed-eating species do not, however, differ only in their total seed consumption. Differences in the diversity of seed species accepted by individuals, referred to as “preference”, has also been reported in several studies (Honek et al., 2011, 2007, 2006; Klimeš and Saska, 2010; Kulkarni et al., 2017; Lund and Turpin, 1977; Petit et al., 2014; White et al., 2007). A better understanding of the seed species that are “preferred” and why a carabid species would choose one seed species over another is of particular interest as selective predation would impose limits on the panel of seeds that might be preyed upon in fields and hence on the potential for a biocontrol service provided by carabids (Honek et al., 2011). In particular, this knowledge would: 1) document whether the ecosystem service of weed regulation is distributed equally among the various weed species; 2) identify those carabid species involved in the service of weed regulation; and, 3) explain the diversity of trophic links between weed and ground beetle species.

5.2.3. Seed feeding preferences in carabids

Preference has mostly been investigated using laboratory choice-test experiments (Box 1) that present relatively small numbers of test weed seed species (e.g. Jorgensen and Toft, 1997) through to studies that use a large numbers of seed species (Honek et al., 2007, 2006, 2003; Lund and Turpin, 1977). These studies appear to show correlations (affinities) between carabid and seed species (see Johan Kotze et al., 2011). These taxonomic affinities were observed for Zabrini species, which prefer seeds of *Taraxacum*, and the species of Harpalini that prefer seeds of *Cirsium* and *Viola* (Honek et al., 2007). Thus, some carabids may have species-specific preferences for weed seeds, which might be a conserved trait at the taxonomic level (Honek et al., 2007).

Carabid feeding preferences might also be shaped by the size of the seeds and of the carabids eating them (Honek et al., 2011, 2007, 2003; Saska et al., 2010). It has been shown that carabid body size is linked to the maximal size of the prey eaten, whereas the smallest body sizes eaten by carabids do not differ between species (Loreau, 1983). The size of the carabid’s mandibles might be of primary importance in determining which seeds could be eaten (Acorn and Ball, 1991), as compatible dimensions between the mandibles of the carabid and diameter of the seeds would allow the carabid to be more efficient in breaking open and consuming the seed (Honek et al., 2011). Harpalini species have been described as unspecialized toward weed seed species (Acorn and Ball, 1991; Forsythe, 1983; Kulkarni et al., 2015b; Zetto Brandmayr et al., 1998), having evolved broad mandibles and massive adductor muscles that are able to crush hard seeds of a range of sizes. They have high rates of seed consumption (Paarmann et al., 2006; Zetto Brandmayr et al., 1998). Being able to feed on several species of seeds, regardless of their shape or size, might be beneficial for a granivorous species. They might survive solely through seed consumption and using the edible seeds available throughout their period of activity (Kamenova et al., 2017). Seed traits also play a role in preference. Seed coat thickness, seed shape and size of the seeds (Honek et al., 2007), the level of imbibition and the chemicals present on the surface of the seed have all been shown to impact individual preference (Honek et al., 2011; Law and Gallagher, 2015; Wheater, 1989). The nutritional content of the seeds, such as the percentages of fats, proteins and carbohydrates, might also influence preference and rates of consumption (Kromp, 1999; Lund and Turpin, 1977).

When tested in the laboratory, the feeding preferences of carabid species do not change over the season, suggesting that preference might be species specific (Honek et al., 2006). Carabids have nonetheless been reported to be able to change their diet according to the quality and/or the availability of the prey (Birkhofer et al., 2011). Thus, carabids might modify their diet according to their physiological needs, which might change during growth (Sasakawa, 2010). Sexually dimorphic needs might also exist, and female carabids were observed consuming more seeds than males (Saska et al., 2010), climbing on plants to reach food (Sasakawa, 2010) and moving more slowly than males when satiated (Szyszko et al., 2004).

5.3. Feeding guilds co-occurring in the wild

5.3.1. Knowledge about the relative importance of guilds in weed control

Given that carabid species might differ in the relative importance of plant *vs*. animal prey in their diet and have species specific preferences for seeds, some studies have examined the role of seed-eating carabid species richness and/or diversity on seed predation (Gaines and Gratton, 2010; Jonason et al., 2013; Trichard et al., 2013). These studies have suggested at some form of complementarity between carabid species in the delivery of weed seed predation. Predation rates would therefore be directly linked to the composition of the carabid community with richer communities of carabids preying upon richer communities of weeds.

In parallel, studies have demonstrated equivocal results for the in-field relationships between carabid abundance and weed seeds predation rates. Various studies have found that even where carabids are usually most abundant, at field edges, weed seed consumption is not always highest there (Saska et al., 2008; Westerman et al., 2008). Saska *et al* (2008) showed that a high abundance of carabids over time does not always translate into more weed seeds consumed. In contrast, Honek *et al.* (2003) found that patterns of abundance of carabid beetles over time are positively correlated with weed seed predation. Moreover, some studies have suggested that only the abundance of granivorous carabid species (i.e. opportunistic omnivores) predict predation rates (Trichard et al. 2013; Diekötter et al. 2016), while other studies, which analyse the links between carabid communities and seed predation, suggest that predation would be better predicted by the abundance of obligate omnivores (Bohan et al., 2011; Jonason et al., 2013). Finally, by showing a clear link between carabids abundance and predation rates, it has also been suggested that both guilds (obligate omnivores and granivores) contribute to seed predation (Kulkarni et al., 2017; Menalled et al., 2007; O'Rourke et al., 2006; Trichard et al., 2013).

These equivocal results, obtained in studies looking at beetle abundance or carabid species richness as predictor of weed seed predation by carabids, have all neglected the role of intraguild interference interactions that can occur within carabid communities. My working hypothesis is that these interference interactions play an extremely important role in seed predation in the field, and explain the apparently equivocal results obtained to date. As carabid beetles are organized in communities in nature, the presence of competitors or predators might be an important criterion for the selection and the consumption of a particular resource (Lima and Dill, 1990; Metcalfe et al., 1987b; Sih, 1980). Moreover, as seed-eating carabids are abundant and diverse in the field, it is likely that interactions within the guild of predators (i.e. intraguild interference), such as intraspecific competition, interspecific competition and intraguild predation would occur frequently between carabid individuals and species (Griffith and Poulson, 1993; Guy et al., 2008). This expectation has led to a renewed interest in the biocontrol exerted by assemblages of mainly generalist predators (Lang, 2003; Snyder and Ives, 2003; Straub et al., 2008). However, testing predictions of pest-control functioning in multi-predator communities has proven difficult because of both positive and negative effects of generalist predator diversity on biocontrol that can arise either from niche complementarity and facilitation or from functional redundancy and predator interference; effects that are not yet well understood (Crowder and Jabbour, 2014; Straub et al., 2008; Tylianakis and Romo, 2010).

5.3.2. Effect of intraguild interference on carabid behaviours and its potential effect on the biocontrol of weeds through change in individual levels of choosiness

5.3.2.1. Competition

Interspecific and intraspecific competition imply the sharing of prey with competitors and, as a consequence, suffering a reduction in energetic intake where resources are scarce. Loreau (1986) showed that only one-third of *Abax parallelepipedus* individuals sampled in fields had eaten the night before and that only few of these individuals were fully satiated. A reduction in feeding income might therefore have serious effects on carabid fitness as undernourished females would be less effective at producing eggs, and undernourished larvae would have a longer development time and in turn produce smaller adults with a shorter life span (Dajoz, 2002). The size of adult carabids also appears to be correlated with their mating success (Juliano, 1985). Given that many species occur simultaneously in fields, at high density, a reduction in feeding income would have serious consequences for individual fitness. Competition has previously been considered a major force affecting the spatial distribution and co-occurrence of carabid species (Niemelä, 1993).

However, work examining the potential effect of interspecific competition in carabid assemblages, has mostly concluded that interspecific competition is not common among carabids (Niemelä, 1993). Co-occurrence is more easily explained by environmental factors rather than by competition interference(Holland et al., 2005; Thiele, 1977). This apparently small effect of competition on the carabid assemblage is further emphasized by studies that show carabid species aggregating to areas where food is abundant (Bohan et al., 2000; Frank et al., 2011; Sunderland and Vickerman, 1980; Thiele, 1977). However, Guy *et al.* (2008) showed that individual *P. melanarius* avoid odors from conspecifics on odor-impregnated papers, and that this response is density-dependent. This behaviour could have two major explanations: i) individuals try to reduce competition, as much as possible, by avoiding areas already exploited by conspecifics where food resources are expected to be scarce; or, ii) individuals try to reduce predatory interference that would result from encountering conspecific cannibals. The finding that *P. melanarius* aggregate where prey are abundant (Bohan et al., 2000) would suggest that the risk of intraspecific competition is not perceived as hazardous enough to induce change in the spatial distribution of foraging carabids. Rather, this avoidance behaviour might suggest at the importance of cannibalism in shaping the behaviour of *P. melanarius* (Thiele, 1977). Another explanatory hypothesis is that individuals accept a higher risk of cannibalism or predatory interference when food items are abundant. In the experiment of Guy et al. (2008) no food items were provided to the test *P. melanarius* in any treatment. Individuals may therefore have chosen the safe response by arresting on the control paper, but this response might have changed if food was provided on impregnated papers, particularly if starving individuals are more willing to take risks (Cartar, 1991; Croy and Hughes, 1991; Godin and Crossman, 1994).

Thus, the absence of proof for interspecific competition effects on carabid assemblages is not proof that competition plays no significant role in biocontrol. Competition might be perceived, but have impacts on other aspects of the foraging behaviour of carabids. The competitive exclusion principle posits that two exactly similar species competing for the same limiting resource cannot coexist. The principle predicts that in order to avoid extinction, coexisting species should use different ecological niches (Den Boer, 1980; Hardin, 1960). These might be due to differences in daily or annual rhythms, as being active during periods of competitor inactivity could help reduce competition. The species *Notiophilus biguttatus* and *Nebria brevicollis*, for example, both compete for collembolan prey, but have different daily rhythms that have been suggested to reduce competition (Dajoz, 2002). It has also been shown that species sharing resources could adjust their temporal activity via behavioural plasticity (Chao et al., 2013; Kamenova et al., 2015; Navarro et al., 2013). When forced to coexist with *Bembidion quadrimaculatum*, *Phyla obtusa* switched from a diurnal activity pattern to become more night active (Kamenova et al., 2015).

In carabids, diet is proposed as a major axis of ecological niche separation (Loreau, 1986). Individuals feeding preferences or morphological differences that restrict the foraging panel were already proposed to reduce competition in coexisting species (Pearson and Mury, 1979). Behavioural plasticity was also observed in feeding behaviours of Tiger beetles; close relatives of the carabids. *Cicindela repanda* individuals were observed changing their feeding panel and rejecting some prey types when they share them as prey with their larvae (Dajoz, 2002). By doing so they reduced intraspecific competition. Competitive interference might thus change the panel of seeds that would be predated by carabids, through indirect interference, and hence, the potential role of each species of seed-eating carabids as an agent of biocontrol.

I have already argued that carabid species differ in both their ability and requirements to consume seeds and their feeding preferences. Consequently, different seed species have different value for carabids. Moreover, direct competition for shared prey in the field, which is absent in most laboratory studies, likely lead to different observations of carabid choice in laboratory and in-field studies (Davis et al., 2011; Dechaume-Moncharmont et al., 2016; Hammerstein and Stevens, 2012). In order to reduce opportunity costs under competition in the field, individuals might reduce their threshold for seed acceptance (i.e. choosiness) and accept a larger panel of food items than in safer, laboratory situations (Amita et al., 2010; Dechaume-Moncharmont et al., 2016). The abundance and diversity of seed-eating carabid species in field might therefore change individual foraging behaviour and hence, the total granivory rate observed in field. Since behaviour, and more specifically individual foraging behaviour, appears to change under interspecific and intraspecific competition, studying carabid choice under both these intraguild interferences is required if we are to better understand how carabids survive in rich communities in arable fields. A change in foraging behaviour could help reduce functional redundancy, improving complementary between species and thus improve biocontrol.

5.3.2.2. Predation

The risk of predation might also impact carabid behaviour. As failing to avoid a predator would likely be at best harmful and at worst lethal, the risk of predation should induce behavioural changes greater than competition. Cannibalism is widespread in adult and larval carabids. Brunsting and Heessen, (1983) showed that larval density was reduced significantly as the carabid population increased, irrespective food availability. Interspecific predation also occurs between carabid species (Currie et al., 1996; Dajoz, 2002) with some species being able to directly impact the survival of other species. Predation by non-carabids can also impact carabid population dynamics. Carabid individuals avoided patches containing predatory rodents (Parmenter and Macmahon, 1988). The risk of predation by rodents can induce behavioural changes in carabid foraging behaviour, with carabids eating more seeds when exposed to rodent urine than in a no-urine control (Blubaugh et al., 2017). Both these studies focused on predation of carabids by mammals and to date and the best of our knowledge, no study has explicitly examined the effect of predation interactions between carabids on the foraging behaviour of carabids. Given the broad range of potential predators of carabids, including birds, small mammals and amphibians (Dajoz, 2002), and other carabid species (Currie et al., 1996; Thiele, 1977), predation is likely to markedly affect carabid-derived services. This is especially true for carabids foraging for seeds in arable fields, simultaneously exposed to many other carabid species from all guilds and experiencing intraguild predation. However, the effect of predation risk on carabid feeding choice (i.e. choosiness) has rarely been studied and the effect of intraguild predation between carabid species largely ignored.

5.3.2.3. Adjustment to the Intensity of the risk

Both competition and predation risk are thus expected to impact the level of choosiness of individuals. It is however impossible for an animal to determine precisely and accurately the intensity of the risk it is foraging under (Abrams, 1994). If neglecting the risk could be detrimental for obvious reasons, overestimating the risk could also be costly for the foraging individuals (Abrams, 1994; Sánchez-González et al., 2017). Predator avoidance behaviours are in conflict with other behaviours such as foraging. Overestimating the risk of encounter with a predator could lead to an unnecessary postponement of foraging and hence, reduction in total feeding income. Overestimating a risk of competition can also be detrimental as it could lead an individual to accept all encountered items, regardless their quality, in order to reduce as much as possible potential opportunity costs (Etienne et al., 2014). Carabids forage in highly disturbed and changing environments and in carabid communities with markedly different compositions, and may thus face high variance in the intensity of risk. The ability to finely adjust their foraging behaviour would increase their chance of survival in these highly disturbed environments (Snell-Rood, 2013; Sol, Lapiedra, & González-Lagos, 2013). Individual are thus expected to adjust to the intensity of the risk (Abrams, 1994; Sánchez-González et al., 2017) and change their level of choosiness according to the intensity of the risk they are foraging under.

5.3.3. Effect of other factors that might impact individuals' choosiness for seeds in carabids.

5.3.3.1. Effect of individual personality

An individual's response to the risk might also be affected by other factors more specific to individuals such as personality traits, physiological characteristics and even sex. Between-individual behavioural variation has been explained either as simple variation around an adaptive mean (Stephens and Krebs, 1986) or as the result of the inherent stochasticity of the environment in which the individuals are observed (Clark and Ehlinger, 1987; Monceau et al., 2017a). These explanations neglect whether, how and why individuals might differ in their behaviour (Clark and Ehlinger, 1987; Réale et al., 2007; Sih et al., 2004; Wilson, 1998). It is now recognised that behaviour can vary significantly between individuals of the same species, even in the same environment (Clark and Ehlinger, 1987; Wilson, 1998). Repeatable patterns of individual behaviours, which are consistent over time and across context, have been found in a wide range of animal taxa and have been termed 'personality'. Personality traits can impact individual fitness and have become the focus of considerable interest, recently, in the behavioural ecology literature (*see* Réale et al., 2007 *for a review*). Personality traits have been successfully linked to individual foraging behaviour in many taxa (Toscano et al., 2016). Reactive, or shy, individuals are expected to be less likely to expose themselves to predation risk than bold individuals. As predator avoidance and foraging are two conflicting tasks (Sih, 1980), shy and bold individuals might respond differently to predation risk according to their position on the "proactive-reactive" personality axis (Quinn et al., 2012). To my knowledge, no study has to date looked at the existence of personality traits in carabids. Thus, to improve biocontrol of weeds by carabids it would be interesting to determine whether personality traits exist in carabids and assess whether individual personality could be linked to an individual level of choosiness.

5.3.3.2. Effect of individual immunity traits

As the level of hunger of a foraging individual increases, the level of risk that it is willing to accept might also increase, leading hungry individuals to invest more energy in foraging or spend more time foraging in risky habitats (Cartar, 1991; Croy and Hughes, 1991; Godin and Crossman, 1994). Immune activity has been shown to increase the overall energetic requirements of individuals (Hess et al., 2015; Ponton et al., 2013; Stahlschmidt et al., 2015). Between individuals differences in level of choosiness could thus be explained by between individual differences in immunity traits. Immunity in insects can be affected by pesticide use (James and Xu, 2012). Linking the immune status and level of choosiness in carabid individuals might help in understanding the observed variability in predation rates observed in man-managed agricultural fields (Saska et al., 2008).

5.3.3.3. Effect of individuals sex and size

Individual traits, such as body size and sex could also impact individual feeding requirement (Cords, 1986; Gill and Hart, 1994; Kulkarni et al., 2015b; Pyke, 1984). Females carabids were observed eating more food than males (e.g. Kulkarni, Dosdall, Spence, & Willenborg, 2015; Sasakawa, 2010; Saska, Martinkova, & Honěk, 2010), that sexually dimorphic energy requirements might exist in carabids. Females might accept therefore higher levels of risk than males in order to meet their energetic requirements and hence differ in their level of choosiness when foraging under intraguild interference. Moreover, bigger individuals are expected to have higher energetic requirement (Gill and Hart, 1994). Change in level of choosiness could thus also be explained by difference in size between foraging individuals of a single carabid species.

5.3.3.4. Effect of the seed species encountered (interaction between preference rank and level of choosiness)

The level of choosiness when foraging for seeds might be impacted by the species encountered in the environment. It might be expected that preferred seeds would increase the level of risk that an individual is willing to accept while foraging. As a consequence, choosiness would likely always be lower for preferred than for non-preferred seeds, when under predation. The rate of predation among all species of seeds encountered in the wild will therefore be variable, and will differ with the relative riskiness of the environment.

6. The brief aims and summary of this PhD

As both competition and predation might be expected to induce change in the foraging behaviour of carabid individuals, both from consideration of the Behavioural Ecological theory and the empirical ecology of carabids, some understanding of how these two risks modify individual choosiness is necessary if we are to improve the biocontrol of weeds by communities of carabids. As predation and competition interference occur between individuals of the same carabid species and between individuals of different species, there is a need to quantify the impact of these different interference interactions on patterns of individual carabid seed consumption and foraging strategy. Specifically, I address how the risk of predation and competition affect choosiness. My task is therefore to better understand how carabid individuals choose their food items at: 1) the between individual scale using specific test carabid species; and, 2) the within species scale, to evaluate the consistency of choice and choosiness and potential differences in foraging strategy. I also examine the effects of individual characteristics, such as sex, personality and physiological state, and environment characteristics, such as intensity of the risk and seed species available, on the foraging behaviour of individuals

This thesis is structured as a series of chapters in which I address these questions as a series of explicit hypotheses. The chapters report on laboratory based experiments that were conducted to address the potential change in level in choosiness that could occur in carabids foraging for seeds. A basic assumption of the testing was that prey assessment and predator/competition avoidance behaviours are tasks in conflict. The core, null hypotheses tested were:

H1: Predation and competition risk, if perceived by an individual carabid, would impact its level of choosiness when foraging for seeds (**Chapter II**)

H2: The intensity (strength and direction) of change in choosiness for seeds will depend on:

- the relative component of seeds in a carabid diet (**Chapter III**)
- specific characteristics of the foraging individual, including personality and physiological traits (**Chapter IV**);
- the perceived intensity of the risk and on the species of seeds available in test (**Chapter V**)

H3: Change in level of choosiness would lead to a change (i.e. an increase or a reduction) in the daily total amount of seeds consumed by foraging carabids (**Chapter V**)

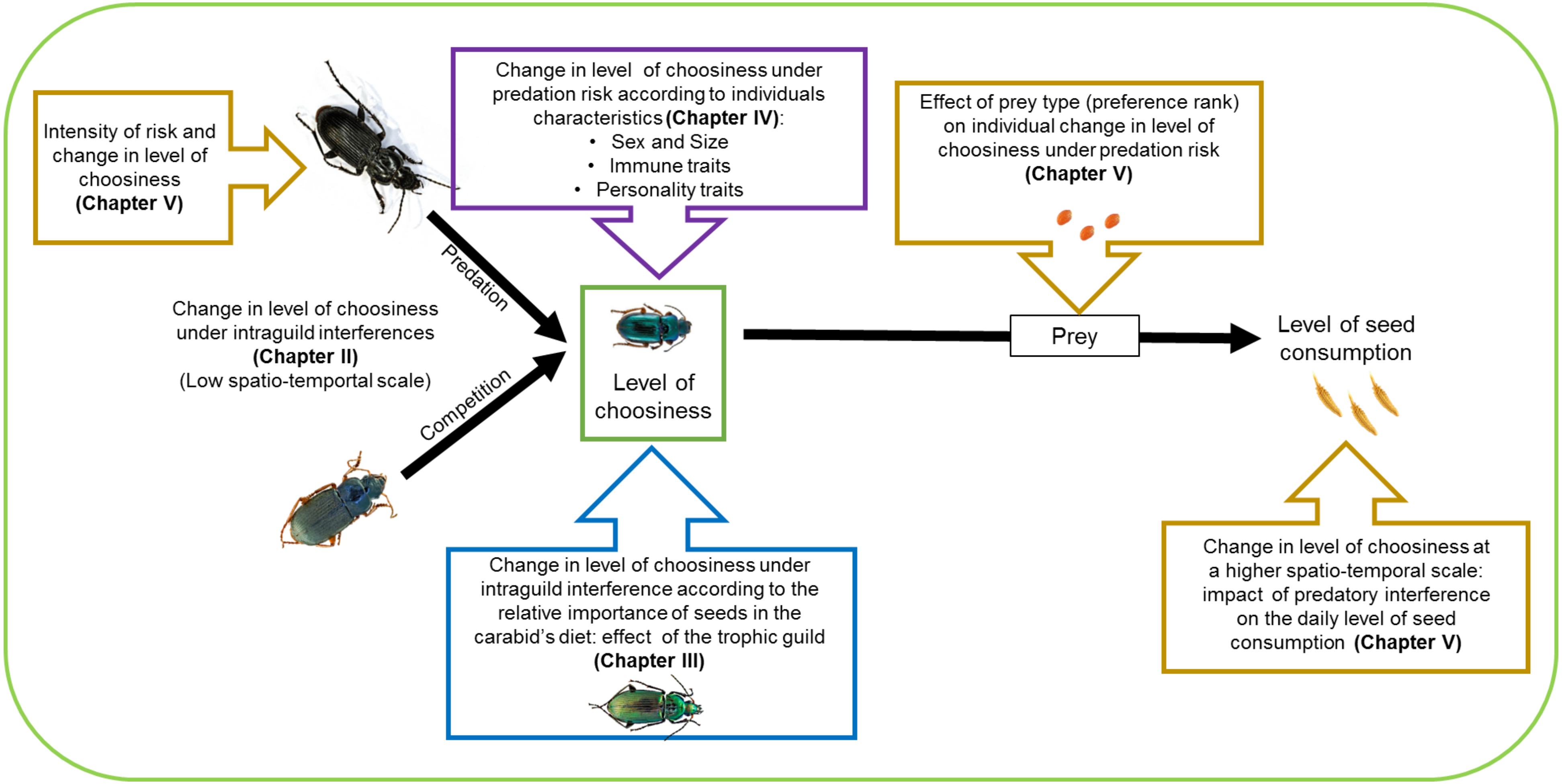


Figure 1: Representation of the potential mechanisms that determine choice in carabids. The chapters are structured by the mechanisms described in the coloured boxes.

7. Building an experimental methodology to assess change in levels of choosiness in foraging carabids

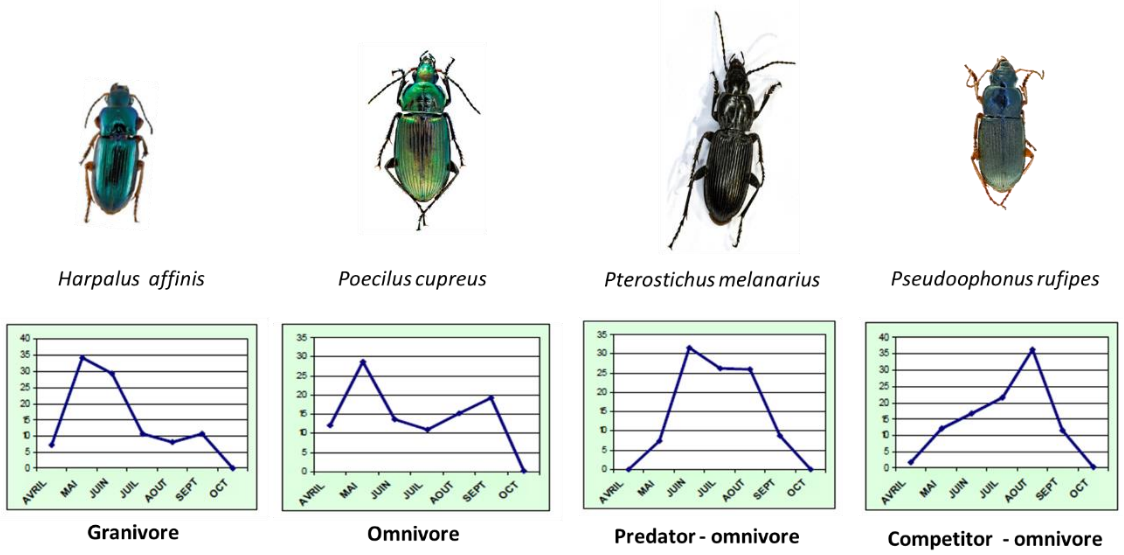
7.1. A laboratory controlled experiment that uses olfactory cues to simulate interference risk in the place of live carabids

Given that very little was known about the carabid foraging decision-making process and, more specifically, carabid choosiness, it was necessary to develop a simplified experiment protocol that would reduce any potential confounding effects of the experimental environment and establish a robust list of factors that might impact individual choosiness. I therefore started with a laboratory experimental design, to be done under highly controlled conditions, which is somewhat distant from what might be termed the ‘reality of the field’. The aim was to specifically control for effects of temperature (Saska et al., 2010), seed imbibition level (Law and Gallagher, 2015), individual hunger (Ernsting and van der Werf, 1988) and light exposure (Allema et al., 2012; Drees et al., 2008) on carabid foraging behaviour. Moreover, the laboratory conditions I established allowed the monitoring, at fine temporal resolution, of the individual behaviour of carabids by direct observation. This would assure that I could observe, parameterise and evaluate how a given *H. affinis* individual would behave toward an encountered seed, allowing the measurement of metrics such as latency to first seed acceptance, handling time, space use, etc.

One of the major problems to be addressed was how to test variation in level of carabid choosiness for seeds under intraguild interference, while also avoiding any confounding effects of direct interaction between the focal individual under test and the intraguild predators and competitors. Exposing the focal individual to live competitor or predator would have made the task of disentangling a genuine response to intraguild interference from reductions in choosiness, due to food items lost directly to intraguild predators or competitors, very much more difficult. Mating-related behaviours, which might have occurred in the intraspecific competition treatment, or predatory interactions, which might have occurred in the predation treatment, would have distracted individuals from foraging. The effects of competitive and predatory ‘intraguild’ interference were therefore simulated using odour cues, produced by individuals of two other standard carabids species and of conspecifics, as was demonstrated by Armsworth et al. (2005) and Guy et al. (2008). I choose to use cues from other highly abundant species in the wild, as standards for the testing, in order to ensure that our simulated encounters would have the greatest probability of being applicable to the in-field situation.

7.2. Choice of the carabid species used in tests

As focal species for our study, I choose to use two carabid species that are highly abundant in the fields: *Poecilus cupreus* (Linnaeus, 1758) and *Harpalus affinis* (Schrank, 1781). Given the aim of the Ph. D. being to assess individual change in the level of choosiness when foraging for seeds, I decided to focus my work on the granivorous carabid species, *H. affinis. P. cupreus*, an omnivore species, was used to test for a potential effect of the omnivore carabid trophic guild on *H. affinis* foraging behaviour. *Pterostichus melanarius* and *Pseudoophonus rufipes* were chosen in order to evaluate intraguild interference effects on our focal species level of choosiness. The choice for all these carabid species was based on their abundance, and therefore their potential conservation biocontrol importance, in the field and that they occurred simultaneously (Fig. 2). Studies using test papers, impregnated with odors from walking *P. melanarius* individuals to simulate *P. melanarius* presence and test for behaviour change in conspecifics or other animals, had already been developed and published (Armsworth et al., 2005; Guy et al., 2008). We were, thus, sure that this method would work at least for that carabid species.



Harpalus affinis — *Poecilus cupreus* — *Pterostichus melanarius* — *Pseudoophonus rufipes*

Granivore — **Omnivore** — **Predator - omnivore** — **Competitor - omnivore**

Figure 2: Graphics of the periods of activity over the agricultural year for each of the carabid species used in the testing during this PhD (adapted from Roger et al., 2010)

Data on the feeding preferences and consumption rates for all weed seed species used in this study were already published for the four carabid species (Table 1), and provided the basic information necessary to start this experimental investigation of choosiness. I would also note that *P. melanarius* was also chosen for its low rates of seed feeding (Table 1), which allowed us to assume that its cues would primarily be perceived as cues of predation and not as cues of competition as with *P. rufipes* odors.

Table 1: Seed consumption rates of the species used in test (adapted from Petit et al., 2014)

Species	*Harpalus affinis*	*Poecilus cupreus*	*Pterosticus melanarius*	*Pseudoophonus rufipes*
Role in this thesis	Focal Granivore	Focal Omnivore	Predator	Interspecific competitor
Used in chapter	All	Chapter III	All	Chapter II & III
Daily seed consumption	11.82	5.26	1.28	26.35
Daily consumption of seeds of *T. officinale*	2.52 (±2.90)	1.12 (±3.04)	0.12 (±0.26)	4.34 (±2.89)
Daily consumption of seeds of *V. arvensis*	4.65 (±3.13)	0.40 (±0.62)	0.15 (±0.24)	15.37 (±6.06)
Daily consumption of seeds of *Senecio vulgaris*	1.12 (±2.35)	1.87 (±3.83)	X	X
Daily consumption of seeds of *Capsella bursa-pastoris*	1.57 (±3.31)	1.40 (±2.58)	X	X

7.3. Choice of a valid metric to evaluate the variation in level of choosiness

I chose to use latency to first acceptance as my main metric of individual variation of choosiness. Counting the amount of seeds manipulated and subsequently rejected would have also been a valid metric of individual choosiness (Holveck et al., 2015). Rejection in carabids is however difficult to quantify objectively. Foraging carabids might assess the quality of food items at a distance; possibly using visual and chemical cues, and by direct contact via mandibular manipulation (Law and Gallagher, 2015; Thomas et al., 2008). Thus, I might have had some individuals not manipulating the seeds but still rejecting them at a distance. As this would potentially represent a high proportion of ambiguous data, I therefore chose to analyse only the latency to first acceptance and total seed consumption as proxies of individual change in level of choosiness (Edward, 2014; Jennions and Petrie, 1997). My justification was that by evaluating latency to first acceptance as choosiness I could: i) unambiguously determine that the seed has been consumed by the focal individual; and, ii) use Cox survival models to censor the data for those individuals not observed eating.

Changes in the use of space within the arena (space use) and in individual velocity under intraguild interference, such as predatory interactions (Ioannou and Krause, 2009), might also have impacted latency to first acceptance in foraging individuals. I therefore scored and analysed trajectometry of all individuals during the course of the experiments to correct for any potential confounding effect of velocity and overall movement of individual on their latency to first seed acceptance.

Second Chapter

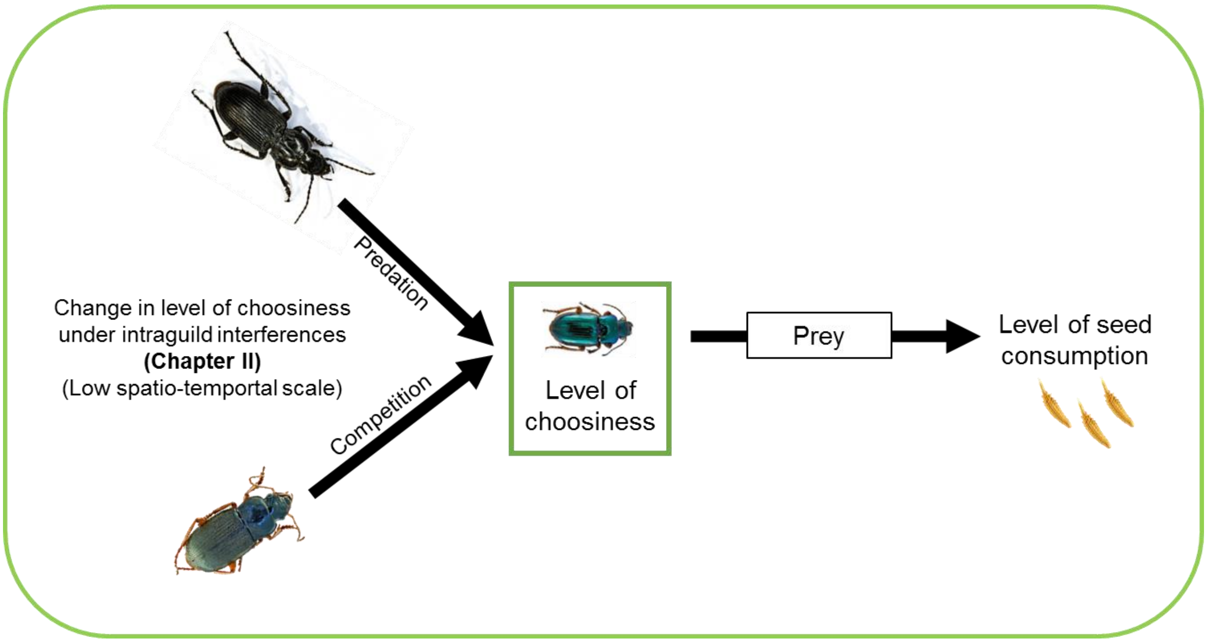
Is individual level of choosiness modified by predatory and competitive interference in carabid beetles: a case study using the granivorous carabid beetle *Harpalus affinis*

1) Introduction to chapter II

One way to improve biocontrol of weeds by carabids would be to understand better how an individual forager chooses seeds and how the decision making of the individual could be modified during foraging. Laboratory studies looking at the feeding behaviour of carabids have typically tested individual feeding preferences using experiments that adopt the choice test paradigm in environment without risk (Honek et al., 2011, 2007, 2006; Petit et al., 2014; Saska et al., 2010). Results from these studies indicate that carabids appear to have strong feeding preferences for seeds of some species of weeds, suggesting that weed species that might be controlled by granivory would depend on the species of carabids present in the carabid community. Laboratory diet assessments have, however, failed to predict feeding in the field (Petit et al., 2014). The range of species of weed seed eaten in the laboratory and in the field do not match as closely as expected. This inconsistency might be explained by the fact that in field conditions, predatory and/or competitive (i.e intraguild) interference are likely to occur and could impact the choices of individual foragers, whereas these interference do not exist in simple laboratory experiments. The occurrence of predatory and intraguild interference is likely to be frequent in carabids communities as many individuals of different species can co-occur within arable fields. If these interferences are perceived by foraging carabids, this could modify significantly foraging decision making and strategies of carabid individuals. The main objective of this chapter is to test explicitly my hypothesis that *interference interactions with other carabid species impacts individual carabid foraging behaviour*.

Given that in theory individual levels of choosiness reflect the willingness to invest in eating in a given situation (Jennions and Petrie, 1997), it is necessary to understand how choosiness varies among foraging carabids, as the first step towards explaining the relative feeding preferences of carabids. As the presence of actual competitors in the arena leads to a reduction in the amount of feeding items available, disentangling a genuine response to intraguild interference from a reduction in choosiness due to a drop in feeding resources can be problematic. To avoid such confounding effects, rather than using competitor individuals, I exposed test individual foragers to olfactory cues from other species as a simulation of the risks of competition and predation interference that these species might pose. I therefore adopted and modified a methodology already developed for exposing carabid individuals to olfactory cues (see Armsworth et al., 2005 and Guy et al., 2008). In addition, as I wanted to test variation in motivation, weed seed species that were known to be of average interest for the test carabids were used. A highly preferred seed might have induced high motivation to feed, irrespective of the level of risk, which would potentially have obscured any feeding adjustment by a forager to the risk treatment in comparison with the control.

In this chapter, I first test whether a granivorous carabid beetle reacts to cues from other carabid species. I then examine whether this reaction impacts choosiness for seeds. Finally, I discuss any observed change in choosiness in the light of the available framework of theory of choosiness and foraging from behavioural ecology.



This chapter is accepted for publication in PLoS One.

2) Article 1

Risk of predation makes foragers less choosy about their food

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ABSTRACT

Animals foraging in the wild have to balance speed of decision making and accuracy of assessment of a food item's quality. If resource quality is important for maximizing fitness, then the duration of decision making may be in conflict with other crucial and time consuming tasks, such as anti-predator behaviours or competition monitoring. Individuals facing the risk of predation and/or competition should adjust the duration of decision making and, as a consequence, their level of choosiness for resources. When exposed to predation, the forager could either maintain its level of choosiness for food items but accept a reduction in the amount of food items consumed or it could reduce its level of choosiness and accept all prey items encountered. Under competition risk, individuals are expected to reduce their level of choosiness as slow decision making exposes individuals to a higher risk of opportunity costs. To test these predictions, the level of choosiness of a seed-eating carabid beetle, *Harpalus affinis*, was examined under 4 different experimental conditions of risk: i) predation risk; ii) intraspecific competition; iii) interspecific competition; and, iv) control. All the risks were simulated using chemical cues from individual conspecifics or beetles of different species that are predatory or granivorous. Our results show that when foraging under the risk of predation, H. affinis individuals significantly reduce their level of choosiness for seeds. Reductions in level of choosiness for food items might serve as a sensible strategy to reduce both the total duration of a foraging task and the cognitive load of the food quality assessment. No significant differences were observed when individuals were exposed to competition cues. Competition, (i.e opportunity cost) may not be perceived as risk high enough to induce changes in the level of choosiness. Our results suggest that considering the amount of items consumed, alone, would be a misleading metric when assessing individual response to a risk of predation. Foraging studies should therefore also take in account the decision making process.

KEYWORD: Predator-prey; intraspecific competition; interspecific competition; food choosiness; foraging behaviour; carabid beetles

A. INTRODUCTION

Mating or feeding enough to maintain fitness is a significant challenge in a world where resources can vary markedly in availability and quality. When sampling resources, individuals encounter items that do not fulfil their needs (Westneat and Fox, 2010) or that are hazardous, either by being poisonous (e.g. stinging insects (Chittka and Osorio, 2007)) or by harbouring predators, such as crab spiders camouflaged in flowers attractive to insect pollinators (Wang et al., 2013; Welti et al., 2016). Thus, the fitness of an individual would increase with its ability to accurately evaluate the quality of a resource, and decide between accepting an item immediately available or waiting for a potentially better future option, but with no guarantees as to the outcome. Such precise evaluation, however, gives rise to incompressible cognitive and time costs. An individual seeking resources should therefore experience a speed accuracy trade-off while choosing which item to exploit (Chittka et al., 2009; David et al., 2014).

Investing too much time in assessing the quality of a resource item could be detrimental for individuals foraging or seeking a mate under hazardous situations, such as risks of predation or competition (Dechaume-Moncharmont et al., 2016; Leaver and Daly, 2003; Metcalfe et al., 1987b; Perea et al., 2011). Under the risk of predation, individuals deal with two conflicting tasks (Beauchamp, 2008; Milinski and Heller, 1978; Sih, 1980; Underwood, 1982; Wang et al., 2013) or mutually exclusive behaviours (Lima and Dill, 1990; Nonacs and Blumstein, 2010): either the avoidance of predators or the acquisition of resources (a vigilance-foraging trade-off). Given the immediate and lethal outcome of failing to avoid a predator, a potential prey individual should adjust its foraging behaviour primarily to the predation risk and only secondarily to starvation (Lima and Dill, 1990). Thus, individuals are expected to postpone foraging tasks and allocate more time and energy to predator avoidance behaviours, when under no energy stress (Higginson et al., 2012).

Postponement of foraging is only a sensible strategy for short periods of predation risk, however, it could be hazardous during extended periods of diffuse predation risk or when the risk of starvation is too high to defer foraging (Higginson et al., 2012). An animal is expected to adjust its foraging effort in respect of its energetic requirements and the likelihood of predator attack (Ferrari et al., 2009; Lima and Bednekoff, 1999). It supposes that the individuals are able to, firstly, assess local predation risk and, secondly, adjust their intensity of an antipredator response according to the level of threat (Berger-tal et al., 2010; Brown et al., 2006; Helfman, 1989; Helfman and Winkelman, 1997; Sivy et al., 2011). When assessing the response to a predation risk during foraging, the authors typically measured the number of food items consumed per unit of time, which is based on the assumption of direct proportionality between the number of items consumed and the “feeding effort” (i.e. the time spent foraging). Under such an assumption, the predicted decrease in the time spent foraging under predation risk would result in an overall decrease of the number of food items consumed (Leaver and Daly, 2003; Sivy et al., 2011). A rarely considered alternative assumption, which we consider in this study, is that an individual adjusts its foraging strategy while keeping constant the number of food items consumed. To mitigate a vigilance-foraging trade-off, the forager might adjust the time spent in assessing a resource item before deciding whether or not to accept it, rather than simply reducing the amount of food collected (Godin, 1990; Houtman and Dill, 1998).

The time or energy that an individual invests in sampling or assessing an available resource item is termed ‘choosiness’ in the behavioural literature (Dechaume-Moncharmont et al., 2016; Jennions and Petrie, 1997). Choosy individuals accept only a few resources in a given time span or spend a substantial amount of time assessing an item before accepting it, whereas less choosy individuals either accept more resource items over the same time or hesitate for a shorter amount of time before consuming a resource item (Edward, 2014; Jennions and Petrie, 1997). Consequently, the time spent in assessment before accepting an encountered resource item is a primary metric for evaluating individual choosiness. When exposed to predation risk, a forager should increase the time allocated to anti-predator behaviours and, thus, reduce the total time invested in foraging (Higginson et al., 2012). This could result in two apparently contradictory foraging patterns: i) a forager could reduce the length of the foraging period, while maintaining a constant level of choosiness, leading to an observed reduction of the number of food items consumed (Leaver and Daly, 2003; Lima and Valone, 1986; Sivy et al., 2011) or, ii) an individual could reduce its level of choosiness, by accepting all prey items encountered irrespective of their quality (Ibrahim and Huntingford, 1989; Metcalfe et al., 1987b), and keep constant the number of food items consumed (Dianne et al., 2014). This last pattern might erroneously be interpreted as an absence of behavioural flexibility in response to predation risk, if the number of prey eaten were recorded alone. The total amount of items consumed should not serve as the sole metric for assessing the behavioural adjustment to risks. More specifically, studies that have found no adjustment of foraging effort in response to predation risk (Ferrari et al., 2009), may have done so because they considered only the total amount of items consumed and neglected the variation in individual choosiness under predation risk.

Adjustment of choosiness may also be an important behavioural response to competition (Amita et al., 2010; Davis et al., 2011; Fox and Morrow, 1981; McNamara and Houston, 1987). In the absence of competition, one sensible strategy would be to select and consume only the most profitable food resources, and neglect most of the encountered items. Where competitors are also present in the same patch, however, such a choosy forager might be unable to fulfil its energetic needs. Neglecting food items of low quality, in this way, is costly because the expected better items could have already been consumed by competitors. Moreover, choosy foragers may not be able to re-adjust their thresholds of prey acceptability, following a lengthy unsuccessful period, because lower choice items that had been previously neglected might have already been consumed by less choosy competitors (Dechaume-Moncharmont et al., 2016). These lost opportunity costs can be sufficiently strong to constrain the evolutionary stable strategy for prey choosiness. Indeed, game-theoretical approaches suggest that optimal level of choosiness is frequency-dependent and decreases with increasing competition (Dechaume-Moncharmont et al., 2016).

Our hypothesis is that both predation and competition risks affect levels of choosiness. As the fitness costs of predation should be higher and more immediate than the costs resulting from competition, differences in the intensity of either an increase or reduction of the level of choosiness (behavioural adjustment) under each of these two risks is expected. We examine whether individuals of a granivorous carabid species, *Harpalus affinis* (Schrank, 1781), modulate their level of choosiness for seeds as a function of either predation risk or competition, from either intraspecific or interspecific competitors.

B. METHODS

a. Study system

The carabid species used in the tests are commonly found together in European farmland. *H. affinis* is a granivorous species that we use as our focal test forager as it is one of the most abundant spring-breeding predominantly granivorous species in arable agriculture. We chose to use *Pterostichus melanarius* (Illiger, 1798) as the potential predator because they have been shown to be voracious predators of live prey (Currie et al., 1996; Foltan, 2004; Hatteland et al., 2010; Kromp, 1999; McKemey et al., 2003). Moreover, *P. melanarius* were observed to prey upon *H. affinis* in experimental situations (Alice Charalabidis, pers. obs.), and upon others species of carabids (Currie et al., 1996). *Pseudoophonus rufipes* (De Geer, 1774) was chosen as the interspecific competitor, given that this granivorous species has been observed to readily eat a large amounts of seeds in laboratory conditions (Petit et al., 2014). We sampled adult individuals of three carabids species, *H. affinis, P. melanarius* and *P. rufipes* on the INRA experimental farm at Epoisses (Côte d'Or, France; 47°14'11.4"N 05°05'53.4"E) using pitfall traps during spring and summer 2015. Individuals of the focal species, *H. affinis,* were maintained in small, mixed sex groups (up to 20 individuals) in plastic boxes (34 x 19 x 11 cm, length x breadth x height) for a minimum of two weeks prior to experimentation. Each box contained two to three cm deep soil and some moistened paper tissue to maintain high humidity and provide the carabids with shelter. The boxes were maintained under temperature- and light-controlled conditions (19°C +/- 1°C, 60% humidity, 14:10h light:dark cycle). Boxes of *H. affinis,* the granivore *P. rufipes* and the omnivore *P. melanarius* were kept in separate rooms to prevent interspecific predation (Currie et al., 1996) or any possible effects of chemical cues. Age, mated status and feeding background were not controlled as we used wild-caught individuals in the tests.

Highly preferred seeds might induce high risk taking by the carabids, and therefore acceptance in all contexts of risk, while disliked seeds would not be accepted at any level of risk. *T. officinale*, a moderately preferred species (Honek et al., 2007; Petit et al., 2014) that is known to be eaten both by *H. affinis* and *P. rufipes,* was therefore selected as the test seed. In order to standardize their feeding background and ensure that *T. officinale* seeds were encountered at least once by all tested individuals prior to the experiment (Hammerstein and Stevens, 2012), individuals of *H. affinis* were fed with a combination of four seeds species, *T. officinale, Viola arvensis* (Murray), *Senecio vulgaris* L. and *Capsella bursa-pastoris* (L.) Medik. All seeds were one year old and were collected on the INRA Dijon experimental farm. All experimental seeds had been soaked in water for 14 hours to become more palatable to and detectable by carabids (Law and Gallagher, 2015). Carabids were provided with water *ad libitum* in an Eppendorf containing moistened cotton wool.

b. Experimental set-up

The 290 experimental *H. affinis* individuals were randomly split into four treatment groups, *control* (n = 70, with 31 females and 39 males), *intraspecific competition (*n = 71, with 32 females and 39 males), *interspecific competition* (n =75, with 32 females and 43 males), and *predation* (n = 74, with 31 females and 43 males). The sexes were identified using protarsi, which are dilated and have hairy undersides in males (Lindroth, 1974). All beetles were tested individually and only once. To standardize the feeding motivation, individuals were isolated in small individual plastic boxes (diameter 9 cm) and starved for the 54 hours prior to testing.

Starvation duration was estimated from pre-test experiments designed to produce individuals motivated to feed, but not so starved that they were too tired to forage. Water was provided *ad libitum* via a moist paper tissue covering the bottom of each individual boxes.

Predation and competition risk were simulated via olfactory cues that carabids leave along their path of movement (Armsworth, 2005; Guy et al., 2008). Using these cues, in place of live predators or competitors, we avoided the confounding effects of direct interactions between the focal individual and predators and competitors. The consistency of the chemicals cues was tested by Guy et al. (Guy et al., 2008), who found that carabids responded to almost 2 day old residual chemicals. To simulate the risk of predation, we used the chemicals cues left by *P. melanarius*. Interspecific competition was simulated using chemicals from *P. rufipes* and intraspecific competition was simulated using chemicals from *H. affinis*. Using the method of Armsworth *et al*. (Armsworth et al., 2005), impregnated papers (white filter paper, Dutscher, Brumath, France) were created by allowing 20 individual beetles (10 females, 10 males) to walk over test papers (40 x 30 cm) for a minimum of 24 hours; this density of stimulus individuals has been previously shown to induce concentration of olfactory cues which is perceived by carabids (Guy et al., 2008). For the control treatment clean test papers, with no carabid chemical cues, were used. We used two different types of competition in order to differentiate potential sexual induced-behaviours in the intraspecific competition treatment from actual behavioural responses to the cues of competition risk. The impregnated test papers were collected immediately prior to the start of each experimental trial. For each experimental arena we arranged 20 seeds of *T. officinale* in two concentric circles of 5 and 16 cm diameter on an impregnated test paper (Fig. 1).

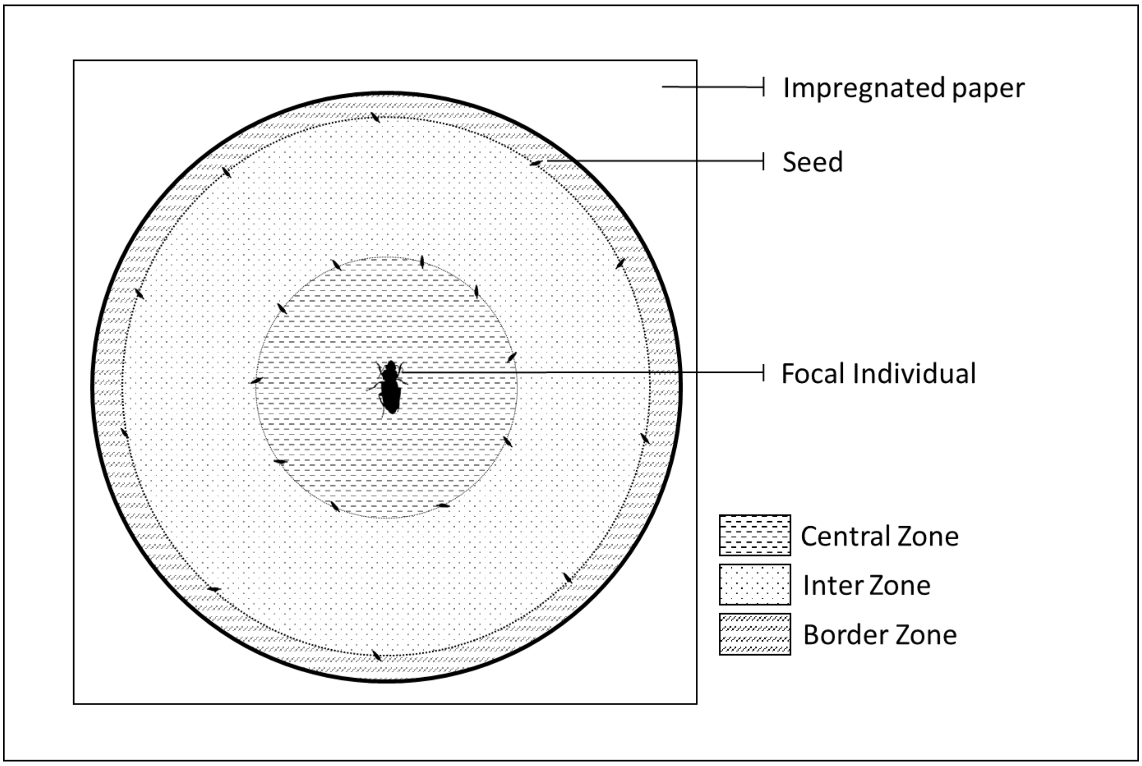

Figure 1: Design of the test arena. Arena was divided intro into three circular parts by two circles of respectively 5 cm and 16 cm diameter: i) the central zone, ii) the inter-zone and iii) the border zone. Ten *T. officinale* seeds were placed around each circle. This representation is approximately to scale: carabids measure ~1 cm and seed ~2.5 mm in length

The focal carabid individual was acclimatized under a plastic pot at the centre of the arena for 8 minutes. The pot was removed and we immediately placed an inverted 18 cm diameter Pyrex petri dish bottom over the arena to delimit and isolate the arena from external perturbations (movement of air, chemical cues). Foraging behaviours were then scored over a one hour period. The test papers were used for only one trial, and between repetitions the petri dishes were washed in a medical dish-washer.

The four experimental conditions and the two sexes of *H. affinis* were tested in random order in controlled temperature room at 19°C +/- 1°C and 60% humidity. The arenas were laid out on an aluminium bench that had previously been cleaned with alcohol to remove any olfactory cues. All treatments and both sexes were tested each day of test in order to prevent any impact of date on the results.

c. Assessment of the level of choosiness

The level of choosiness of *H. affinis* was examined in test arenas under the 4 different experimental treatment levels of risk. We evaluated, at the individual carabid level, choosiness for a weed seed food item. Individual level of choosiness was assessed in "no-choice" tests in which only one food type is offered to individuals (Dougherty and Shuker, 2014). Since most resources are encountered sequentially, animals cannot easily make comparative choices. Hence, no-choice tests have been described as more ecologically realistic experimental designs (Allison and Cardé, 2008; Larrinaga, 2010; Rapport and Turner, 1970). No-choice tests have been proven useful and relevant in many studies (Dougherty and Shuker, 2015, 2014; Martel and Boivin, 2011; Wagner, 1998) and are considered to be particularly suitable for measuring choosiness since an individual offered only one seed, and rejecting it, would be considered choosier than an individual accepting the seed (Reinhold and Schielzeth, 2015; Rodríguez and Greenfield, 2003; Rothbart and Hennig, 2012). In tests with multiple choices, alternative resources might impact on the choices an individual makes toward other resources, potentially leading to false negatives or positives (Edward, 2014; Murray et al., 2010). Moreover, no-choice tests are easier to standardize than multiple choice tests, which require that the focal individual has the sensory capability and the cognitive skills to compare several items simultaneously (Dougherty and Shuker, 2014; Murray et al., 2010; Raffa et al., 2002). Lastly, longer latencies to acceptance of a food item, when there are no other simultaneously available options, might be interpreted as evidence for higher levels of choosiness (Murray et al., 2010).

The level of choosiness was assessed by scoring four behaviours (Fig. 2.): i) the latency to the first movement of an individual (i.e. motion of more than the average body length); ii) the latency to first acceptance of a seed (i.e. from the first movement of an individual until it actually accept its first seed); iii) the handling time (i.e. the duration of the seeds consumptions) and, iv) the number of seeds eaten per individual during the 1 hour test. Given that the total number of seeds eaten might hide variation in behaviour in the test population, the proportion of individuals eating at least one seed during the test was also used in the analysis.

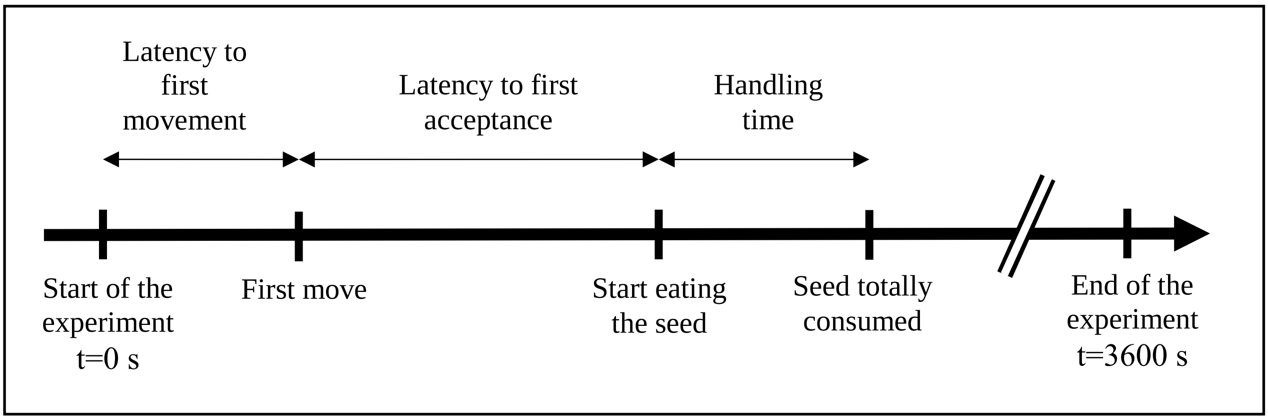

Figure 2: Schematic diagram of the chronological course of the experiment and the temporal metrics use in the tests. Latency to first movement was measured from the release of the test carabid to its first movement greater than its average body length; the latency to first acceptance of a seed was measured as the time from the first movement of an individual until it accepted the first seed; handling time is the duration of the seed consumption starting from an individual seizing the seed in its mandibles until it released the empty tegument. The experiment ended after a duration of 3600 s.

d. Trajectometry

The presence of predators is expected to induce predator avoidance behaviours, such as reduced exploration or increased velocity. It is to be expected that such a change in locomotion or space use would reduce the probability of seed encounter and consequently the number of seeds eaten, irrespective of an individual's level of choosiness. The trajectometry of each individuals was recorded during the one-hour test using a monochrome camera (IMAGINGSOURCE – model: DMK 31AU03) suspended above the arenas and connected to a computer. The video files of 29 individuals, from all treatments were lost due to a hard disk failure. The trajectometry data (n = 261 individuals: n = 66 for the control, n = 69 for the intraspecific competition, n = 63 for the interspecific competition and n = 63 for the predation treatments) were analysed using Ethovision (Noldus Information Technology, Wageningen, The Netherlands).

Differences in exploration behaviours were analysed as a function of the treatment. The tendency to stay in physical contact with borders of the arena (thigmotaxis) and to avoid open space (centrophobicity) were also assessed as proxies of an individual's anxiety levels (Soibam et al., 2012; Tremmel and Muller, 2013) and were expected to vary with the presence of predator cues. We therefore defined three annular zones corresponding to the "central zone" (0-5 cm), "inter-zone" (5-8 cm) and the "border zone" (8-9 cm) regions of the arena, delimited by the seed circles described above (Fig. 1). The cumulative time spent within the central zone was scored as a measure of thigmotaxis and centrophobicity. The experimental area was divided up into 1 cm x 1 cm squares. We estimated the proportion of space used by scoring the number of squares visited at least once, by the focal carabid, as a proportion of the total number of squares (mean total number of squares per arena = 332.5, 95% CI = [331.4; 333.7]). Finally, mean velocity was scored as a proxy measure of activity, calculated by dividing the total distance travelled (cm) by the cumulative amount of time during which individuals were in movement (s).

e. Statistical analysis

The data were analysed in R version 3.3.2 (R Development Core Team, 2016). The number of seeds eaten per individual during the 1 hour test was modelled as a generalized linear model, assuming a negative binomial distribution. Because zero-inflated negative binomial model fitted the data better than the negative binomial model (Vuong's test for non-nested models: $p = 8.4 \times 10^{-5}$, $\Delta AIC = 37.9$), we used 'zeroinfl' function from the 'pscl' package (Jackman, 2015). The proportion of individuals eating at least one seed during the test was analysed in each of the four different treatment levels using generalized linear modelling and binomial errors. The times of latency to first movement and first seed acceptance, and handling were analysed by means of the Cox proportional hazard models (Dechaume-Moncharmont et al., 2005) in the 'cox.ph' function from the package 'survival' (Therneau, 2006). The Cox model allowed the analysis of censored data produced when a replicate was terminated before the end of the observed behaviour. For each Cox regression model fit, the proportional hazards assumption was assessed using the 'cox.zph' function. The velocity data and the cumulative time spent within the central zone were analysed using ANOVA. The data for the proportion of space used was arcsine transformed in order to meet the condition of normality for ANOVA.

For all parametric analyses, the full model included as effects the treatment level (control, intraspecific competition, interspecific competition and predation), the sex of the focal individual and their interactions. Significant effects of sex, treatment and their interactions were identified by sequential comparison of the nested sub-models, with and without a given covariate, using backward, stepwise elimination of non-significant variables and interaction terms. Where a global effect of treatments was detected, a post-hoc contrast analysis was performed.

To facilitate future meta-analysis or comparisons, we also reported effect size indices and the corresponding 95% confidence intervals (Lakens, 2013; Nakagawa and Cuthill, 2007). When comparing means with non-normal data we used Cliff's delta (Cliff and Keats, 2003;

Monceau et al., 2017b). The measure of effect size for the latencies was the hazard ratio, estimated as the exponent of the regression coefficient, exp(beta), of the Cox model (Dechaume-Moncharmont et al., 2003). The hazard ratio was calculated either for the sex effect or the treatment effect. A sex hazard ratio above one indicates that the females had a longer latency time than that of the males. A treatment hazard ratio above 1 indicates that the treatment decreased the latency time compared to the control.

f. Ethical note

This work followed the ABS/ASAB guidelines for the treatment of animals in behavioural research. Information about individuals' origin, and housing conditions are described below. Transport between sampling site and laboratory, housing conditions, as well as monitoring of experimental arena, were done to reduce stress and maximise animal welfare.

C. RESULTS

a. Latency to first movement

The latency to the first movement of an individual differed significantly between treatments (Cox model, χ^2_3= 17.1, P < 0.001, Fig. S1). Compared to the control, it increased in the predation and intraspecific competition treatments but not in the interspecific treatment (Table 1). It was affected neither by the sex of the individual (Cox model, χ^2_1= 0.25, P = 0.62, hazard ratio = 1.06, 95%CI = [0.74; 1.19]) nor the interaction between sex and treatment (Cox model, χ^2_3= 3.40, P = 0.34).

Table 1: **Contrast analysis between treatments for the latency to first movement**

	P	Hazard ratio	95%CI
Control - Predation	0.024	0.68	[0.49 ; 0.95]
Control - Intraspecific competition	0.0033	0.60	[0.43 ; 0.84]
Control - Interspecific competition	0.61	1.09	[0.79 ; 1.51]
Intraspecific competition - interspecific competition	< 0.001	1.82	[1.30 ; 2.54]
Intraspecific competition - predation	0.44	1.14	[0.82 ; 1.58]
Interspecific competition - predation	0.0052	0.63	[0.45 ; 0.87]

b. Latency to first acceptance of a seed

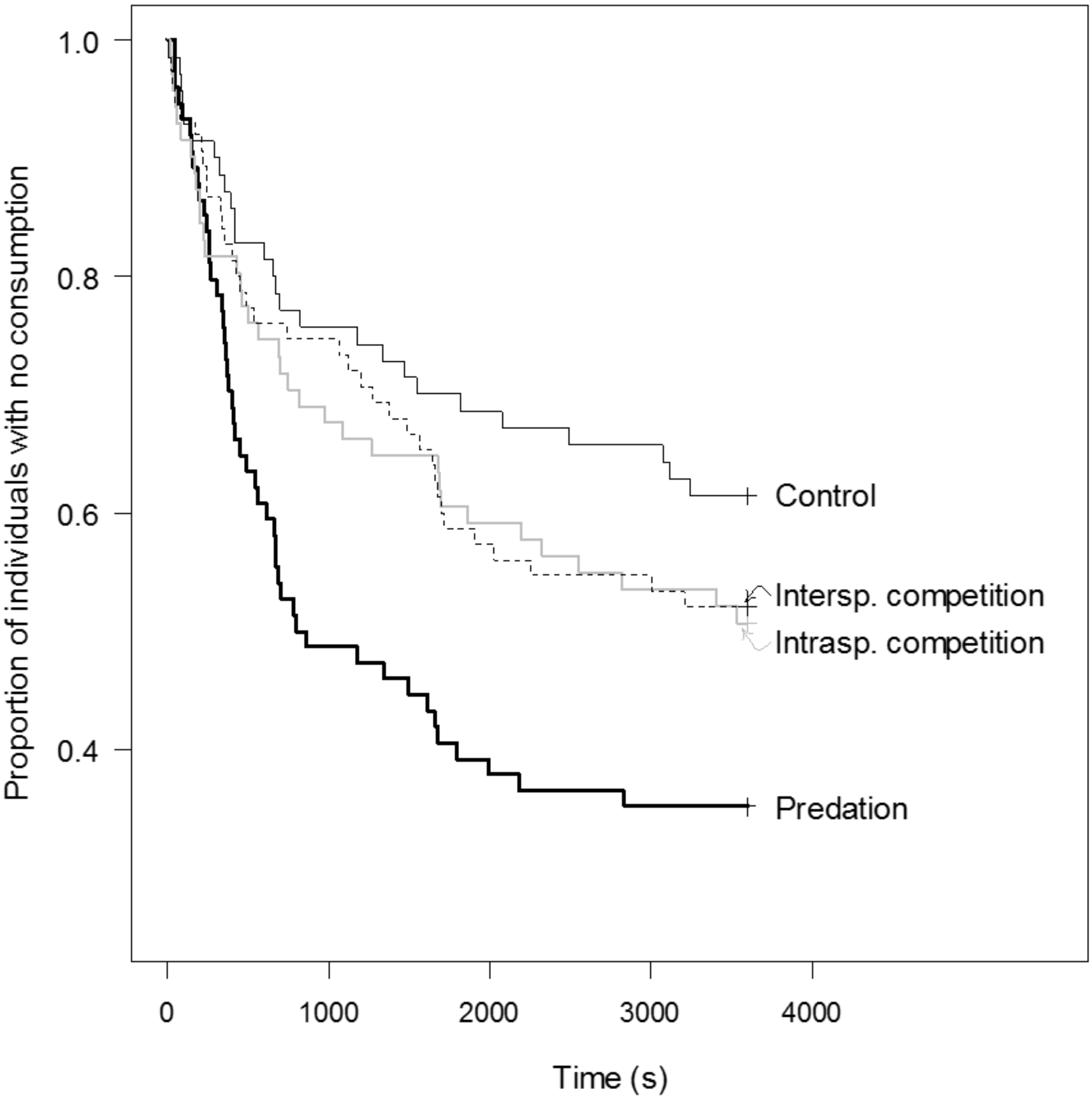

Figure 3: Kaplan-Meier plot for the latency to first acceptance as a function of the treatments. Each curve represents, for a given treatment level, the proportion of individuals with no consumption as a function of the time since the first move: control (continuous line, n = 70), intraspecific competition (grey line, n = 71), interspecific competition (dotted line, n = 75) and predation (bold line, n = 74). Individuals not eating before the end of the observation at time t = 3600 s were treated as censored data in the model.

The latency to first acceptance of a seed significantly differed between treatments (Fig. 3, Cox model, χ^2_3= 12.1, P = 0.007). The latency to first acceptance of a seed was shorter in the predation treatment than in all the three others treatments (Table 2)

Table 2: Contrast analysis between treatments for the latency to first acceptance of a seed

	P	Hazard ratio	95%CI
Control - Predation	< 0.001	2.22	[1.38; 3.56]
Control - Intraspecific competition	0.19	1.39	[0.84; 2.30]
Control - Interspecific competition	0.26	1.33	[0.81; 2.19]
Intraspecific competition - interspecific competition	0.84	1.05	[0.66; 1.67]
Intraspecific competition - predation	0.04	1.59	[1.03; 2.46]
Interspecific competition - predation	0.02	1.67	[1.08; 2.57]

While non-significant, the values of effect size suggested that the latency to first acceptance of a seed was consistently shorter under the interspecific competition and intraspecific competition treatment than under the control treatment (Table 2). An *a posteriori* power analysis showed that such trends would have required a doubling of the sample size to become significant, provided that the mean value of effect size does not change. The latency to first acceptance of a seed did not differ between the two competition treatments (Table 2). It was also not affected by sex (Cox model, χ^2_1= 2.22, P = 0.14, hazard ratio = 1.28, 95%CI = [0.92; 1.78]) or the interaction between sex and treatment (Cox model, χ^2_3= 0.60, P =0.90).

c. Number of seeds eaten per individual and handling time

There was no significant effect of treatment on the handling time (Cox model, χ^2_3= 1.9, P= 0.59, Fig. S2). There was a significant effect of the treatment on the mean number of seeds eaten per individual during the one hour test (Generalized linear model, χ^2_6 = 17.22, P = 0.009). The mean number of seeds eaten was significantly higher under the predation treatment than in the other treatments (Fig. 4, Cliff's delta for the difference between control and predation δ = 0.28, 95%CI = [0.10; 0.44]).

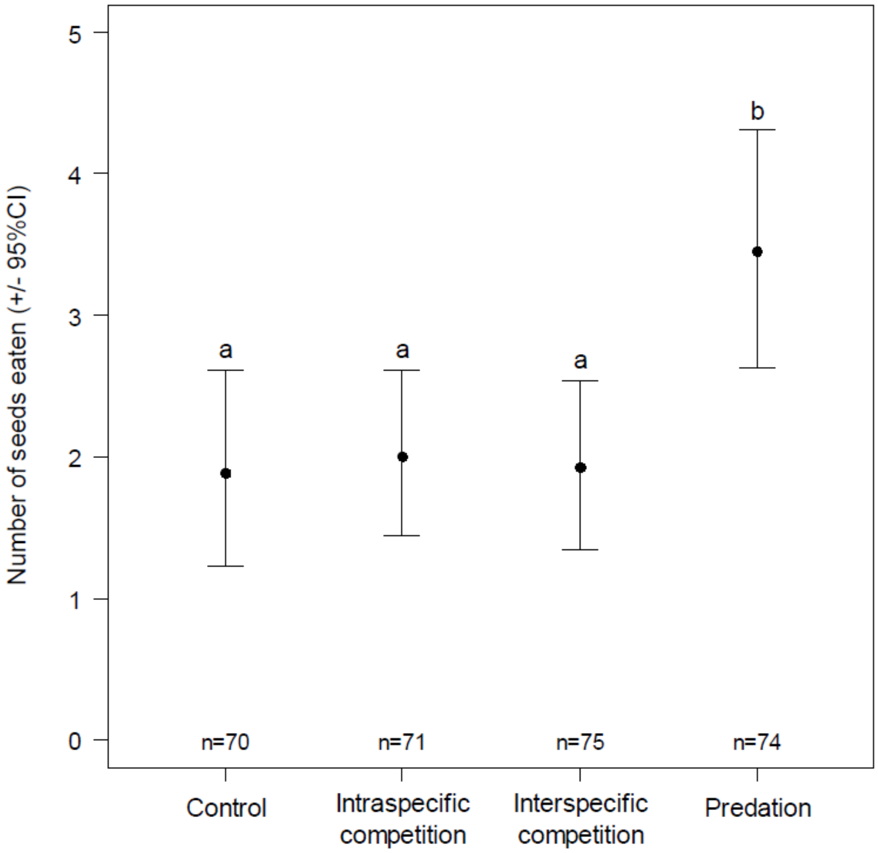

Figure 4: Mean number (bootstrapped +/- 95%CI) of seeds eaten per individuals after one hour of test in each treatment. Different letters correspond to statistically significant difference between treatments (post-hoc pairwise comparison with Tukey adjustment for multiple comparisons). The sample sizes are shown above the x-axis.

There was no statistical difference among the control and competition treatments. There was a significant effect of sex (Generalized linear model, χ^2_2= 6.58, P = 0.037), but no sex by treatment interaction term (Generalized linear model, χ^2_6= 1.47, P = 0.96). Females consumed more seeds than males (Cliff's delta δ = 0.11, 95%CI = [0.01; 0.24], Fig. S3), with females having a mean consumption of 2.8 seeds (95%CI = [2.22; 3.43]) and males consuming 1.95 seeds (95%CI = [1.55; 2.39]) over the hour of testing.

The proportion of individuals that ate at least one seed in the hour of the test also differed between the treatments (Generalized linear model, χ^2_3= 10.45, P = 0.015). Post-hoc comparisons with the control treatment showed that this proportion was significantly higher under the risk cues of predation (P = 0.003, odds-ratio = 2.94, 95%CI = [1.49; 5.79]), but not under the risk cues of intraspecific (P = 0.31, odds-ratio = 1.47, 95%CI = [0.76; 2.85]) or interspecific competition (P = 0.24, odds-ratio = 1.54, 95%CI = [0.79; 3.02]). There was no significant effect of sex (Generalized linear model, χ^2_1= 1.35, P = 0.25) and no interaction between the sex and treatment effects (Generalized linear model, χ^2_3= 0.23, P = 0.97).

d. Trajectometry

All individuals moved during the test. The mean velocity was not affected by the treatment (ANOVA, $F_{3,\ 257}$=0.36, P = 0.78), sex (ANOVA, $F_{1,\ 259}$ = 1.51, P = 0.22) or the interaction between treatment and sex (ANOVA, $F_{253,\ 256}$ = 1.74, P = 0.16). The proportion of space used differed between the two types of competition (ANOVA, $F_{3,\ 257}$ =3.36, P=0.019), but did not differ between the predation treatment and the control (Fig. 5). The cumulative time spent in the central zone was not affected either by treatment (ANOVA, $F_{3,\ 257}$=1.58, P = 0.19), sex (ANOVA, $F_{1,\ 259}$ = 0.034, P = 0.85) or the interaction between treatment and sex (ANOVA, $F_{253,\ 256}$ = 0.26, P = 0.86).

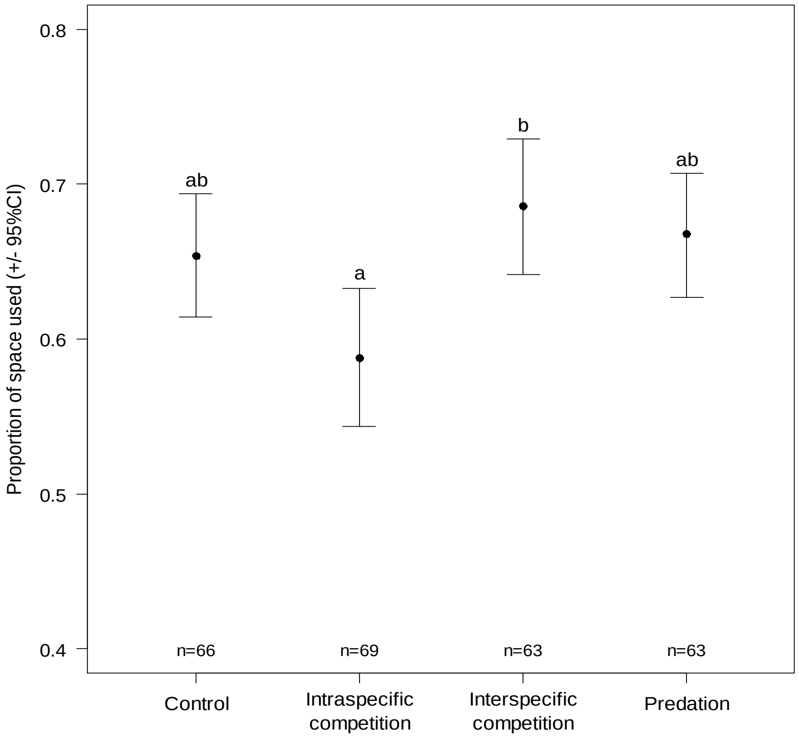

Figure 5: Proportion of space used (bootstrapped +/- 95%CI) after one hour of test in each treatment. Different letters correspond to statistically significant differences between treatments (post-hoc pairwise comparison with Tukey adjustment for multiple comparisons). The sample sizes are shown above the x-axis

D. DISCUSSION

a. Adjustment of the foraging effort in response to predation risk

In order to allocate more time and energy to predator avoidance behaviours when exposed to predation risk, individuals should postpone foraging task (Higginson et al., 2012). This decrease of the foraging effort should not straightforwardly be interpreted as a reduction of the number of items consumed. Indeed, our results show that considering the number of items consumed as the sole metric of the intensity of an individual's response to a risk of predation could be misleading. Individuals of the granivore, *H. affinis*, when exposed to chemicals cues of a potential predator were found to significantly increase the total number of food items consumed in comparison to the control or the competition treatments. This increase in the number of food items consumed suggest that individuals *H. affinis* reduced their level of choosiness toward feeding items. *H. affinis* showed a marked reduction of the latency to first acceptance of a seed in comparison to the control or competitions treatments, suggesting that the effort that an individual is willing to invest in the acquisition of a resource (i.e. choosiness) is reduced under predation. Such foraging patterns cannot be interpreted as a lack of behavioural adjustment to the risk of predation or be explained by differences in handling time or trajectometry, as there were no differences in the handling time or the trajectometry metrics between the treatments.

Reductions in individual levels of choosiness could lead to the consumption of prey items that would be rejected under control conditions, but it might also provide important benefits. It could allow a greater focus on predator avoidance, for example, by reducing the cognitive load attributable to food item selection (Block et al., 2010). Metcalfe et al. (Metcalfe et al., 1987a, 1987b) found that salmon exposed to a fake predator reduced their level of choosiness for passing food pellets. Given that salmon use vision to acquire information both for predator vigilance and for assessing the quality of their prey they might accept a potential reduction in food quality in order to focus on vigilance. Bees were observed to lower their threshold of acceptance of flower quality when exposed to potential ambush predation by cryptic crab spiders in flowers. In doing so, the bees were able to minimize conflict between foraging and predator vigilance and the high energetic costs of foraging flights (Wang et al., 2013).

The performance of any two tasks that use similar sensory machinery, such as vision or chemoreception, can result in "dual task interference" (Lawrence, 1985; Pashler, 1994). Due to limitations of cognitive load either one of the tasks could be detrimental to the other, thus producing an “outcome conflict” (Lawrence, 1985; Navon and Miller, 1987). Even where these two tasks could be performed simultaneously, this will be both energy and time consuming (Wang et al., 2013) and many taxa do not succeed in solving the conflicts of dual task interference. Birds (Dukas, 2000) and humans (Joseph et al., 1997) have been observed failing to divide their attention between two complex visual tasks (Wang et al., 2013), for example. Hence, one solution to managing the limited available cognitive load, and the potential associated extra costs, might be to apply a weighting to each task (Pashler, 1994). In the vigilance-foraging trade-off this would be expressed by a reduction in the weight assigned to the foraging task, as was observed for salmon and bees (Metcalfe et al., 1987a, 1987b; Wang et al., 2013). Such difficulties in making acute choices, while performing a high-load cognitive task, were reviewed by Block *et al*. (Block et al., 2010), who noted that individuals typically respond by reducing their period of judgment and making more rapid choices. Rodents living in patches without refugia have been shown to reduce their time exposed to predators by reducing the time spent choosing seed food items (Perea et al., 2011), lowering both the risk of starvation and the risk of predation (Lawrence, 1985; Lima and Bednekoff, 1999).

Reductions in levels of choosiness for food items, as found for *H. affinis*, might therefore serve as a sensible strategy to reduce both the total duration of a foraging task and the cognitive load of the food quality assessment (Leaver and Daly, 2003). Our results therefore serve to extend the predation risk allocation hypothesis (Lima and Bednekoff, 1999), by suggesting that individuals could adopt one of several alternative strategies, with both reductions and increases in their level of choosiness for food items being possible in risky situations. Future experimental assessments of the risk allocation hypothesis should, therefore, try to define “foraging effort” and take into account the process of decision making itself.

b. Response to competition risk

A core expectation of our study was that the individuals should also decrease their level of choosiness in response to the risk of competition, due to opportunity costs (Dechaume-Moncharmont et al., 2016). We found that the effects of competition on the level of choosiness (i.e. latency to first acceptance and mean number of seeds eaten) were similar across the two competition treatments. Latency to first acceptance of a seed and mean number of seed eaten per individuals were also not significantly different between the competition treatments and to the control. However, the values of the effect size for the latencies to first acceptance would suggest at a reduction in individual levels of choosiness and that it would be misleading to interpret these results as evidence for absence of a competition effect (Nakagawa and Cuthill, 2007). Rather, it suggests that we may not have taken into account all possible co-variates of competition that affect foraging, such as individual personality (David et al., 2011; Royauté and Pruitt, 2015), and future studies should seek to evaluate the importance of these co-variates.

In order to avoid agonistic behaviours or competitive interference between individuals, our protocol was based on indirect competition or predation risks in the form of olfactory cues impregnating the arena paper. It may be that the use of odour as a competition cue, in place of test competitor individuals and the associated reduction in food items that would have ensued, might have lowered the perceived risk of competition enough that the *H. affinis* individuals did not modify their foraging effort, irrespective of the potential linked costs (Mohamad et al., 2014). Moreover, given that individuals were maintained in groups of up to 20 individuals prior to experiment, which matched the amount of individuals used to impregnate the tests papers, the focal individuals might have become habituated to situations of competition similar to the one under test potentially reducing our power to test for competition risk perception (Milinski, 1982; Mohamad et al., 2014).

While changes in level of choosiness were not observed under both competition treatments, our results did demonstrate a difference in latency to first movement and in space use between the two competition treatments. *H. affinis* individuals were found to move later and visit fewer squares of the arena in the intraspecific competition treatment. Similar patterns in the use of space were observed for *P. melanarius* in avoiding papers impregnated with chemical cues from conspecifics (Guy et al., 2008). We hypothesise that this lower space use and increased latency to first movement may be due to an effect of sex, with male and female arresting in the presence of odours from the opposite sex. An alternative hypothesis is that the perceived risk of competition itself affects space use. For example, individuals of the Bullethead Parrotfish, *Chlorurus spilurus*, do not change their feeding rate under competition, but modify the way that they use space during foraging (Davis et al., 2017).

c. Carabid beetles in agroecosystem

Our study group of choice is the carabid beetles that naturally inhabit arable farmland. Many thousands of individuals exist in farm fields in communities of granivore, omnivore and predatory species that can be cannibalistic and inter-specific predators (McKemey et al., 2003; Charalabidis pers.obs.). Reductions in the level of choosiness, in an environment filled with predation cues, might lead to an increase in the number of weed seeds accepted by the granivorous carabids. Counterintuitively, therefore, predation risk might be a mechanism for a biodiversity-ecosystem function (Hines et al., 2015; Reiss et al., 2009) relationship amongst the carabids. Rather than the commonly held expectation that communities formed of granivores alone should have the highest weed seed predation (Petit and Bohan, 2017), our results predict that the ecological function of weed seed predation would increase with the diversity of the carabid community.

E. ACKNOWLEDGEMENTS

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F. SUPPLEMENTARY MATERIALS

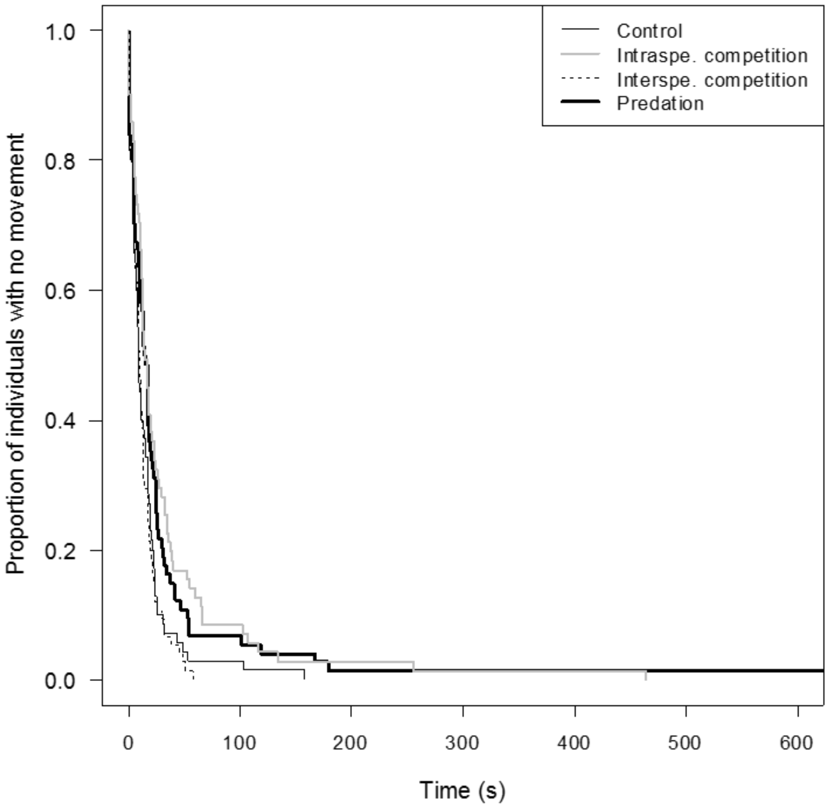


Figure S1: Kaplan-Meier plot for the latency to first movement as a function of the treatments. Each curve represents, for a given treatment group, the proportion of individuals with no movement as a function of the time since the start of the experiment: control (continuous line, n = 70), intraspecific competition (grey line, n = 71), interspecific competition (dotted line, n = 75) and predation (bold line, n = 74). Individuals having not being observed moving before the end of the observation at time t = 3600 s were treated as censored data in the model.

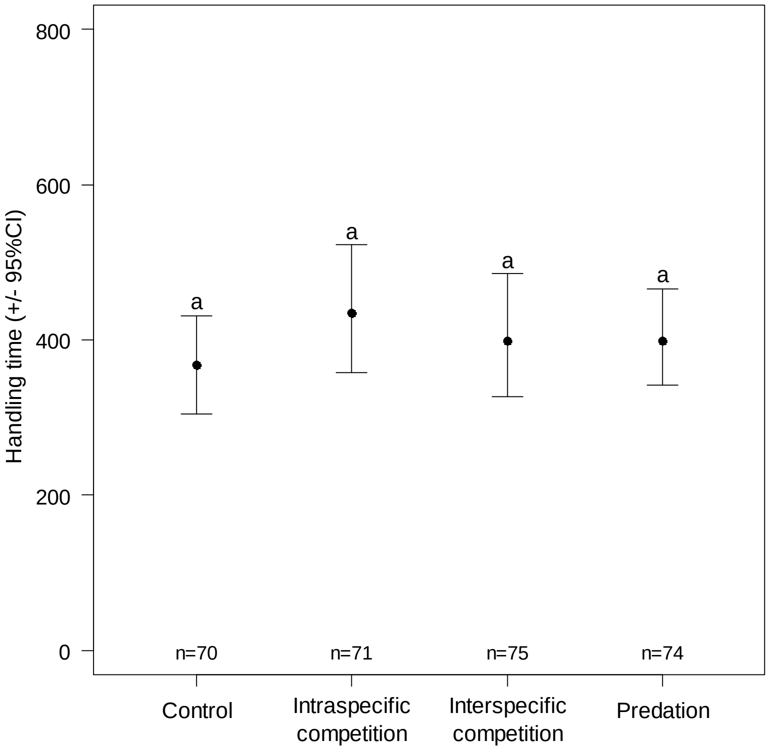


Figure S2: Mean duration (bootstrapped +/- 95%CI) of handling time in each treatment. Different letters correspond to statistically significant difference between treatments (post-hoc pairwise comparison with Tukey adjustment for multiple comparisons). The sample sizes are shown above the x-axis.

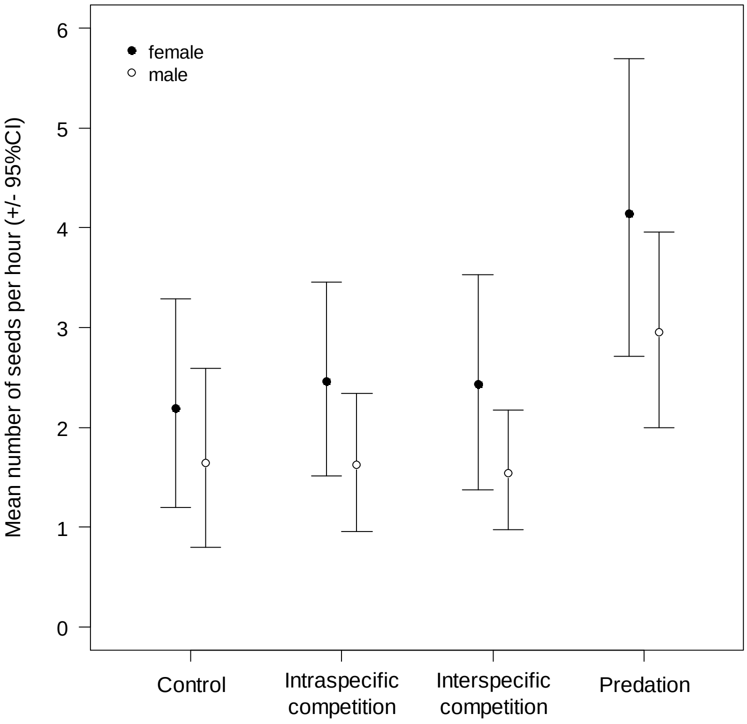


Figure S3: Mean number (bootstrapped +/- 95%CI) of seeds eaten per individuals after one hour of test in each treatment separated by sex. Different letters correspond to statistically significant difference between treatments (post-hoc pairwise comparison with Tukey adjustment for multiple comparisons). The sample sizes are shown above the x-axis.

3) Chapter conclusion

These results clearly demonstrate that individuals of *H. affinis* perceived cues of other species while foraging on impregnated papers. Moreover, these foraging individuals were able to differentiate the cues left on the papers by different carabid species. This implies that the perception of the carabid community, mediated by chemical cues, might differ in between carabid species.

H. affinis expressed a stronger behavioural adjustment to cues of predation risk than to competition. The tested individuals significantly reduced the effort that they were willing to invest in assessing seeds before accepting a seed as a food item (choosiness *sensu* Jennions & Petrie (1997)), when exposed to predatory cues. The number of seeds consumed, over the experimental period, also increased in the predation treatments. Importantly, the internal control of an absence of a difference in the trajectometry data between treatments, meant that all individuals had similar encounter rates with the seeds in all treatments. The observed changes in seed consumption and latency before first seed acceptance are therefore better explained by a reduction in choosiness than by a difference in the patch exploration. We interpreted this reduction in choosiness as a strategy of reducing the cognitive load and time of food assessment to make this load and time available to other critical behavioural tasks such as predator vigilance.

Looking at the effect size in isolation, the foraging individuals also responded to competition by appearing to consistently lower their choosiness, as predicted by current models (Dechaume-Moncharmont et al., 2016). These results did not significantly differ between the competition treatments and the control, however, and we were therefore not able to conclude that competition also impacts choosiness for seeds in *H. affinis*.

Third Chapter

Effect of the diet of a carabid species on its level of choosiness for seeds when foraging under intraguild interferences

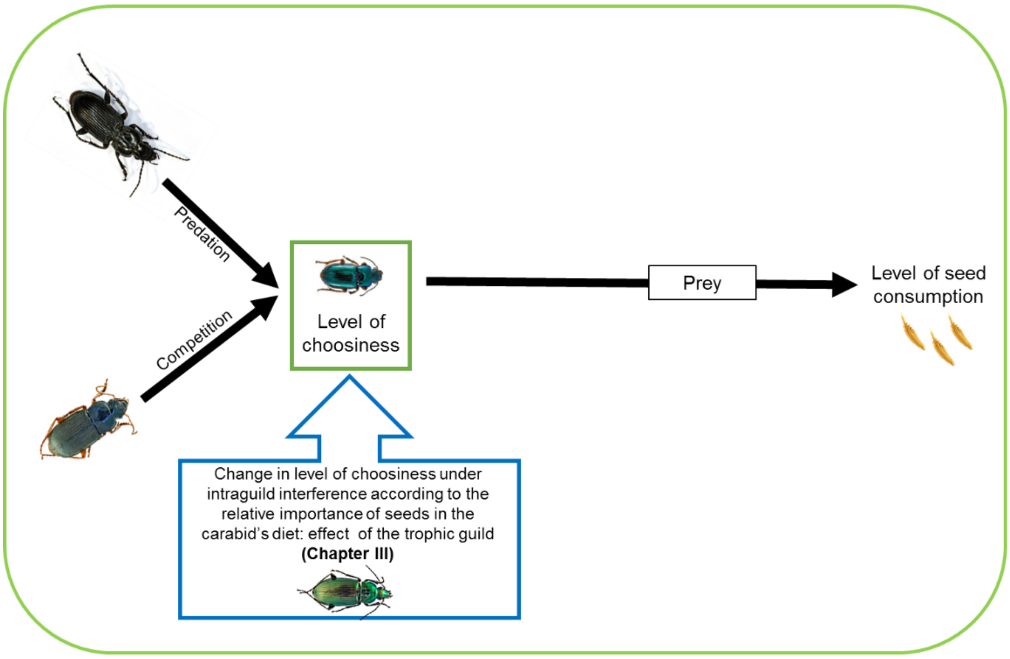
1) Introduction to chapter III

The experiment in Chapter II demonstrated that *H. affinis* individuals could modify their foraging behaviour when exposed to cues of carabids. The foraging individuals reduced their choosiness for seeds food items when exposed to predatory cues from another carabid species. Reduction in choosiness was not significant under cues of competitive interference.

The generality of these findings might depend on the relative importance of seeds in the diet of a carabid species. *H. affinis* is one of the more abundant granivorous species of carabids in arable fields in Europe. The daily consumption of seeds by *H. affinis* can be extremely high (Honek et al., 2006; Kulkarni et al., 2015b; Petit et al., 2014) and individuals rely on seeds as their main food source to meet their energetic requirements (Fawki and Toft, 2005; Kulkarni et al., 2015b; Saska, 2005; Saska and Jarošík, 2001). The rejection of an eatable seed might thus have a different impact on the fitness of *H. affinis* individuals than for individuals of more opportunist omnivorous species. A reduction in an individuals' level of choosiness might thus assure a non-zero supply of food, when exposed to predatory interference over an indefinite period. However, the consumption of resources, regardless of their quality, might also lead to the consumption of resources of low quality that ultimately would fail to fulfil the energetic needs of the forager. Moreover, eating whilst being vigilant might still reduce the ability of individuals to mount and effective response to an attack from a predator (Blanchard and Fritz, 2007).

Omnivore carabids, in contrast, rely on both animal and plant prey to meet their energetic requirements. They may, therefore, be more willing to reject a seed when foraging under predation risk than granivorous individuals. Given that one would expect an encounter with a predator to strongly impact individual fitness, we might hypothesise *that omnivore individuals would reject more seeds than H. affinis individuals and only accept seeds if considered as good enough to compensate for the risk of foraging under predation risk*. Moreover, we expect that *an omnivore would be less sensitive to opportunity cost for seeds than H. affinis, and maintain its choosiness for seeds when foraging under cues of competition*.

To test these expectations, I used the most abundant omnivorous carabid species found in fields in Burgundy, *Poecilus cupreus.* As it was not clear how species from the trophic guilds of granivores and omnivores would behave toward different seed species, when no other alternatives are available, I examined individual levels of choosiness for four different species of weeds commonly found in arable fields. These results were used to weight the relative interest that any given carabid species would have toward a particular weed seed species. I then reused the protocol from Chapter II, appropriately adapted for *P. cupreus*, to test whether omnivore individuals similarly change their level of choosiness for seeds of *T. officinale* when exposed to both to predatory cues and cues of competition. I discuss the results obtained by initially analysing *P. cupreus* alone and then by comparison to the results previously obtained in Chapter II for *H. affinis.*



This chapter was submitted for publication in Biological control

2) Article 2

Contrasted foraging strategies, predator interference and weed suppression in seed-eating carabid beetles

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ABSTRACT

Seed-eating carabid beetles have been shown to consume large amounts of weed seeds and are considered as potential biocontrol agents in arable agriculture. Seed-eating carabids range from ‘specialist’ (opportunistic omnivores) to more ‘generalist’ predators (obligate omnivores), but the relative contribution of these two guilds to weed suppression is still under debate. In this paper, we report on two experiments that: (i) characterize the level of choosiness of two carabid species, the obligate omnivore *Poecilus cupreus* and the opportunistic omnivore *Harpalus affinis* on four weed species; and, (ii) evaluate the change in level of choosiness of the two carabid species for seeds of *Taraxacum officinale* under intraspecific and interspecific competition and predation risk intraguild interference. The two carabid species differed strongly in their foraging strategy. *Poecilus cupreus* exhibited strong interest for only two of the four weed species offered in test and overlooked the others and this high level of interest remained unchanged under intraguild interference whereas *H. affinis* showed no difference of interest between the four weed species but a strong response to intraguild interference. These results suggest the coexistence of two distinct foraging strategies in seed-eating carabids that could be complementary in the delivery of weed seed regulation, giving support to the hypothesis of a positive effect of predator biodiversity on the provision of this regulation service.

KEYWORD:

Weed regulation; trophic guild; foraging strategy, level of choosiness, behavioural flexibility, predation risk

A. INTRODUCTION

Generalist predators are often considered less efficient than specialist predators as biocontrol agents, notably because of their exploitation of multiple food resources, which include other predators that suppress pests (Snyder and Ives, 2003). However, successful biocontrol has been reported for generalist predators in a variety of cropping systems, leading some authors to question the expected inferiority of generalists (Parshad et al., 2016; Rosenheim et al., 1995; Symondson et al., 2002). This has led to a renewed interest in the biocontrol exerted by assemblages of mainly generalist predators (Lang, 2003; Snyder and Ives, 2003; Straub et al., 2008). Predictions of pest-control functioning by multi-predator communities has proven difficult, possibly because of positive and negative effects of generalist predator diversity on biocontrol that can arise either from niche complementarity and facilitation or from predator interference (Crowder and Jabbour, 2014; Straub et al., 2008; Tylianakis and Romo, 2010). The complexity of species interactions within the guilds of predators of a community and the foraging strategies that individual predators adopt remains largely unstudied. Characterizing predator decision making process, diet breadth and spatial exploration, in effect the behavioural traits that determine the choice of the predator to attack a prey and how, where, and when this decision is taken, would aid the prediction of differences in foraging strategies and the relative efficacy of generalist and specialist predator species sharing a common suite of prey. In turn, behavioural information at a fine spatio-temporal scale would allow predictions for the occurrence of intraguild predation, functional redundancy and niche complementarity (Straub et al., 2008), and ultimately biocontrol (Wilby et al., 2013) in communities composed of both predator types; this could potentiallyprovide a mechanism to explain relationships between carabid biodiversity and the ecosystem function of biocontrol (Hines et al., 2015; Loreau, 2001).

Carabid beetles are common and abundant predators in agroecosystems that eat substantial amounts of weed seeds (Honek et al., 2003), and thereby contribute to weed control in arable fields (Bohan et al., 2011; Kulkarni et al., 2015b). Most carabid species are true omnivores (sensu Coll and Guershon, 2002), feeding on both plant and animal prey (R Hengeveld, 1979). Their preferences appear to be shaped by the most abundant and the easiest to capture or consume prey items (Frank, 2007), but carabids can rapidly switch to alternative prey species and between animal and plant feeding when necessary (Lundgren and Harwood, 2012). Some carabid species exhibit strong behavioural aggregation responses, either to weed seeds (Frank et al., 2011) or to animal prey such as slugs (Bohan et al., 2000). Differences in the relative importance of plant *vs*. animal prey in the diet of carabids mean that seed-eating carabids are found along a continuum between rather specialist granivores that only occasionally on animal prey (i.e. opportunistic omnivores) to more generalist predators that are obligate omnivores feeding both on plant and animal prey. These two feeding guilds coexist within carabid communities of arable fields, but as yet the relative contribution of these two guilds to weed suppression is not resolved. Field studies analysing the links between carabid communities and seed predation have indeed led to equivocal results. Seed predation can be predicted by total seed-eating carabid abundance, suggesting that both guilds contribute equally to seed predation (Menalled et al., 2007; O'Rourke et al., 2006; Petit et al., 2017), by opportunistic omnivore abundance (Diekötter et al., 2016; Trichard et al., 2013) or conversely by obligate omnivore abundance (Bohan et al., 2011; Jonason et al., 2013). Other studies have highlighted the role of seed-eating carabid species richness and/or diversity on seed predation (Gaines and Gratton, 2010; Jonason et al., 2013; Trichard et al., 2013) suggesting some complementarity between carabid species in the delivery of weed seed predation.

From an ecological viewpoint, obligate omnivorous carabids might be required to consume seeds to increase their fitness (Kulkarni et al., 2015b; Saska and Jarošík, 2001) but may also be limited in biocontrol efficacy by their metabolic machinery that is not well adapted to consume and digest many different species of weed seeds (Lundgren and Lehman, 2010). As a consequence, obligate omnivores could be limited in the amount of seeds and/or in the range of weed seed species that they can consume. Conversely, one could hypothesise that opportunistic omnivores are well-adapted to digesting plant material and could thus accept a wider range of weed seed than obligatory omnivores. Analysing the diet breadth of individual carabid species to weed seeds in controlled conditions at a fine temporal resolution would shed some light on the behavioural processes underpinning potential differences in the relative contribution of individual species to weed seed suppression.

Given the abundance and diversity of seed-eating carabids in the field, it is likely that interactions within the guild of predators, such as intraspecific competition, interspecific competition and intraguild predation occur frequently between carabid individuals and species (Griffith and Poulson, 1993; Guy et al., 2008). Potential impacts of intraguild interference on the consumption pattern of predators (i.e. functional response) have been described in the literature (e.g. Kratina et al., 2009; Rudolf, 2006). None of these studies, however, have looked at individual-level changes in foraging investment under intraguild interference. Predation avoidance and competition monitoring are considered as conflicting task with foraging as they, most of the time, can't be executed simultaneously (Beauchamp, 2008; Lima and Dill, 1990;

Milinski and Heller, 1978; Nonacs and Blumstein, 2010; Sih, 1980; Underwood, 1982; Wang et al., 2013). There is, thus, a trade-off between intensity of the foraging investment and intraguild interference avoidance. The effort and time that an individual should thus invest in finding what is an acceptable feeding item, referred to as "level of choosiness" in behavioural literature (Dechaume-Moncharmont et al., 2016; Jennions and Petrie, 1997), should therefore change according to the perceived intensity and risk of intraguild interference in order to reduce this trade-off (Amita et al., 2010; Davis et al., 2011; Ibrahim and Huntingford, 1989; Metcalfe et al., 1987b). The higher the risk, the lower the choosiness is expected to be. Quantifying the impact of interactions between carabid individuals on their level of choosiness for seeds would help to predict the importance of such interference on their efficacy as weed biocontrol agents as a lower choosiness might increase the range of prey accepted by a foraging predator under predation risk.

In this study, we compare the level of choosiness of two seed-eating carabid species common in European arable fields; the opportunistic omnivore *Harpalus affinis* (Schrank, 1781) and the obligate omnivore *Poecilus cupreus* (Linnaeus, 1758). In the first experiment, we conduct a no-choice test (where only one seed species is proposed to one individual) to assess the potential variation in the effort that individuals from each carabid species would put in finding an acceptable feeding items, when foraging for four different weed species, before finally accepting one (i.e. choosiness). We score individual latency to first seed acceptance, seed handling time, amount of seed consumed and time spent in a shelter as proxy for individual choosiness. High levels of choosiness observed for a given seed species (i.e. long latency to first seed acceptance) in a no-choice paradigm (no alternative species of weed available) would indicate a low level of interest of the carabids for that particular species of weed seeds, while low choosiness (i.e. short latency to first seed acceptance) would indicate a strong interest of the carabids for the offered species of weed. In a second experiment, we extend the study by Charalabidis et al (see Chapter II) that assessed the variation in level of choosiness in *H. affinis* foraging for seeds of *T. officinale* under predatory and competitive interferences. Using the same methodology, here we assess the variation in level of choosiness of *P. cupreus*. We score individual foraging strategy under different conditions of predator interference to assess potential differences in between obligate and opportunistic omnivorous carabids on individuals' variation in level of choosiness. The seed predation strategies emerging from these results are discussed.

B. METHODS

a. The study system

All carabids species used in tests are commonly found in local fields simultaneously (Petit et al., 2017). The obligate omnivore, *P. cupreus*, and the opportunistic omnivore, *H. affinis*, are both medium sized spring breeding carabids. Elytra length of tested individuals was measured under a binocular microscope (Zeiss Stemi ® 2000-C, magnification x10, accuracy: ± 0.05 mm) and weights estimated to an accuracy of 0.01mg (Mettler Toledo® XS204), following a fasting period of 54h to standardized individuals feeding states. *P. cupreus* individuals had a mean left elytra length of 7.30 mm (± 0.3) and a mean mass of 0.078 g (± 0.009) and *H. affinis* individuals had a mean left elytra length of 5.67 mm (± 0.3) and a mean mass of 0.055 g (± 0.008).

The four weed species tested, *Capsella bursa-pastoris* (L.) Medik. (0.1 mg, 0.8 mm), *Senecio vulgaris* L. (0.2 mg, 1.75 mm), *Taraxacum officinale* Weber (0.7 mg, 2.67 mm), *Viola arvensis* Murray (0.9 mg, 1.36 mm) are common in farmland and readily consumed by both carabid species, both in field and laboratory conditions (Petit et al., 2014; Trichard et al., 2014). *Pseudoophonus rufipes* (De Geer 1774, 11-16 mm), an opportunistic omnivore weed seed consumer (Petit et al., 2014) was chosen as the competitor species. *Pterostichus melanarius* (Illiger 1798, 12-19 mm), an obligate omnivore and carabid interspecific predator (Currie et al., 1996), was chosen as the predator species. Carabids were collected using pitfall trapping and kept under temperature and light-controlled conditions (19°C +/- 1°C, 60% humidity, 14:10 h light:dark cycle) in small groups in plastic boxes (34 x 19 x 11 cm length x breadth x height). Boxes were filled with soil, a moistened paper tissue sheet and water provided *ad libitum* in an Eppendorf tube containing moistened cotton wool. The species were held in different boxes to prevent interspecific predation (Currie et al., 1996) and in different rooms to prevent exposure to one another chemical signatures for at least 2 weeks prior to the test. Opportunistic omnivores were fed with the four weed seeds and the obligate omnivores were presented with *Tenebrio molitor* larva and frozen beef as an additional meat diet. The seeds used were collected locally and were soaked in clean water for 14 hours prior to each experiment, to become more palatable to and detectable by carabids (Law and Gallagher, 2015).

The experiments were conducted in a temperature controlled room at 19°C +/- 1°C and 60% humidity on an aluminium bench. Each carabid individual was tested alone and only once, following allocation at random to a treatment. To avoid any possible behavioural modification via volatile olfactory cues, species were always tested separately. Prior to testing, individuals were isolated and starved for 54 hours, a duration calibrated from preliminary experiments designed to produce individuals motivated to feed without sapping their strength and affecting their locomotion behaviours. To avoid a potential effect of date / hour and the status of individuals, all treatments and both sexes were tested each day in a random order. In both experiments we used no-choice tests, where only one food type was presented to individuals (Dougherty and Shuker, 2014). This method was preferred over ‘cafeteria tests’ as such comparative choice apparatus can artificially decrease the attractiveness of a given resource item, through a contrast effect with other resources offered simultaneously (Dougherty and Shuker, 2014; Edward, 2014; Larrinaga, 2010; Murray et al., 2010; Raffa et al., 2002; Underwood et al., 2004). Cafeteria tests thus provide an assessment of relative (Dougherty and Shuker, 2014; Murray et al., 2010; Raffa et al., 2002) and simultaneous (Allison and Cardé, 2008; Dougherty and Shuker, 2014) preference. This is problematic because, in the field, prey items are encountered sequentially: individuals must decide to accept, or not, an item without the possibility to return to it later, which limits the opportunity for comparative evaluation of the preys (Stephens, 2008). Moreover, in no-choice tests, a longer latency to acceptance of a food item can be interpreted as evidence for higher levels of choosiness for a particular food items (Jennions and Petrie, 1997; Murray et al., 2010; Reinhold and Schielzeth, 2015; Rodríguez and Greenfield, 2003; Rothbart and Hennig, 2012).

b. Estimation of carabid species diet breadth and level of choosiness for four different weed species

Experimental design

For each weed species, we tested respectively 10 males and 10 females of *H. affinis* (n= 80) and 9 males and 9 females of *P. cupreus* (n= 72). Individuals were isolated in a 9 cm diameter arena covered with a moist paper tissue, providing shelter and water *ad libitum.* Just prior the start of a test, 20 seeds were evenly positioned within the arena. During the first hour of the test, we monitored the proportion of individuals eating and the latency to first seed acceptance as metrics of the choosiness level of carabid individuals. We also monitored the mean number of seeds consumed and the individual shelter usage by scoring the total number of seed consumed and the position of the tested carabid at every sample date (i.e. every hour of the test :1h, 2h, 3h, 4h, 5h, and 13h after the beginning of the test). The mean number of seeds consumed was used to assess individual diet breadth and complete information on the choosiness level of individuals when offered seeds, while shelter usage was scored as a covariate that could affect the number of encounters with seeds. Individual were considered hiding under the moist paper at the bottom of the arena when their head, at least, was invisible. The proportion of shelter usage was then calculated by dividing the hiding score of an individual (i.e. number of sample dates were it was found hiding under the moist paper) by the total number of sample dates during the experiment.

Damaged seeds and the debris from eaten seeds were removed at each sample date to avoid double accounting. All individuals were measured and weighed after the last behavioural experiment to limit handling stress.

Statistical analyses

The proportion of individuals eating was analysed as a generalized linear model, assuming a binomial distribution. Where the seed species effect was significant, the difference between seed species was analysed using 2 by 2 table analysis using Epi package (Carstensen et al., 2017).

Latency to first seed acceptance was analysed using Cox proportional hazard models in the ‘cox.ph’ function from the package ‘survival’ (Therneau, 2006). This model allows censored data (when the observed behaviour happens after the end of the experiment duration). Proportional hazards assumption were assessed using the ‘cox.zph’ function. For each analysis, sex effect and its interaction with the seed species were tested. We reported the effect size indices and the corresponding 95% confidence intervals to allow meta-analysis or comparisons in future studies (Lakens, 2013; Nakagawa and Cuthill, 2007). The measure of effect size for all latencies was the hazard ratio estimated as the exponent of the regression coefficient, exp(beta), of the Cox model (Dechaume-Moncharmont et al., 2003).

The mean number of seeds consumed after 1 hour and at the end of the experiment was analysed using beta regressions with the function ‘betareg’ from the betareg package (Cribari-Neto and Zeileis, 2010). Where the weed species effect was significant, differences between specific pairs of weed species were tested using *post-hoc* multiple comparisons with Tukey adjustment. Individual shelter use was modelled as a generalized linear model assuming a binomial distribution. Individual body size and weight were compared between carabid species using a *t*-test as data met the condition for normality. The data were analysed in R version 3.3.2 (R Development Core Team, 2016).

Effect of light on the foraging strategy of H. affinis

Preliminary experiments showed that seed consumption of *H. affinis* was low during the initial four hours of a test and that individuals frequently used shelters. we ran additional trials under red light condition method often use to observe natural night time behaviour in carabids (Allema et al., 2012; Drees et al., 2008), to assess whether lighting conditions affected the experimental outcomes. The proportion of individuals consuming seeds and the latency to first seed acceptance did not differ between the light and red light treatments (respectively χ^2_1= 2.67, P = 0.1021 and P =0.47, hazard ratio = 0.79, 95%CI = [0.423; 1.496]). Latency to first acceptance was not affected by the sex of individual (χ^2_1= 2.96, P = 0.08, hazard ratio for the males compared with the females =1.75, 95%CI= [0.92; 3.227]) or by the interaction between sex and light condition (χ^2_1= 0.63, P =0.43). There was also no effect of light or seed species (χ^2_3= 3.24, P = 0.36). The mean amount of seed consumed did not differ between light and red light treatments during the first hour of the test (χ^2_6=2.885, P=0.8231) or by the end of the experiment (χ^2_6=5.58, P=0.4723).

c. Measuring variations in individuals level of choosiness when foraging for seeds under intraguild interference

Experimental design

We selected *T. officinale* as the experimental test weed as it was highly consumed by both carabid species in the first experiment. The experimental design follows Charalabidis et al. (see Chapter II). Intraguild interferences were simulated using test papers (white filter paper, Dutcher, Brumath, France) impregnated during the 24h prior to testing with non-volatile cuticular hydrocarbon chemicals cues released by walking carabids (Armsworth et al., 2005; Guy et al., 2008). Chemical cues from the focal carabid species were used to simulate intraspecific competition. Chemicals from *P. rufipes* simulated interspecific competition and chemicals from *P. melanarius* simulated intraguild predation. As sexual olfactory cues in the intraspecific competition treatment could induce mating related behaviours and distract individuals from foraging, we treated interspecific competition as a control of these potential cues interactions.

A total of 20 seeds of *T. officinale* were arranged on impregnated papers in two concentric circles of 10 seeds of respectively at 5 and 16 cm diameter, the latter circle corresponding to the border of the arena. Across treatments, a total of 288 *P. cupreus*, mature males and females, were tested (Table 2). Test individuals were acclimatized under a plastic pot at the centre of the arena for 8 min. The pot was then removed and a circular 18 cm diameter Pyrex petri dish bottom was inverted and placed on the top of the arena in order to create a circular arena boundary that isolated the arena from external perturbation. Individuals were then observed for one hour. We recorded the proportion of individuals eating, the latency to first seed acceptance and the mean number of seeds consumed. In addition, we recorded the handling time as the duration of consumption of a single seed. Individual exploration was estimated as the proportion of space used by individuals by counting the number of 1 x 1 cm cells visited at least once divided by the total amount of cells available in the arena. These trajectometry data were collected using a monochrome video camera (IMAGINGSOURCE DMK 31AU03) suspended over the arena and analysed using Ethovision (Noldus Information Technology, Wageningen, The Netherlands). The same set of variables for *H. affinis* individuals offered with *T. officinale* were reused from Charalabidis et al. (see Chapter II).

Statistical analysis

The proportion of individuals eating was modelled as a generalized linear model, assuming a binomial distribution. The mean number of seed consumed was modelled as a generalized linear model assuming a negative binomial distribution with zero-inflation, in the 'zeroinfl' function from the 'pscl' package (Jackman, 2015). The proportion of space used by the individuals was analysed using ANOVA. Latency to first seed acceptance and handling time were analysed using Cox proportional hazard models (see section above). For each analysis, the possible effect of the sex of individuals or its interaction with the treatment was tested.

C. RESULTS

P. cupreus individuals were larger ($t = -32.1$, $df = 136.53$, $P < 0.001$) and heavier ($t = -15.59$, $df = 138.22$, $P < 0.001$) than *H. affinis* individuals. *P. cupreus* had a mean left elytra length of 7.30 mm (± 0.3) and a mean mass of 0.078 g (± 0.009) and *H. affinis* had a mean left elytra length of 5.67 mm (± 0.3) and a mean mass of 0.055 g (± 0.008).

a. Estimation of carabid species diet breadth and level of choosiness for four different weed species

Estimates for the five variables measured during the first hour of the experiment are presented in Table 1. Potential effect of the sex of individuals and of interactions between sex and weed species are presented in the Supplementary Materials (Table S4) and are mentioned in the text when significant.

Table 1: Variable estimates (mean and SD) per carabid species and sex during the first hour of test for the four species of weeds.

	Poecilus cupreus		*Harpalus affinis*	
	Males	Females	Males	Females
T. officinale				
# individuals tested	9	9	10	10
% individuals consuming	88.9% (±33)	88.9% (±33)	40% (±52)	10% (±32)
Latency 1st seed (seconds)	809 (±1184)	1026 (±1410.5)	2455.5 (±1545.6)	3392.5 (±656.2)
Mean # seed consumed	5.55 (±2.92)	5.22 (±3.23)	3.6 (±5.12)	0.4 (±1.26)
Shelter use	22% (±44)	11% (±33)	50% (±53)	90% (±32)
S. vulgaris				
# individuals tested	9	9	10	10
% individuals consuming	78 (±44)	67 (±50)	40 (±52)	18 (±40)
Latency 1st seed (seconds)	1519.1 (±1498.8)	1519.2 (±1637.4)	2502.5 (±1567.5)	3348.5 (±599.7)
Mean # seed consumed	6.89 (±5.35)	6.67 (±6.61)	2.4 (±3.83)	0.45 (±1.03)
Shelter use	11% (±33)	11% (±33)	50% (±53)	82% (±40)
V. arvensis				
# individuals tested	9	9	10	10
% individuals consuming	100	89 (±33)	20 (±42)	22 (±44)
Latency 1st seed (seconds)	566.1 (±475.9)	1185.8 (±1086.6)	3199.6 (±872.3)	3265.1 (±776.4)
Mean # seed consumed	3.89 (±3.22)	2.33 (±2.55)	0.6 (±1.07)	0.78 (±1.99)
Shelter use	0% (±0)	22% (±44)	50% (±53)	78% (±44)
C. bursa-pastoris				
# individuals tested	9	9	10	10
% individuals consuming	33 (±50)	22 (±44)	20 (±42)	10 (±32)
Latency 1st seed (seconds)	2531.4 (±1615.2)	3037.8 (±1147.8)	2973.7 (±1328.9)	3562.9 (±117.3)
Mean # seed consumed	1.44 (±3.13)	3.11 (±6.25)	1.8 (±3.9)	0.3 (±0.95)
Shelter use	11% (±33)	22% (±44)	60% (±52)	80% (±42)

Proportion of individuals eating during the first hour

The proportion of *P. cupreus* individuals consuming seeds differed between weed species (χ^2_3 = 24.41, P < 0.001). More *P. cupreus* consumed seeds when offered *S. vulgaris* (P = 0.016), *T. officinale* (P = 0.0042) and *V. arvensis* (P = 0.002) compared with *C. bursa-pastoris* (Table S1). For *H. affinis*, the proportion of individuals eating did not vary between weed species (χ^2_3 = 1.33, P = 0.72). More individuals *P. cupreus* than individuals *H. affinis* were scored eating when offered with *S. vulgaris* (χ^2_1 = 7.64, P = 0.0057), *V. arvensis* (χ^2_1 = 17.21, P < 0.001) or *T. officinale* (χ^2_1 = 23.33, P < 0.001) whereas, in the two carabid species, the same of proportion of individuals consumed *C. bursa-pastoris* (χ^2_1 = 0.93, P = 0.72).

Latency to first seed acceptance

P. cupreus accepted *C. bursa-pastoris* significantly later than *S. vulgaris* (P = 0.0085), *T. officinale* (P < 0.001) and *V. arvensis* (P < 0.001) (Table S2). For *H. affinis*, latency was similar for the four weed species (χ^2_3 = 1.56, P = 0.67). The two carabid species differed in their latency (χ^2_1 = 48.77, P < 0.001) with *P. cupreus* accepting their first seed earlier than *H. affinis* individuals for all weed species (hazard ratio for *P. cupreus* compared with *H. affini*s = 6.1, 95%CI= [3.52, 10.60], P < 0.001). There was no interaction between species of carabids and species of seeds (χ^2_3 = 3.73, P = 0.29).

Total number of seeds consumed

The amount of seeds consumed by *P. cupreus* differed between weed species during the first hour (χ^2_3 = 11.58, P = 0.0090, Fig. 1), with T. *officinale* being consumed more than *C. bursa-pastoris* (P = 0.013, Table S3). There was also a difference at the end of the experiment, (χ^2_3 = 41.17, P <0.001) for pairs of weed species (Table S3). *T. officinale* was more consumed than *C. bursa pastoris* (P < 0.001) and *V. arvensis* (P < 0.001) and *S. vulgaris* was consumed more than *C. bursa-pastoris* (P < 0.001) and *V. arvensis* (P = 0.001). The mean amount of seed consumed by *H. affinis* did not differ between weed species in the first hour (χ^2_3 = 0.66, P = 0.88, Fig. 1) and at the end of the experiment (χ^2_3 = 4.74, P = 0.19).

Overall, *H. affinis* consumed more weed seeds than *P. cupreus* (χ^2_1 = 17.67, P < 0.001), with mean amounts of respectively 14.6 and 11 seeds at the end of the experiment. The two carabid species differed in their mean consumption of specific weed seeds (χ^2_3 = 9.08, P =

0.028). *H. affinis* consumed more seeds of *C. bursa-pastoris* (χ^2_1 = 20.72, P < 0.001) and *V. arvensis* (χ^2_1 = 12.17, P < 0.001) than *P. cupreus*. *P. cupreus* consumed more seeds of *T. officinale* (χ^2_1 = 16.37, P < 0.001). The two carabid species did not differ in their mean consumption of *S. vulgaris* (χ^2_1 = 0.23, P = 0.63) (Fig 1). There was no interaction between the species of carabids and the species of seeds (χ^2_3 = 5.44, P = 0.14).

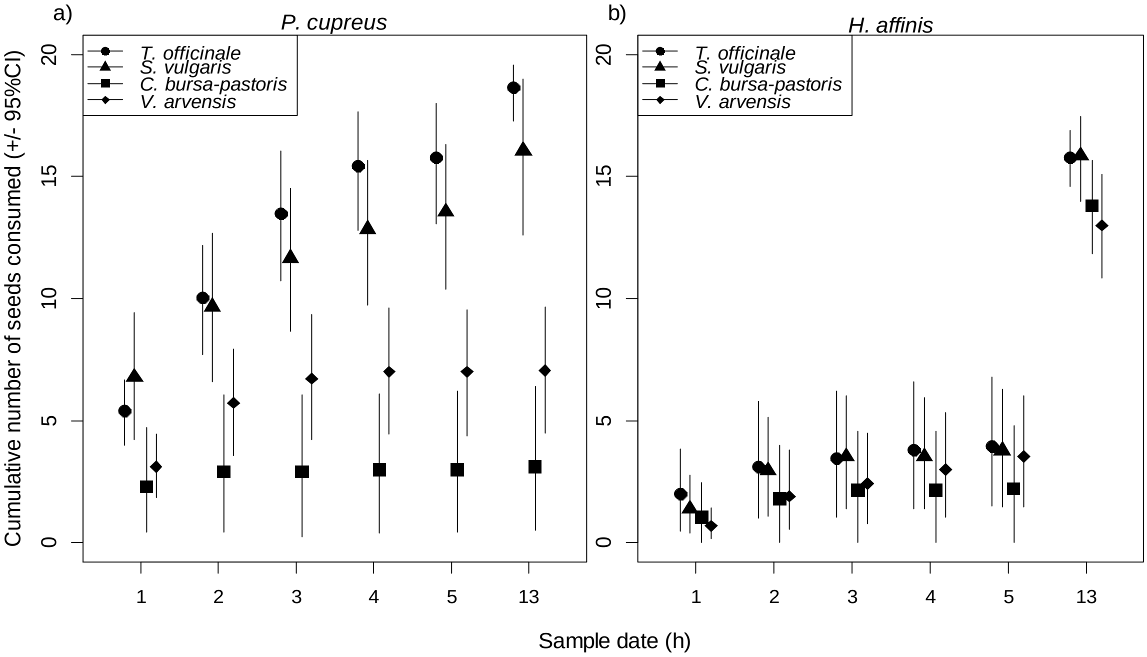

Figure 1: **Cumulative number of seed consumed** (bootstrapped +/- 95%CI) by *P. cupreus* (a) and *H. affinis* (b) individuals at each sample date for seeds of *T. affinis* (●), *S. vulgaris*(▲), *C. bursa-pastoris* (■) and *V. arvensis* (♦)

Pattern of carabid shelter use

There was an effect of the sex of individuals on shelter use with females hiding more than males both in *P. cupreus* (χ^2_1 = 8.45, P = 0.0036) and *H. affinis*. (χ^2_1 = 54.12, P < 0.001). Weed species did not affect shelter use in *P. cupre*us (χ^2_3 = 1.26, P = 0.74) or in *H. affinis* (χ^2_3 = 2.04, P = 0.56). There was no interaction between seed species and sex of individuals for *P. cupre*us (χ^2_3 = 5.76, P = 0.12) and for *H. affinis* (χ^2_3 = 2.83, P = 0.42).

H. affinis individuals were observed hiding more often than *P. cupreus* individuals whether it be the females (χ^2_1 = 156.33, P < 0.001) or the males (χ^2_1 = 71.55, P < 0.001). Weed seed species affected the shelter use of individuals neither for *females* (χ^2_3 = 1.08, P = 0.78) and nor for *males* (χ^2_3 = 4.21, P = 0.24) and there was no interaction between seed species and carabid species for *females* (χ^2_3 = 5.57, P = 0.13) or for males (χ^2_3 = 1.03, P = 0.79).

b. Effect of intraguild interference on individuals level of choosiness

Variable estimates per carabid species and sex for each treatment are presented in Table 2 Results for the potential effects of the sex of individuals and interactions between sex and the treatments are presented in Table S5.

Table 2: Variable estimates (mean and SD) per carabid species and sex for each treatment

	Poecilus cupreus		*Harpalus affinis*	
	Males	Females	Males	Females
Control				
# individuals tested	35	36	39	31
% individuals consuming	86 (±35)	72 (±45)	36 (±5)	42 (±5)
Handling time (seconds)(seconds)	750.13 (±519.7)	562.6 (±713.5)	397.07 (±224)	335.38 (±87.5)
Latency 1st seed (seconds)	1006.7 (±1250.2)	1617.2 (±1454.2)	2533.2 (±1552.2)	2157.6 (±1743.8)
Mean # seed consumed	2.97 (±2.2)	3.33 (±3.0)	1.64 (±3.0)	2.19 (±3.0)
% of space used	62 (±22)	74 (±20)	64 (±17)	67 (±15)
Intraspecific Competition				
# individuals tested	36	36	39	32
% individuals consuming	72 (±45)	61 (±49)	46 (±50)	53 (±51)
Handling time (seconds)(seconds)	716.65 (±600)	607.54 (±352.8)	510.72 (±293.4)	354.35 (±171)
Latency 1st seed (seconds)	1355.4 (±1494.7)	1756.2 (±1573.2)	2089.7 (±1738.7)	1783.7 (±1768.5)
Mean # seed consumed	2.92 (±2.6)	2.61 (±2.7)	1.18 (±1.7)	1.53 (±2.0)
% of space used	63 (±20)	66 (±18)	59 (±19)	58 (±18)
Interspecific Competition				
# individuals tested	36	36	43	32
% individuals consuming	86 (±35)	72 (±45)	46 (±50)	50 (±51)
Handling time (seconds)	614.45 (±304)	420.56 (±273.3)	493.2(±289.7)	281.38(±102.2)
Latency 1st seed (seconds)	1033.8 (±1267))	1417.6 (±1467.6)	2135.5 (±1679.9)	1915.5 (±1741.7)
Mean # seed consumed	3.14 (±2)	2.69 (±2.5)	1.39 (±1.9)	2.44 (±3.2)
% of space used	67 (±20)	70 (±19)	67 (±18)	71 (±17)
Predation				
# individuals tested	36	36	43	31
% individuals consuming	75 (±44)	72 (±45)	60 (±49)	71 (±46)
Handling time (seconds)(seconds)	664.97 (±409.5)	529.15 (±307.2)	430.42 (±275.5)	361.5 (±129.5)
Latency 1st seed (seconds)	1161.7 (±1460.5)	1558.4 (±1463.3)	1526.7 (±1715)	1069.9 (±1647.2)
Mean # seed consumed	3.14 (±2.5)	2.64 (±2.3)	2.98 (±3.2)	3.26 (±3.9)
% of space used	68 (±20)	71 (±24)	68 (±16)	64 (±17)

Proportion of individuals consuming weeds

Across treatments, the proportion of *P. cupreus* males consuming weeds was higher than for that of females ($\chi^2 1 = 4.1$, $P = 0.04$). The proportion of individuals consuming weeds did not differ between treatments for *P. cupreus* ($\chi^2 3 = 3.91$, $P = 0.27$). A treatment effect was observed for *H. affinis* ($\chi^2 3 = 10.62$, $P = 0.014$), with the proportion of individuals consuming weeds being higher in the predation risk than in the control treatment ($P = 0.0025$, odds-ratio = 2.94, 95%CI = [1.49, 5.79]). The proportion of individuals consuming weeds was not affected by intraspecific competition ($P = 0.31$, odds-ratio = 1.47, 95%CI = [0.76, 2.85]) and interspecific competition ($P = 0.24$, odds-ratio = 1.54, 95%CI = [0.79, 3.02]).

There was an effect of the carabid species and of the treatment on the proportion of individuals consuming ($\chi^2 3 = 8.82$, $P = 0.032$). More individuals of *P. cupreus* consumed seeds in the control ($\chi^2 1 = 24.44$, $P <0.001$), intraspecific competition ($\chi^2 1 = 4.45$, $P = 0.035$) and interspecific competition treatments than *H. affinis* ($\chi^2 1 = 15.77$, $P <0.001$). There was no significant difference in seed consumption by the two carabid species in the predation treatment ($\chi^2{}_1 = 1.31$, $P = 0.25$).

Latency to first seed acceptance and total amount of seed consumed

Across all treatments, *P. cupreus* females accepted their first seed later than the males ($\chi^2 1 = 8.09$, $P = 0.004$). Treatment, however, did not affect the latency to first seed acceptance for *P. cupreus* ($\chi^2 3 = 1.99$, $P = 0.57$, Fig. 2b). There was a treatment effect in *H. affinis* ($\chi^2_3 = 12.6$, $P < 0.001$, Fig. 2a), with a shorter latency in the predation treatment compared to the other treatments (control: $P < 0.001$, hazard ratio = 2.22 , 95%CI = [1.38, 3.56]; intraspecific competition: $P = 0.032$, hazard ratio = 1.59, 95%CI = [1.02, 2.47]; interspecific competition: $P = 0.020$, hazard ratio = 1.67, 95%CI = [1.08, 2.57], Fig. 2a). Latency to first seed acceptance differed between the two carabid species ($\chi^2 3 = 8.14$, $P = 0.043$). *P. cupreus* started consuming seeds earlier than *H. affinis* in all four treatments (Control: $\chi^2 1 = 28.76$, $P < 0.001$; Intraspecific competition: $\chi^2 1 = 4.51$, $P = 0.034$; Interspecific competition: $\chi^2 1 = 22.66$, $P < 0.001$ and Predation: $\chi^2 1 = 4.51$, $P = 0.034$).

Treatment did not affect the mean amount of seeds consumed in *P. cupreus* ($\chi^2 6 = 5.10$, $P = 0.53$, Fig. 2d), but did in *H. affinis* ($\chi^2 6 = 17.22$, $P = 0.0085$, Fig. 2c) with an effect of sex

($\chi^2 2$ = 6.58, P = 0.037), but no interaction between sex and treatment ($\chi^2 6$ = 1.47, P = 0.96). *H. affinis* consumed significantly more seeds in the predation treatment than it did in the other treatments (control P = 0.030; intraspecific competition P = 0.031; interspecific competition P = 0.019 (Fig. 2c). There were no other significant differences between treatments (Intraspecific – Interspecific competition (P = 0.99); Control – Interspecific competition (P = 1); Control – Intraspecific competition (P = 0.99, Fig. 2c). There was an effect of the carabid species and treatment ($\chi^2 6$ = 12.78, P = 0.047).

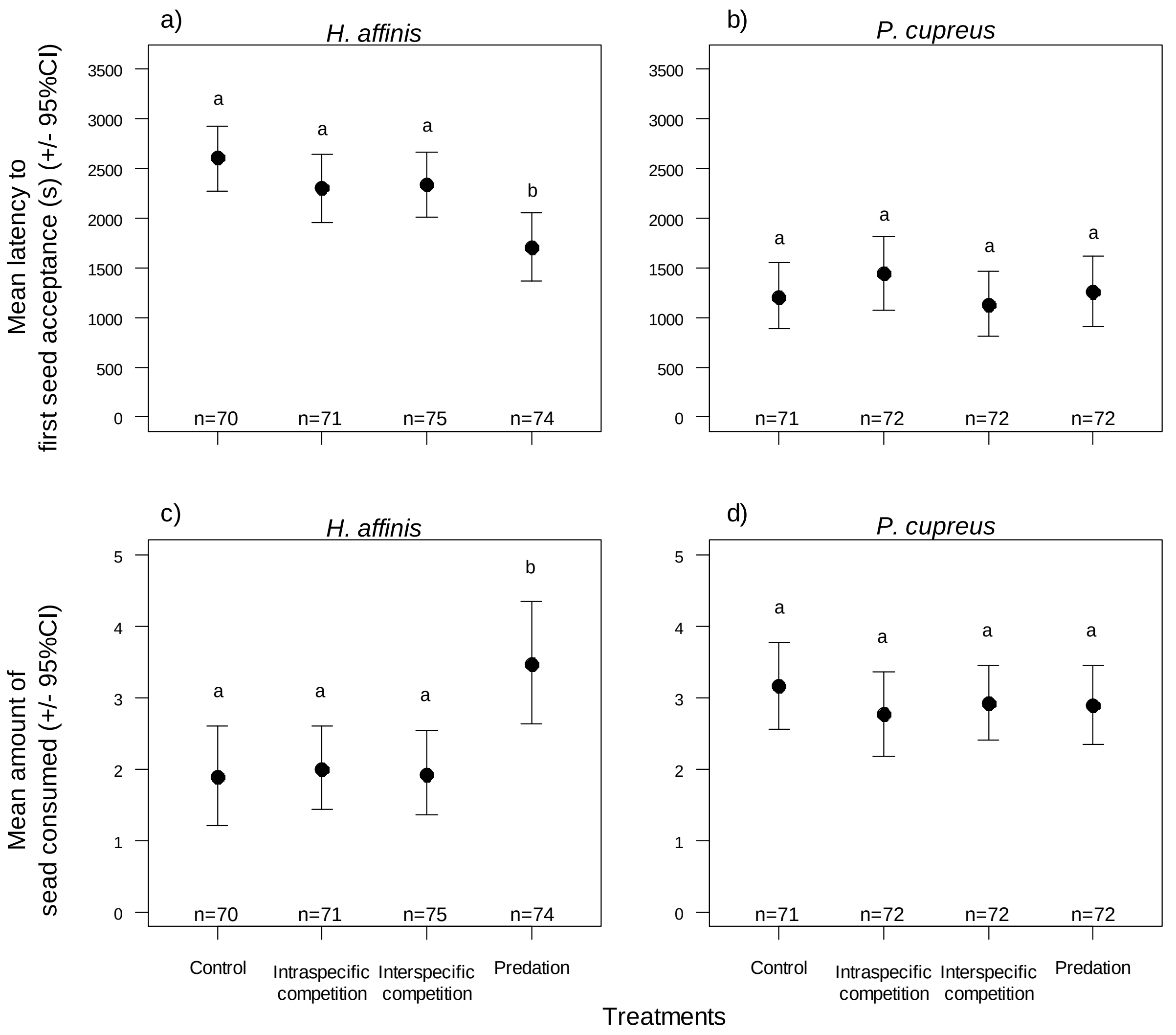

Figure 2: a-b) **Mean latency (bootstrapped +/- 95%CI) before first seed acceptance** in each treatment for *H. affinis* (a) and *P.cupreus* (b), c-d) **Mean number (bootstrapped +/- 95%CI) of seed consumed** by *H. affinis* (c) and *P. cupreus* (d) individuals during the hour of the test in each treatment. Different letters correspond to statistically significant difference between treatments (post-hoc pairwise comparison with Tukey adjustment for multiple comparisons). The sample sizes are shown above the x-axis. Figure 2c is derived from Charalabidis et al. (*see Chapter II*)

Handling time

Handling time did not vary with treatment for *H. affinis* ($\chi^2_3 = 1.40$, P = 0.71) nor for *P. cupreus* ($\chi^2_3 = 3.46$, P = 0.32) There was a sex effect in both species, with females consuming seeds faster than males irrespective of the treatment (for *P. cupreus:* $\chi^2_1 = 7.8$, P = 0.005, for *H. affinis*: $\chi^2_1 = 16.45$, P < 0.001). Moreover, across treatments *P. cupreus* individuals spent more time handling seeds of *T. officinale* than individuals of *H. affinis* ($\chi^2{}_1 = 33.60$, $P < 0.001$, results for the control: $\chi^2{}_1 = 8.46$, $P = 0.0036$; predation: $\chi^2{}_1 = 12.60$, $P < 0.001$; intraspecific competition: $\chi^2{}_1 = 7.65$, $P = 0.0057$; interspecific competition: $\chi^2{}_1 = 4.45$, $P = 0.035$). There was no interaction between carabid species and treatment ($\chi^2{}_3 = 2.26$, $P = 0.52$).

Proportion of space used

Space use by *P. cupreus* did not differ between treatments ($F_{282,285} = 0.73$, $P = 0.53$) There was an effect of sex, with female individuals exploring more than males ($F_{282,283} = 4.33$, $P = 0.038$), but no interaction between sex and treatment ($F_{279,282} = 0.86$, $P = 0.46$). Space use by *H. affinis* differed between treatments ($F_{256,259} = 3.95$, $P = 0.0088$), being higher under interspecific competition than under intraspecific competition ($F_{3,257} = 3.36$, $P = 0.019$). The proportion of space used did not differ between the two carabid species ($F_{1,543} = 3.06$, $P = 0.08$). There was no interaction between carabid species and treatment ($F_{3,540} = 0.51$, $P = 0.67$).

D. DISCUSSION

In this paper we quantified sets of behavioural traits characterising the foraging strategy of two common seed-eating carabid species. Our results show that the two carabid species exhibit two contrasted foraging strategies, with potentially important implications for their relative contribution to weed seed biocontrol.

The quantification of individual levels of choosiness demonstrates that the two carabid species differ in their seed diet breadth. The behaviour of the obligate omnivore *P. cupreus* changed with the species of weed offered. *P. cupreus* expressed a low level of choosiness (i.e. higher interest) for *T. officinale* and *S. vulgaris* seeds, with individuals accepting seeds earlier, eating more seeds and overall, a higher proportion of individuals consuming seeds. Generalist predators are able to make choices, by discarding prey from their diet, in order to maximize their fitness (Eubanks and Denno, 2000). Here, we suspect that the low choosiness of *P. cupreus* is linked to the ease of consumption of the seeds with individuals discarding those weed species that are too difficult to consume. This is supported by our observations that the initial interest of *P. cupreus* for *V. arvensis* declined dramatically after the first hour of the experiment, and that these seeds were subsequently discarded. *P. cupreus* individuals were observed having difficulties handling seeds of *V. arvensis* and often lost seeds while trying to open them (Pers. Obs.). Honek et al (2007), showed that larger individuals prefer larger seeds (Honek et al., 2011, 2007, 2003). Their efficiency at opening a seed may partly be explained as a dimensional compatibility between the mandibles of the carabid and the seeds (Honek et al., 2007). The drop off in interest observed in our study for seeds of *V. arvensis* by *P. cupreus* individuals might, hence, be explained by the bigger size of *P. cupreus,* in comparison to *H. affinis,* and the fact that seeds of *T. officinale*, whereas having a similar weight, are two times as long as seeds of *V. arvensis*. The lack of interest of *P. cupreus* individuals for seeds of *V. arvensis* could also be explained by an inability of the individuals to effectively digest *V. arvensis* seeds (R. Hengeveld, 1979c; Lundgren and Lehman, 2010; Schmid et al., 2014)

In contrast, the opportunistic omnivore *H. affinis* consumed all seed species indifferently and showed no difference in relative level of choosiness for each seed species. *Harpalini* species have been described as unspecialized toward a particular seed species (Acorn and Ball, 1991; Forsythe, 1983; Kulkarni et al., 2015b; Zetto Brandmayr et al., 1998). *Harpalus sp.* have evolved broad mandibles with massive adductors that are able to crush hard seeds and, hence, can have high consumption rates of seeds (Paarmann et al., 2006; Zetto Brandmayr et al., 1998). Their greater ability to consume seeds, as compared to *P. cupreus,* is supported by differences in the handling time of *T. officinale,* a weed preferred by both carabid species. Although *P. cupreus* consumes more seeds of *T. officinale* in total than *H. affinis, P. cupreus* individuals have a longer handling time. The ability of *H. affinis* individuals to feed on several species of seeds, regardless of their shape or size, is beneficial for an opportunistic omnivore as they survive predominantly by seed consumption (Kamenova et al., 2017) and require edible seeds throughout their period of activity. Discarding seeds could result in strong opportunity costs (Stephens, 2008) either because of competition (Dechaume-Moncharmont et al., 2016) or because uneaten seeds quickly become unavailable by entering the seed bank.

Differences were apparent in the foraging strategy of these two carabid species. *H. affinis* appeared much slower to adopt seed consumption behaviours than *P. cupreus*, in both experiments. During the first five hours of the no-choice experiment, *P. cupreus* accepted their first seed earlier and ate significantly more seeds than *H. affinis*, irrespective of the weed species, and a similar pattern was observed in the control treatment of the second experiment. This apparent lack of interest for the seeds in *H. affinis* is unlikely to be due to the weed species offered, as these weed species have been tested successfully for *H. affinis* in cafeteria-test studies (Honek et al., 2011, 2007, 2006; Petit et al., 2014; Saska et al., 2010). Light conditions did not impact the foraging strategy of *H. affinis*. Rather, the pattern could simply result from a lower activity in *H. affinis* than in *P. cupreus* (Thiele, 1977). Smaller species, such as *H. affinis* have been shown to be typically less active than larger species like *P. cupreus*

(Greenslade, 1964; Lang, 2000; Luff, 1975). We also observed that most *H. affinis* individuals sought shelter and hid during the no-choice test, reducing the period they were observed actively foraging for seeds.

Finally, in contrast to *H. affinis* individuals that were reported to reduce their level of choosiness for seeds when facing predatory interference (see Chapter II), no change was observed in *P. cupreus.* Under predation risk, *H. affinis* reduced its latency by half and almost doubled its mean seed consumption when compared to the control treatment. This is consistent both with other research showing an increase in seed acceptance in carabids exposed to predatory cues (Blubaugh et al., 2017) and with the hypothesis that predator interactions could make individuals less choosy (Leaver and Daly, 2003; Metcalfe et al., 1987; Perea et al., 2011). Individuals would reduce the effort or energy used to assess a ressource (i.e. choosiness as defined by Jennions and Petrie 1997) and accept all encountered items, regardless of their quality. This ability to adjust choosiness when facing a risk of predation would enable *H. affinis* to maintain its feeding income, especially in arable fields situations, where carabid predator such *P. melanarius* are common and abundant. In contrast, situations of intraspecific and interspecific competition triggered no behavioural adjustment in *H. affinis*, even if competition could expose too choosy individuals to the loss of reasonably good quality resource items by opportunity costs (Dechaume-Moncharmont et al., 2016).

The lack of change in the level of choosiness of *P. cupreus* foraging under predation risk might be explained by the potential encounters with *P. melanarius* not being hazardous enough to select for a change in their foraging strategy. It is also possible that the interest of *P. cupreus* for *T. officinale* seeds in the control treatment was already as high as it could be (i.e. individuals were consuming seeds quickly and to satiety) and therefore choosiness for this particular weed species could not be reduced. Being an obligate omnivorous carabid, *P. cupreus* can rely on both plant and animal material (Coll and Guershon, 2002; Frank et al., 2011). This wide feeding range pattern could explain the lack of change in level of choosiness under the risk of competition observed in our study. Under competition, individuals could always switch to focus on a prey type that is not shared with the competitor. Hence, they might not need to reduce their choosiness in order to maintain energetic incomes. Since an encounter with a potential predator is more directly lethal than the opportunity costs resulting from competition, we would have expected a stronger behavioural adjustment (i.e. intensity of the change in level of choosiness) in the predation treatment. The lack of difference between the two competition treatments and the predation risk treatment could be explained by *P. cupreus i*ndividuals perceiving *P. melanarius* as a potential feeding competitor, as they both feed on animal materials (Brooks et al., 2012). Cues of *P. melanarius* could, hence, have been considered as same type of risks than *P. rufipes* (i.e. interspecific competition) or *P. cupreus* (i.e. intraspecific competition) individuals' cues. Lastly, if olfactory cues have already proved useful to induce behavioural response in carabids (Guy et al., 2008), it could be that *P. cupreus* do not rely on olfactory cues to assess risks but rather on mechanical cues (Kratina et al., 2009). Hence, individuals may not perceive odours as effective cues of risks.

The differences in observed change in level of choosiness under different intraguild interference in our study could have implications in terms of the relative contribution of both species to the regulation of weeds in arable agriculture. The carabid fauna of arable fields is, in most situations, dominated by a few obligate omnivorous species for which the consumption of seeds is important for their fitness (Kulkarni et al., 2015b; Saska and Jarošík, 2001). If obligate omnivores have different level of choosiness for each encountered species of weeds (i.e. different level of interest for given seed species), because of physiological limits, and forage actively on seeds in arable fields, patches of weed species with high level of interest will be rapidly found and cleared and will therefore not be available for opportunistic omnivores if their latency to seed consumption is too high. This could lead opportunistic omnivores to accept only those weed species still available to them in the field. Field consumption may therefore not match the preferences observed in cafeteria-tests, explaining the difficulty in extrapolating laboratory results to field situations (Petit et al., 2014). We might hypothesise that obligate and opportunistic carabids should be complementary in their contribution to weed seed predation, with a rapid and selective effect of obligate omnivores complemented by a delayed but non-selective effect of opportunistic omnivores (Crowder and Jabbour, 2014). Moreover, biological control could be further enhanced if granivorous species, as shown here for *H. affinis*, can lower their choosiness for seeds when exposed to predation risk, further widening the range of weed seed consumed.

E. CONCLUSION

Our comparison of a set of behavioural traits in two common seed-eating carabid species provides evidence of contrasted specific change in level of choosiness for seeds within this group of generalist predators. It also suggests some complementarity between the two foraging strategies, hence providing a mechanism to explain a positive relationship between carabid biodiversity and the ecosystem function of weed biocontrol Future studies characterizing the foraging strategy (e.g. change in levels of choosiness) of opportunistic and obligate carabid species should be conducted in order to assess whether the two strategies described here are generic and/or if other foraging strategies exist in carabid beetles. This knowledge would advance our understanding of the ecological processes underlying the delivery of weed biological control by carabid communities in arable fields

F. ACKNOWLEDGEMENTS

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G. SUPPLEMENTARY MATERIALS

Table S1: Pairwise comparison between seed species for the proportion of individuals of *P. cupreus* that consumed during the first hour of the test. The index of effect size (odds ratio) for the difference between seed species was estimated using 2 by 2 table analysis performed with 'Epi' package (Carstensen et al., 2017)

Seeds species	P-value	Odds ratio	IC 95%
T. officinale - V. arvensis	1	1.0625	[0.43, 2.64]
S. vulgaris - V. arvensis	0.50	1.3816	[0.56, 3.41]
C. bursa-pastoris - V. arvensis	0.002	0.2032	[0.074, 0.56]
T. officinale - S. vulgaris	0.65	0.7690	[0.31, 1.88]
T. officinale - C. bursa-pastoris	0.0042	0.2159	[0.079, 0.59]
S. vulgaris - C. bursa-pastoris	0.016	0.2807	[0.10, 0.76]

Table S2: Pairwise comparison between seed species for the latency of first seed acceptance for *P. cupreus* individuals

Seeds species	P-value	Hazard ratio	IC 95%
T. officinale - V. arvensis	0.76	0.89	[0.45, 1.78]
T. officinale - S. vulgaris	0.15	0.58	[0.28, 1.21]
T. officinale - C. bursa-pastoris	<0.001	0.14	[0.053, 0.39]
V. arvensis- S. vulgaris	0.24	0.64	[0.31, 1.34]
V. arvensis- C. bursa-pastoris -	<0.001	0.16	[0.058, 0.44]
S. vulgaris - C. bursa-pastoris	0.0085	0.25	[0.088, 0.70]

Table S3: Pairwise comparison between seed species for the mean number of seed consumed for *P. cupreus* individuals (post-hoc pairwise comparison with Tukey adjustment for multiple comparisons)

First hour of the test	
Seeds species	P-value
T. officinale - *V. arvensis*	0.39
S. vulgaris - *V. arvensis*	0.80
C. bursa-pastoris - *V. arvensis*	0.38
T. officinale - *S. vulgaris*	0.90
T. officinale - *C. bursa-pastoris*	0.013
S. vulgaris - *C. bursa-pastoris*	0.073
After. 13hours	
T. officinale - *V. arvensis*	<0.0001
S. vulgaris - *V. arvensis*	0.0001
C. bursa-pastoris - *V. arvensis*	0.24
T. officinale - *S. vulgaris*	0.84
T. officinale - *C. bursa-pastoris*	<0.0001
S. vulgaris - *C. bursa-pastoris*	<0.0001

Table S4: Effect of sex of the individuals and interactions between sex and species of seeds for the experiment on individual diet breadth and level of choosiness for four different weed species.

Section title	**Duration**	**Carabid species**	**Interaction Sex * Species of weed**			**Effect of the sex**		
				df	***P***		***df***	***P***
Number of individuals consuming weeds	t=1h	*P. cupreus*	$\chi^2 = 1.089$	3	0.78	$\chi^2 = 0.91$	1	0.34
		H. affinis	$\chi^2 = 1.45$	3	0.69	$\chi^2 = 2.73$	1	0.098
Latency to first seed acceptance	t=1h	*P. cupreus*	$\chi^2 = 0.66$	3	0.88	$\chi^2 = 1.20$	1	0.27
		H. affinis	$\chi^2 = 1.48$	3	0.69	$\chi^2 = 3.42$	1	0.06
Total number of seed consumed	t=1h	*P. cupreus*	$\chi^2 = 0.57$	3	0.90	$\chi^2 = 0.45$	1	0.50
		H. affinis	$\chi^2 = 0.80$	3	0.85	$\chi^2 = 2.013$	1	0.16
	t=13h	*P. cupreus*	$\chi^2 = 0.99$	3	0.80	$\chi^2 = 1.081$	1	0.29
		H. affinis	$\chi^2 = 0.66$	3	0.88	$\chi^2 = 1.24$	1	0.26

Table S5: Effect of sex of the individuals and interactions between sex and intraguild interferences on individuals' change in level of choosiness.

Section title	**Carabid species**	**Interaction Sex * intraguild interference**			**Effect of the sex**		
			df	***P***		***df***	***P***
Number of individuals consuming weeds	*P. cupreus*	$\chi^2 = 1.087$	3	0.78	$\chi^2 = 4.097$	1	0.04
	H. affinis	$\chi^2 = 0.23$	3	0.97	$\chi^2 = 1.34$	1	0.25
Latency to first seed acceptance	*P. cupreus*	$\chi^2 = 0.43$	3	0.93	$\chi^2 = 8.09$	1	0.004
	H. affinis	$\chi^2 = 0.60$	3	0.89	$\chi^2 = 2.22$	1	0.14
Total amount of seed consumed	*P. cupreus*	$\chi^2 = 5.69$	6	0.46	$\chi^2 = 4.65$	2	0.098
	H. affinis	$\chi^2 = 1.47$	6	0.96	$\chi^2 = 6.58$	2	0.037
Handling time	*P. cupreus*	$\chi^2 = 0.66$	3	0.88	$\chi^2 = 7.8$	1	0.005
	H. affinis	$\chi^2 = 5.7$	3	0.12	$\chi^2 = 16.45$	1	< 0.001
Space use	*P. cupreus*	F = 0.86	282, 283	0.46	F = 4.33	282, 283	0.038
	H. affinis	F = 0.61	253, 256	0.61	F = 0.042	256 257	0.84

3) Chapter conclusion

These results demonstrate that even though currently classified as an omnivorous species, the mean consumption of seeds by *P. cupreus* was relatively high in a no-choice paradigm test. Individuals consumed a mean amount of 11 seeds after 13 hours of exposure. In comparison, the granivore *H. affinis* ate a mean amount of 15 seeds over the same time span. Clearly, when exposed to seeds and no other food item alternatives, *P. cupreus* could eat a relatively high amount of seeds.

The panel, or range, of seed species that *P. cupreus* individuals would eat in testing is narrower than for *H. affinis*. *P. cupreu*s individuals overlooked two of the four species of seed presented in the no-choice tests, eating only seeds of *T. officinale* and *S. vulgaris.* Given that the seed species were offered without alternatives for a period of 13 hours, such a consistent lack of interest for some seeds would suggest that they are not interesting to the carabids. Individual behaviour toward seeds of *V. arvensis,* which included initial high rates of attack but subsequent rejection, might suggest that either the energetic investment necessary to eat *V. arvensis* seeds is higher than for seeds of *T. officinale* and *S. vulgaris* or their handling is difficult for *P. cupreus* individuals. At face value, the latter hypothesis would seem the most credible because *H. affinis* readily ate *V. arvensis* seeds, which might indicate that the energetic value of this seed species might not differ from the other seed species offered in test. Moreover, the seed species used in test were chosen because they had similar percentage lipid contents. *V. arvensis* seeds are rounder than the seeds of *T. officinale* and *S. vulgaris*. The narrow mandibles of *P. cupreus* might make it difficult to handle seeds of *V. arvensis*. A high energetic investment necessary to crush them (unfitting mandibular parts) or an inability to properly digest them might explain why *V.* arvensis seeds were overlooked and future studies should try to link carabid feeding preference with the efficiency of handling, eating and digesting weed seeds.

My results also show that the foraging behaviour of *P. cupreus* differed from *H. affinis* when foraging under intraguild interference. *P. cupreus* individuals demonstrated a very low choosiness for seeds of *T. officinale* irrespective of the cues they were exposed to. This relative lack of change in response to intraguild interference, by the *P. cupreus* individuals in our test, could mean that the foraging behaviour of *P. cupreus* is more consistent, than *H. affinis,* between different carabids communities.

Fourth Chapter

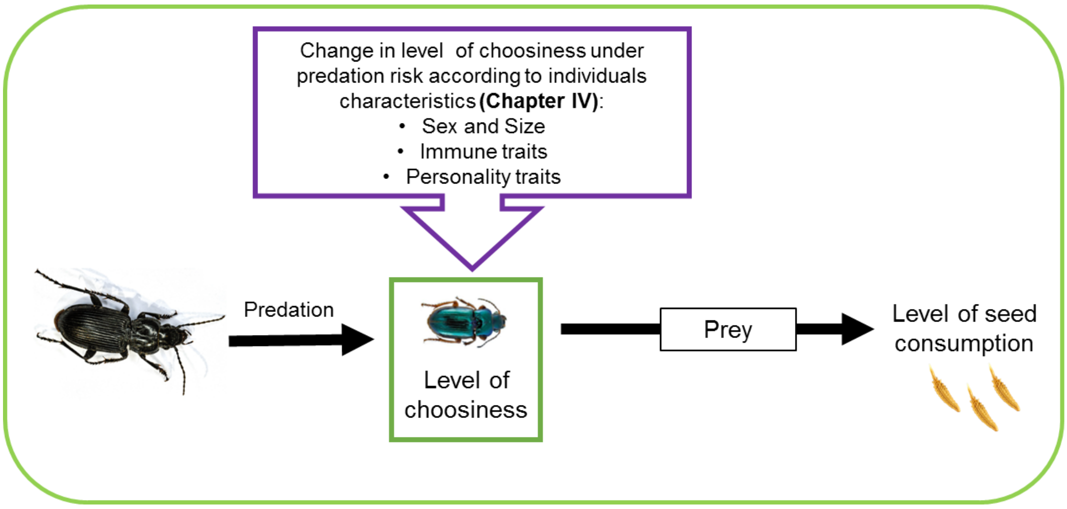
Effect of individual personality traits and immune defences on the level of choosiness.

1) Introduction to chapter IV

Between-individual behavioural variation has frequently been observed in studies of animal behaviour and decision making. Thus, the observation of systematic variation in an individuals' level of choosiness for weed seeds, irrespective either of predatory and intraguild interference cues or of trophic guild effects, would not be surprising in my results. The sizes of the confidence intervals observed for the metrics of choosiness, in Chapter II and III, indeed suggest that there is a diversity of behavioural adjustments levels between the individuals that were tested. This between-individual variation may be due to intrinsic characteristics of individuals themselves, such as personality traits, and physiological and morphological characteristics.

Immune activity has been shown to increase the overall energetic requirements of individuals (Hess et al., 2015; Ponton et al., 2013; Stahlschmidt et al., 2015). Given that the carabids used in our tests were wild caught, their individual immune traits might differ based on their previous encounters with pathogens. Exposure to pathogens, therefore, provokes individual immune traits and changed energetic requirements that may, in turn, explain individual levels of choosiness. Moreover, studies on carabid immunology also shows that males and females can differ in their total immune activity (Giglio et al., 2017, 2016). The sex related differences observed in the total number of seed consumed by *H. affinis*, described in Chapter II, might also be explained as sexually dimorphic energy requirements due to sex differences in immune defence characteristics. As immunity can be linked to the quality of an environment and to pesticide use (James and Xu, 2012), better understanding the impact of immune responses on individual choosiness for seeds might improve biological control of weeds by carabids in arable fields.

Personality traits, as defined in Réale, Reader, Sol, McDougall, & Dingemanse (2007), have already been successfully linked to individual foraging behaviour in many taxa (Toscano et al., 2016). Reactive, or shy, individuals are expected to be less likely to expose themselves to predation risk than bold individuals. As predator avoidance and foraging are two conflicting tasks (Sih, 1980), shy and bold individuals might respond differently to predation risk according to their position on the "proactive-reactive" personality axis (Quinn et al., 2012). The existence of personality traits in carabids could therefore explain the between-individual variation observed for behavioural adjustment in our results. The objective of this chapter is therefore to examine three linked expectations that: *i) personality traits exist in carabid beetles; ii) carabid* *individuals differ in overall immune traits, potentially by sex; and, iii) these two different characteristics, of personality and immunity, can explain individual variation in the level of choosiness for seeds of T. officinale*. Given that previous research suggests that both immunity and personality traits may be correlated through a "*Pace of life syndromes*" (Reale et al., 2010), I tested expectation iii) using the characteristics of personality and immunity in combination (interaction) and individually.



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Initially, the aim was to assess individual personality using a behavioural syndrome. Behavioural syndromes are defined by Sih et al. (2004) as a "suite of correlated behaviours reflecting between-individual consistency in behaviour across multiple (two or more) situations". To do this I scored three different behavioural traits: 1) activity; 2) photophobia; and, 3) exploration of a new area (i.e. neophobia). The results were not conclusive, however, with no clear syndrome being apparent that could provide insight into the foraging behaviour of carabids. The methods and results for the two traits of activity and photophobia were removed from the study, as it was decided to assess personality using only the exploration behavioural trait (see (Toscano et al., 2016)). I report the results for the activity and photophobia in the supplementary materials of this chapter, in the hope that they might be useful for future studies assessing carabid personality and foraging.

I would also note that the assessment of foraging presented in this chapter was originally planned differently. Initially, I wanted to analyse the potential variation in an individuals' level of choosiness by comparing latency to first seed acceptance, between control and predation treatments following the methods developed in Chapter II and III. However, there was a marked lack of response among the individuals in the control treatment: only 7% of the individuals ate during the test. It was therefore decided to analyse only the results for the predation treatment using the measures of individual level of choosiness under predation risk.

2) Article 3

The variability in foraging strategies is better explained by sex than by immunology or personality traits in carabids

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ABSTRACT

Individuals of the same species can vary significantly in their foraging behaviour, showing consistent patterns across contexts that are termed personality. Individually-based traits, such as physiology, body size, sex and levels of immune defence are expected to shape individual foraging behaviour. *The Pace of Life Syndrome* (POLS) hypothesis posits that individual physiological, life history and personality traits are intimately linked. For instance, explorative individuals that forage more widely encounter parasites more often thus necessitating better immune defences and a food intake to support it. Here we test in a granivorous model species, the carabid beetle *Harpalus affinis*, if patterns of weed seed foraging can be predicted from i) their personality scores; and, ii) their levels of immune response. Total distance travelled and space use were used as repeatable personality traits. Our experimental investigation provides no evidence of a quantitative link between foraging behaviour and personality. In addition our results suggest that personality and immune response are independent of one another in *H. affinis*, providing no support for the POLS. Female *H. affinis* had consistently greater immune response and ate more seed than males. These findings of sexual dimorphism in the immune response appear consistent with Bateman's principle that females increase their fitness through longevity by investing more in immunity than males, necessarily supporting this investment with higher amounts of food eaten.

Keyword

Foraging, Insect immunity, Personality, Pace of life syndrome, Carabids

A. INTRODUCTION

It is now recognised that individuals from the same species and the same population can vary significantly in their foraging behaviour in the same environment (Clark and Ehlinger, 1987; Wilson, 1998). This between-individual behavioural variation has been explained either as simple variation around an adaptive mean (Stephens and Krebs, 1986) or as the result of the inherent stochasticity of the environment in which individual are observed (Clark and Ehlinger, 1987; Monceau et al., 2017a). These systematic differences could also be explained by a fast-slow continuum of life-history variation. Fast life strategy favour rapid growth and early reproductive effort at the cost of elevated mortality. Slow life strategy, conversely, is based on delayed reproduction, if it comes with higher risk of mortality (Nakayama et al., 2017; Reale et al., 2010). According to their life-history strategy, individuals would differ in their foraging effort (Abrams, 1991). As reproductive success is conditioned by feeding input (Fawki and Toft, 2005; Jorgensen and Toft, 1997; Kulkarni et al., 2015b; Wallin et al., 1992), fast-living individuals should accept to forage in higher risk situations than slow-living individuals (Abrams, 1991).

Differences observed in individuals foraging behaviour, could solely be explained by differences in individually-based physiological characteristics or by other individual traits such as body size and sex (Cords, 1986; Kulkarni et al., 2015b; Pyke, 1984). For example, the maintenance of elevated levels of immune defence requires considerable energy resources to maintain, and might this lead individuals to adjust their foraging behaviours in order to satisfy their energetic needs (Ponton et al., 2013). Foraging behaviour could thus be the direct consequence of individual levels of satiation that can differ between individuals. As the level of hunger of a foraging individual increases, the level of risk that it is willing to accept might also increase, leading hungry individuals to invest more energy in foraging or spend more time foraging in risky habitats (Cartar, 1991; Croy and Hughes, 1991; Godin and Crossman, 1994).

The Pace-of-Life Syndrome hypothesis (POLS) suggest that life-history strategy of individuals would be linked to physiological characteristic such as metabolic, hormonal, immunity traits. Life-history strategy would indeed results from ecological conditions in which individuals live. Tropical birds, for example, were shown to have a slow-life history strategy (small clutch, slow development, etc.) concurrent with a low metabolic rate (Wiersma et al., 2007). More recently, suggestion were made that individual behavioural traits could be linked with the POLS hypothesis (Reale et al., 2010). Between individuals behavioural differences have become the focus of considerable interests in recent behavioural ecology literature (*see* Réale et al., 2007 *for a review*). Repeatable patterns of individual behaviours, consistent over time and across context, have been found in a wide range of animal taxa and have been termed ‘personality’. One of the main studied personality continuum is the *bold-shy personality axis*. The personality score along this continuum of an individual is expected to determine its foraging behaviour (David et al., 2011; Toscano et al., 2016). As they would be more risk prone than shy individuals, bolder individuals would more often accept to forage in high risk habitats (Griffen et al., 2012). These high risk habitats often differ from low risk ones in available food resources (Godin, 1990; Houtman and Dill, 1998; Marín et al., 2003). Personality score measured in non-foraging context would help to predict the foraging activity of an individual predator (Toscano et al., 2016). However, since shy individuals are consistently more neophobic, slower to explore and more risk averse than bold individuals, behavioural traits were also suggested to be correlated with individual life-history traits. It is, however, still unclear how strongly individual personality and physiological characteristics are connected in a generalisation of life history traits (Reale et al., 2010). Immune defence is expected to be linked to personality because bolder individuals should encounter parasites more often than shy individuals (Barber and Dingemanse, 2010; Reale et al., 2010) since their relative activity would be higher. Thus, immune response and personality might be hypothesised to form a syndrome of characteristics that together overall impact individual behaviour and hence foraging. To date, however, tests for the presence and effects of the POLS on behaviours have produced equivocal results (Jacques-Hamilton et al., 2017; Monceau et al., 2017a; Niemelä et al., 2013).

Carabid communities of species, like *H. affinis*, can consume a substantial number of weed seeds (Frank et al., 2011; Honek et al., 2003; Menalled et al., 2007; Thiele, 1977; Ward et al., 2014) and are thus considered as credible biological control agents of weeds. However, individuals carabids’ feeding rates, when measured in laboratory studies, are highly variable. High standard deviation or standard error values (i.e. dispersion of individual observations around the population mean) suggest high variation in individuals foragers consumption rates in studies (e.g. Honek et al., 2006, 2003; Petit et al., 2014). To date, and to the best of our knowledge, there has been no study of personality in carabids. As both personality traits and individuals level of immune defenses could explained individual variation in foraging behaviour, better understanding the personality and physiological underpinnings of the differences in foraging observed in the fields could help to improve the biocontrol of weeds by carabids. In this paper, we assess the relationship between the foraging behaviour of individuals of the seed eating carabid, *Harpalus affinis* (Schrank, 1781), which is a potentially important biocontrol agent of weeds in arable fields, and their personality and/or immune characteristics. Foraging behaviour was assessed as the individual levels of choosiness for weed species, which has been shown to vary with environmental conditions such as the presence of predator cues (see Chapter II). The personality of individual foragers was evaluated as the repeatability of exploration behaviours across the test arena i.e. distance travelled and space use (Royauté and Pruitt, 2015). Finally, the immune response of an individual was measured using the prophenoloxidase (PPO) system.

B. METHODS

a. Study system

All carabids used in tests were wild caught individuals collected during spring and summer 2016 using pitfall traps on the INRA experimental farm at Epoisses (Côte d'Or, France; 47°14'11.4"N 05°05'53.4"E). Individuals were kept in plastic boxes (34 x 19 x 11 cm length x breadth x height) for a minimum of two weeks prior to experimentation. The boxes were kept in temperature- and light-controlled conditions (19°C +/- 1°C, 60% humidity, 14:10h light:dark cycle). Each box contained a few centimetres depth of soil and some moistened paper tissue to maintain high humidity and provide the carabids with shelter. Carabids were provided with water *ad libitum* in an Eppendorf containing moistened cotton wool. All boxes contained individuals of only one species of carabid to prevent interspecific predation (Currie et al., 1996). Boxes of *H. affinis* and the omnivore *P. melanarius* were maintained in separate rooms to prevent any possible effects of chemical cues prior to experiment (see Chapter II). *H. affinis* were fed with seeds of four weed species (i.e. *Taraxacum officinale*, *Viola arvensis*, *Senecio vulgaris*, *Capsella bursa-pastoris*). *P. melanarius* individuals were presented with *Tenebrio molitor* larva and frozen beef as an additional meat diet. Seeds used in test were collected locally and were soaked in clean water for 14 hours prior to each experiment, to become more palatable to and detectable by carabids (Law and Gallagher, 2015).

b. Experimental chronology and morphological measurement

Experimental measurement commenced with the assessment of personality in *H. affinis*. Once completed for all individuals we started the assessment of the foraging behaviour of all individuals. Individuals were house individually between the two behavioural experiments.

After the last behavioural experiment, hemolymph samples were collected from each individual to measure their immune response parameters.

All individuals were measured and sexed after their death to limit handling-stress effects on the experimental results. The sexes were identified using protarsi, which are dilated and have hairy undersides in males (Lindroth, 1974). In the carabids, elytra length is a good invariant indicator of body size (Juliano, 1986). The elytra lengths of all carabids was measured under a binocular microscope (Zeiss Stemi ® 2000-C, magnification x10, accuracy: ± 0.05 mm).

c. Assessment of individual personality

The personality of 110 individuals was assessed by looking at their exploration behaviour on a test arena made out of a white plastic board square of 160x160 cm. Twenty four hours before their first test, individuals were isolated in plastic petri-dishes (9 cm diameter) with few centimetres depth of soil and some moistened paper tissue to maintain high humidity and provide the individual with a shelter. Prior to the test, the focal carabid individual was acclimatized within the arena under a plastic pot for 2 minutes, in order to reduce stress due to manipulation, before the pot was removed and the recording of the behaviour began. Trajectometry data were recorded for 10 minutes using a monochrome camera (IMAGINGSOURCE – model: DMK 31AU03) suspended overhead the arena and connected to a computer. Distance travelled by the individuals (in cm) and the percentage of space explored by the individuals was then analysed using Ethovision software (Noldus Information Technology, Wageningen, The Netherlands) by dividing the arena into 1 cm x 1 cm squares (corresponding to the average *H. affinis* body length ~1cm) and scoring the number of square visited at least once as a proportion of the total number of squares in the arena (a method adapted from Chapter II). The exploration rate and the total distance travelled by an individual were used as proxies of its boldness-shyness continuum score. Individuals exploring more, moving on greater total distance and/or having greater space use were defined as more proactive (i.e. bolder) and individual exploring less were defined as reactive (i.e. shy) individuals (Royauté and Pruitt, 2015). The full arena and all equipment was cleaned with alcohol in between experimental replicates to prevent interaction with odours along successive tests (Blubaugh et al., 2017; Guy et al., 2008, see Chapter II & III). To assess behavioural repeatability, the exploration test was repeated once for each individual with a 6 days interval between the two sessions. No resource (water or food) was provided within the test apparatus. The test were performed in a different room to avoid perturbation due to chemical cues, but temperature and humidity conditions in test were the same as those used for in insect rearing and individuals were only tested in the afternoons and kept in their individual box in between repetition.

d. Evaluating foraging behaviour

Following the protocol developed by Charalabidis et al. (see Chapter II), foragers were individually tested in a circular 18cm diameter arena. The bottom of each arena was made of a white filter papers previously impregnated with *P. melanarius* chemical cues to simulate a predation risk situation. Previous work has shown that *H. affinis*, subjected to the risk of predation while foraging, reduce their level of choosiness and thus increase their feeding rate while foraging under a risk of predation (see Chapter II). This allowed us to assess individuals level of choosiness still using a short test duration (one hour). Papers were impregnated using a method developed by Armsworth (2005) and Guy, Bohan, Powers, & Reynolds (2008) (see Chapter II & III). Walking carabids release cuticular hydrocarbon chemicals cues along their path of movement (Armsworth, 2005; Guy et al., 2008). Test papers impregnated with predator cues were created by allowing 20 individual beetles of *P. melanarius* (10 females, 10 males), an obligate omnivore and carabid interspecific predator (Currie et al., 1996), to walk over white filter papers (Dutscher, Brumath, France) for a minimum of 24 hours. Once created, two concentric circles of 5 and 16 cm diameter were inscribed in pencil on the test papers, around which 20 seeds of *T. officinale* were evenly arranged. In order to standardize the feeding motivation, all carabids were starved for 54 hours prior to the experiment. The focal carabid individual was acclimatized under a plastic pot at the centre of the arena for 8 minutes. At the start of the experiment, the pot was removed and an inverted 18 cm diameter Pyrex petri dish bottom immediate placed over the arena to delimit and isolate the arena from external perturbations. Individuals level of choosiness were measured by looking at the latency before an individual first seed acceptance. Test papers were used for only one repetition. Petri dishes were washed in a medical dish-washer between repetitions to prevent interaction with odours along successive tests (Blubaugh et al., 2017; Guy et al., 2008, see Chapter II).

e. Measurement of the immune response

Once the foraging tests were completed, we measured three key insect immune parameters (Monceau et al., 2017a) from all test carabids: (i) the concentration of circulating hemocytes; (ii) the phenyloxidase (PO) activity; and, (iii) total-PO activity. Each individual was chilled on ice for 20 min, and 1.37 (±0.77) µl of hemolymph was first extracted with a sterile glass capillary tube (Hirschmann Laborgeräte, Eberstadt, Germany) from a wound made in a soft part not protected by the exoskeleton between the head and thorax. The extract was diluted immediately in 20 µl of cold sodium cacodylate/CaCl2 buffer (0.01 M sodium cacodylate, 0.005 M CaCl2; pH 6.5). A 10 µl sample of this solution was immediately removed for the counting of haemocytes. The remaining solution was stored at -27°C for measurement of the enzymatic activity of the prophenoloxidase (PPO) system.

The concentration of haemocytes was measured immediately after hemolymph extraction. This measurement was done using a Neubauer Improved Haemocytometer under phase contrast microscopy (magnification x 400), as described in Vogelweith et al. (2011). The activity of the PPO system was estimated by measuring the enzymatic activity of naturally activated PO enzymes (PO activity), and the activity of the proenzyme (PPO) together with that of the activated PO (total-PO activity). These measurements were based on a spectrophotometric assay described by Vogelweith et al. (2014, 2013, 2011).

f. Statistical analysis

The data were analysed in R version 3.3.2 (R Core Team 2016). Difference in size between sexes was analysed using a t-test. Repeatability of the behavioural measures for personality assessment were tested using the intraclass correlation coefficient (Nakagawa and Schielzeth, 2010). Correlation between the behavioural traits (i.e. total distance moved and space use) was assessed with a spearman correlation. Effects of sex and size of individuals on their behavioural traits were analysed using ANOVA. In order to avoid inflation of type I error arising from multiple comparisons, we estimated a synthetic immune score using PCA. Effects of sex and size of individuals on their immune traits, i.e. numbers of hemocytes, PO and total PO-activity (PPO) and their immune score were analysed using ANOVA.

All results for the latency to first seed acceptance were analysed using Cox proportional hazard models in the ‘cox.ph’ function from the package ‘survival’ (Therneau, 2006). This model allows censored data (when the observed behaviour happens after the end of the experiment duration). Proportional hazards assumption were assessed using the ‘cox.zph’ function. Effects of sex and size of individuals on the proportion of individuals eating during the test were analysed using a generalized linear model with a binomial distribution. Link between immune traits, individuals’ personality and proportion of individuals eating during the test was analysed using a generalized linear model assuming a binomial distribution.

C. RESULTS

a. Morphological traits

In average, females were larger than males (females mean elytra size: 7.43 mm [7.31, 7.55], males mean elytra size: 6.98 mm [6.86, 7.09], (t = 5.429, df= 95.611, P < 0.001).

b. Behavioural traits

Considering all the data pooled together regardless of the sexes, all traits were found repeatable (Table 2).

Table 1: Repeatability of behavioural traits. Repeatability was assessed by the interclass correlation coefficient and 95% intervals (in brackets) for the four behavioural traits. Traits which intervals do not cross 0 are significantly repeatable (bold).

Behavioural traits	Repeatability
Distance total moved	R= 0.59 [0.444,0.707]
Space used	R= 0.48 [0.334,0.624]

There was no effect of the size of individuals on their behavioural traits (Generalized linear model, distance total moved: χ^2_1= 57051, P= 0.77, Space usage: $\chi^2_1 = 4.57 \times 10^{-5}$, P= 0.70) nor effect of the sexes of individuals on the total distance moved (Generalized linear model, distance total moved: χ^2_1= 206883, P=0.58, Space usage: χ^2_1= 7.06×10^{-5}, P=0.63). There was no interactions between sexes and size of individuals (Generalized linear model, distance total moved: $\chi^2_1$83418, P= 0.73, Space usage: $\chi^2_1 = 2.54 \times 10^{-5}$, P=0.77). Distance moved and space used were highly correlated (Spearman correlation ρ = 0.96) hence only the total distance moved as used as individual behavioural trait.

c. Immune traits

Females had significantly more hemocytes than males (Generalized linear model, χ^2_1=2015.9, P = 0.038, Table 1). There was no effect of the size of individual on their number of hemocytes (Generalized linear model, χ^2_1=168.41, P=0.55) and no interaction between sexes of individuals and their size on their number of hemocytes (Generalized linear model, χ^2_1=

351.43, P=0.39). There no effect of the sex of individuals (Generalized linear model, χ_1^2=47985, P=0.09, Table 1) or of their size (Generalized linear model, χ_1^2=657.02, P=0.84) on their PPO. There was no sex and size interaction on the PPO of individuals (Generalized linear model, χ_1^2= 67.06, P=0.95). Similar results were observed for PO with no effect of the sex (Generalized linear model, χ_1^2=1839.6, P=0.48) or the size (Generalized linear model, χ_1^2=450.89, P=0.73) of individuals and no sex and size interaction (Generalized linear model, χ_1^2=438.46, P=0.73).

Table 2: Mean number (bootstrapped 95%CI) of hemocytes and PPO for females and males in *H. affinis* carabids.

	Females	Males
Hemocytes	39.3 [32.2, 47.4]	29.3 [23.8, 35.3]
PPO	172 [126, 227.7]	113.4 [85.9, 146]

The first axis of the PCA explained 57 % of the total variance. PO and PPO mostly contributed to the first axis of the PCA (Table 2), while total number of haemocytes contributed to the second axis of the PCA.

Table 3: Loading of the three immune traits on to the two principal components. The immune score used to characterize the individual immune score was derived from the first principal component (PC1)

	PC1	PC2
Haemocytes	0.35	-0.94
PO	0.67	0.26
PPO	0.67	0.23
Percentage of variance explained	0.57	0.30
Eigenvalue	1.30	0.95

The immune score (PC1) was not explained by individuals' body size (Generalized linear model, χ_1^2= 0.25, P= 0.69). There was no effect of the sexes of individuals on their immune score (Generalized linear model, χ_1^2= 4.00, P = 0.12) and there was no interaction between the sexes and the size of individuals on their immune score (Generalized linear model, χ^2_1=0.29, P= 0.68).

d. Foraging behaviour explained by morphological, immune or personality traits

The proportion of individuals eating at least one seed during the experiment is higher for females than males (Generalized linear model, χ^2_1= 7.20, P = 0.0073, Fig. 1a). There was no effect of the size of individuals on the proportion of individuals eating (Generalized linear model, χ^2_1 = 0.007, P = 0.93) and no interaction between sexes and size (Generalized linear model, χ^2_1 = 0.39, P = 0.53). There was no effect of females' size on their willingness to consume a seed during the experiment (Generalized linear model, χ^2_1=0.033, P= 0.856). Same for the males (Generalized linear model, χ^2_1= 0.37, P= 0.54). Females accepted they first seed earlier than males (Cox model, χ^2_1= 6.93, P=0.0085, hazard ratio = 5.7, 95%CI [1.25, 26.07], Fig. 1b). There was no effect of the size of individuals on their latency to first seed acceptance (Cox model, χ^2_1= 0.048, P = 0.83) and there was no interaction between the sexes of individuals and their size (Cox model, χ^2_1 = 0.31, P=0.57).

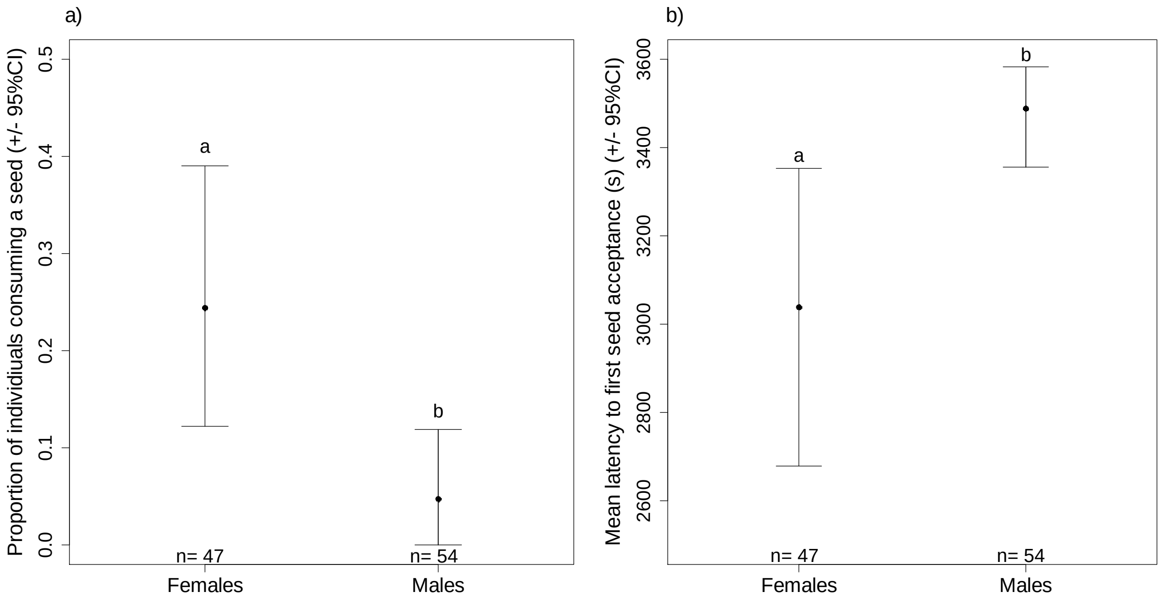


Figure 1: A) **Proportion of individuals (bootstrapped +/-95%CI) eating at least one seed during the test.** B) **Mean latency to first seed acceptance (bootstrapped +/- 95%).** Different letters correspond to statistically significant difference between treatments (post-hoc pairwise comparison with Tukey adjustment for multiple comparisons). The sample sizes are shown above the x-axis.

The proportion of individuals eating was not explained by individuals immunity score (Generalized linear model, χ_1^2= 1.55, P=0.21, Fig 2a). There was no interaction between sexes of individuals and their immune score and the proportion of individual eating (Generalized linear model, χ_1^2= 0.018, P = 0.89). Latency before first seed acceptance was also not explained by individuals' immunity score (Cox model, χ_1^2=1.39, P= 0.24, Fig 2c). There was no interaction between sexes of individuals and their immune score on their latency to first seed acceptance (Cox model, $\chi_1^2 = 5 \times 10^{-4}$, P=0.98).

Individual's personality traits were not correlated to the proportion of individuals eating (Generalized linear model, χ_1^2=0.28, P=0.59, Fig 2b). There was no interaction between individual behavioural traits and individual sexes (Generalized linear model, $\chi_1^2 = 3.59 \times 10^{-6}$, P = 0.99). Latency before first seed acceptance was also not explained by individuals' personality traits (Cox model, χ_1^2=0.33, P=0.56, Fig 2d). There was no interaction between sexes of individuals and their immune score on their latency to first seed acceptance (Cox model, χ_1^2=0, P=0.99).

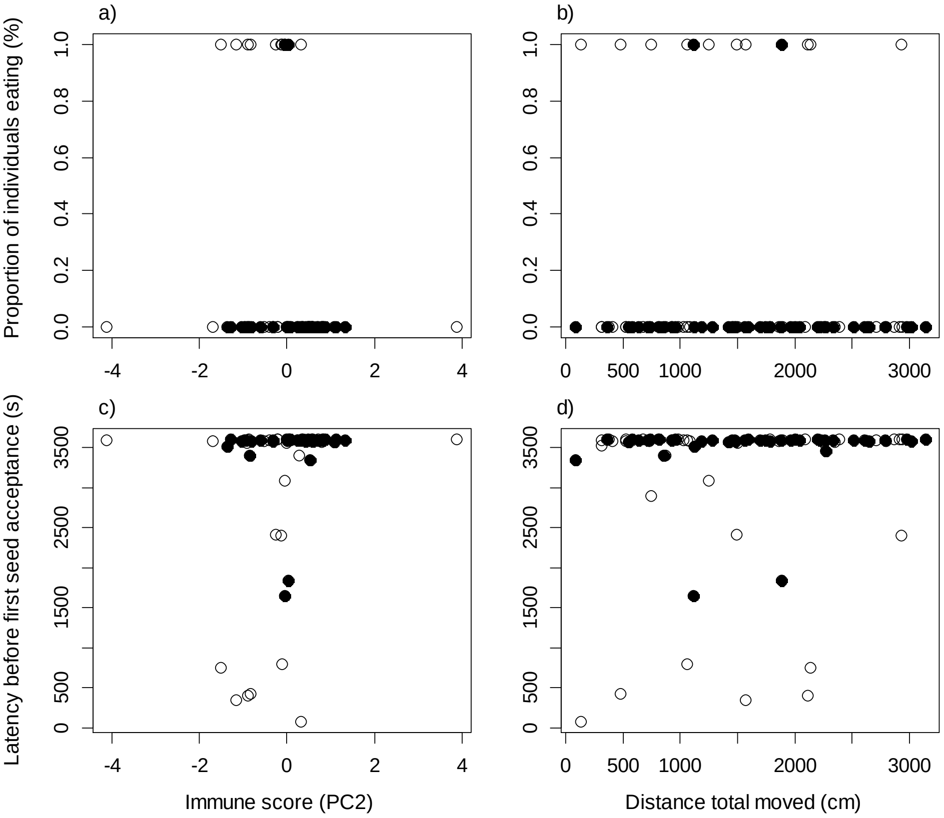


Figure 2 : Relationships between the proportion of individuals eating during the test and **a)** their immune score or **b)** their personality and the latency to first seed acceptance of individuals and **c)** their immune score or **d)** their personality. High immune score implies high PO-PPO and hemocytes concentration. Proactive individuals have higher distance moved while reactive ones have lower distance moved. Females are in white dots (○) and males in black dots (●). 95% confidence interval, in grey, are for both sexes combined.

e. Link between individuals personality and basal immune parameters

There was no correlation between individuals personality and immune score (Generalized linear model, χ_1^2==611.13, P= 0.98, Fig 3). There was no effect of the sexes of individuals (Generalized linear model, χ_1^2==2425.5, P=0.95) nor interactions (Generalized linear model, χ_1^2=X=717502, P=0.31).

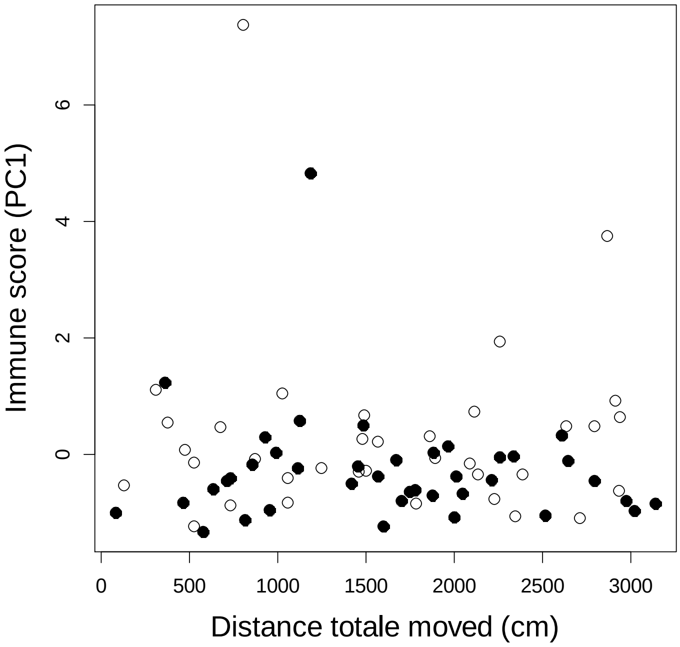


Figure 3: Relationship between the personality of individuals and their immune score. High immune score implies high PO-PPO and hemocyte concentrations. Proactive individuals have higher distance moved while reactive ones have lower distance moved. Females are in white dots (○) and males in black dots (●). 95% confidence interval, in grey, are for both sexes combined

D. DISCUSSION

Individual personalities and immune responses did not appear to drive foraging in *H. affinis,* at least for the choosiness metric for foraging used in our experiment. We did not found any quantitative link between either of these two individual characteristic and individual foraging behaviour. Therefore, neither personality traits nor immune responses could be used in order to predict *H. affinis* individuals foraging behaviour. The measured immunological and personality characteristics also appear to be independent of one another, and provide no support for the pace of life syndrome hypothesis.

We did find qualitative effects, however. Personality was evident in the repeatable patterns of distance total travelled and space used by *H. affinis* individuals. Female *H. affinis* also had consistently greater amounts of hemocytes and significantly lower choosiness for seeds of *T. officinale than* males. Higher investment in immune components by females has already been observed in other insect species (Vogelweith et al., 2017). Rolff (2002) interpret this result in the light of the 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. Our findings of sexual dimorphism in the immune response appear consistent with this difference in reproductive strategies between males and females. A greater immune response is energetically costly, and thus requires larger food intakes (Ponton et al., 2013). Such difference in reproductive perspectives could also explain the differences in the foraging behaviour between sexes. Female insects invest higher energy resources in eggs production than males in sperm production (Hayward and Gillooly, 2011). The number of eggs produced is thus linked to the amount of food available in carabids (Currie et al., 1996; Juliano, 1986; Murdoch, 1966). The seed diets of females carabids has effects on the survival and overall growth of their offspring (Saska, 2005; Saska and Jarošík, 2001). This important requirement for seeds might explained why females had lower level of choosiness for seeds than males, regardless personality or immune traits. Higher consumption in females might also simply result from their larger body size in comparison to males. This is, however, unlikely since no link was found in this experiment between the size of individuals and their foraging behaviour (neither for the all population tested nor for females alone). Difference between sex might also be explained by a seasonal variation in seed predation by carabid beetles (Honek et al., 2006). *Harpalus affinis* is a spring breeder and our tests were carried in early fall. Individual propensities to eat has been observed to decrease slowly after July, which might explained why a large number of individuals did not eat during our experiment (Honek et al., 2006), females might forage with a lower choosiness than males during this post-July period to maximise food intake before hibernation (Baranovska et al., 2014; Lövei and Sunderland, 1996).

Although personality traits in carabids could not be linked with individual choosiness, it would be interesting for further studies to assess a potential link between personality and spatial or temporal (across day time) distribution pattern of carabids in arable fields. For now the distribution and abundance of carabids was shown to depend on many factors such as temperature, humidity, food availability, food preferences and life history traits (Lövei and Sunderland, 1996). Other anthropogenic factors such as intensity of crop management (Holland and Luff, 2000), agricultural practices (Miñarro et al., 2009) as well as the structure and dynamics of landscape (Burel and Baudry, 1995; Varchola and Dunn, 2001) also affect the abundance and composition of carabids communities in semi-natural environments. Personality, and more specifically boldness, was shown to be linked with individual propensity to spread out in their environment (Toscano et al., 2016). Also, as bolder individuals might have access to relatively more good quality items as their use of space would help lowering competition (Guy et al., 2008), personality could also impact condition factor of wild caught carabids.

E. ACKNOWLEDGEMENTS

The authors would like to thank Aurelie Tasiemski and her PhD student for their help with immunity levels assessment in our carabids. We also wish to thank the staff at INRA Dijon and INRA experimental farm for their technical support, and Benjamin Carbonne for his help with trapping and handling the carabids. The PhD of Alice Charalabidis was co-funded by the Institute Nationale de la Recherche Agronomique (INRA) and the Region of Burgundy Franche-Comté. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

F. SUPPLEMENTARY MATERIALS

Assessment of the existence of a behavioural syndrome in *H. affinis* individuals

a. Methods for Activity and photophobia assessment

Activity test:

The arenas were made of a 4 cm diameter plastic tube fixed upside down in the center of a 18 cm diameter pyrex petri dish bottom, to form a 7 cm-wide pathway between the sides of the dish and the plastic tube. This arena was then inverted over a clean paper sheet on which a circle of 18 cm diameter was drawn, divided into eight equal radial sectors (Fig. S1). Tested carabids were released after and acclimatization period of 2 minutes. The number of transitions between sectors was recorded during 5 min as the individual score of activity. To prevent bias caused by chemical cues left on the papers, test papers were used for only one repetition. Between repetitions, the petri dishes were washed in a medical dish-washer and the aluminium bench was cleaned with alcohol.

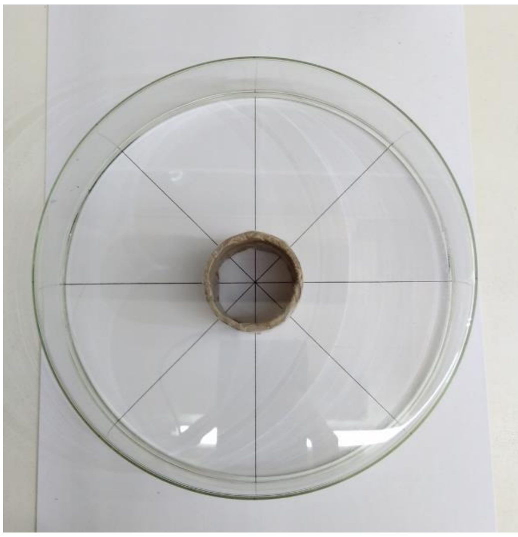


Figure S1: Picture of the experimental set-up used in activity test.

Photophobia test:

The arena was made using a closed Pyrex petri dish of 18 cm diameter. Pyrex is extremely slippery. The bottom of the arena was therefore lined with a plastic foil to improve carabids locomotion. The arena was divided in two equal halves, through the centre of the dish. One of halves was lined with card to completely block light entry and create a ‘dark’ half. The other side was left transparent and was illuminated during the test. Tested carabids were released after and acclimatization period of 2 minutes in the 'light' half. The location of the individual in either the dark or light half was scored at 10 sec, after the start of the experiment, and then every 30 sec, for 7 min and 40 sec to give a total of 16 time points.

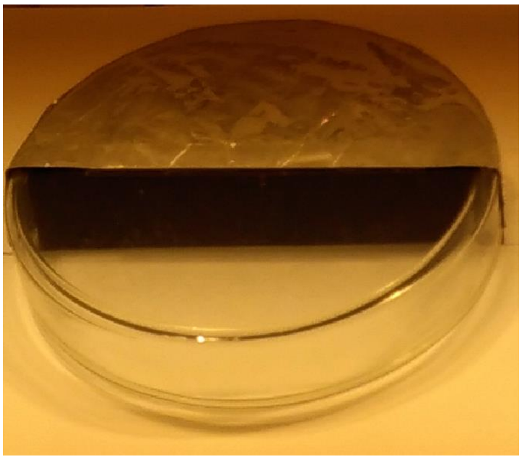


Figure S2: Picture of the experimental set-up used in photophobia test

b. Results for the behavioural syndrome assessment

Repeatability of the behavioural traits

Table S1: Repeatability of behavioural traits. Repeatability was assessed by the interclass correlation coefficient and 95% intervals (in brackets) for the four behavioural traits. Traits which intervals do not cross 0 are significantly repeatable.

Behavioural traits	**Repeatability**
Activity	R= 0.67 [0.564,0.763]
Distance total moved	R= 0.59 [0.444,0.707]
Space used	R= 0.48 [0.334,0.624]
Photophobia	R= 0.44 [0.27,0.59]

Correlation between the behavioural traits

Table S2: Correlations between the behavioural traits used to define the behavioural types. Spearman correlation (rho) with 95% confidence interval between the four behavioural traits.

	Distance total moved	Space used	Photophobia
Activity	0.22	0.18	-0.19
Distance total moved		0.96	-0.17
Space used			-0.17

Behavioural syndrome assessment

Table S3: Loading of the four behavioural traits on to the three principal components

	PC1	PC2	PC3
Activity	0.24	0.67	0.69
Distance total moved	0.67	-0.24	0.02
Space used	0.62	0.25	-0.01
Photophobia	-0.25	-0.65	0.72
Percentage of variance explained	0.52	0.27	0.20
Eigenvalue	1.45	1.03	0.90

3) Chapter conclusion

The results of this chapter show that observed differences in choosiness were better explained by sex than by either personality traits or immune characteristics. *H. affinis* females ate more than males, irrespective of the individual personality, size or immune scores.

Females had more hemocytes than males, however, which may explain their overall higher consumption of weed seeds. Correlations between hemocyte levels and foraging behaviour were not significant for the population of individuals in our study. There were significant spearman correlation between individuals levels of hemocytes and individuals choosiness (ρ= -0.32, P= 0.0039), which suggest that immunity can be linked to individual foraging behaviour in *H. affinis*. This suggestion is supported by a significant correlation between immunity and foraging amongst females (ρ= -0.35, P=0.036). Females with higher level of hemocytes appeared to have lower choosiness than females with a lower level of hemocytes. The absence of significance for the population as a whole might result from the low number of individuals that ate seeds during our experiment, i.e. 18%. This result was puzzling, given that in Chapter II more than 60% of individuals ate at least one seed during the 1 hour experiment, when exposed to *P. melanarius* cues. It is possible that this was due to the season in which we tested our individuals. *H. affinis* is a spring breeder and while the tests in Chapter II were obtained between July and early autumn those presented here only started in early autumn, finishing during winter. Individual propensities to eat have been shown to decline after July, which might explain the large number of individuals that did not eat here (Honek et al., 2006).

The observed higher level of hemocytes in females was particularly interesting given that previous studies on *Carabus lefebvrei* did not find any evidence of sexual differences in hemocyte amounts in cell-free hemolymph (Giglio et al., 2016). The study of Giglio et al. (2016) did demonstrate that plasmatic protein content, as a measure of *C. lefebvrei* immune status, can vary with individual reproductive status, both in male and female.

It is also possible that the metrics of foraging behaviour used here do not respond to immunity level, and hence to higher energetic requirement in insects (Ponton et al., 2013). Immunity might have been better explained by the total number of seed eaten by individuals. In the future, it would be valuable to assess how many seeds would be eaten by individuals according to their immunity level, and whether the number of seed eaten per individual changes through season according to reproductive status and immunity level. As immunity in insects can be affected by pesticides use (James and Xu, 2012), linking immunity and number of seeds eaten by a wild caught carabid individual could help understanding the variability in predation rates observed in arable fields (Saska et al., 2008).

On another note, our results also confirmed that personality traits exist in carabids and could be linked to exploration behaviour. Difference between proactive (more explorative, less neophobic) and reactive (shyer, less aggressive, more neophobic) individual may reflect more their strategy of prospection and space use on large scale than their energetic need. Some authors (Royauté and Pruitt, 2015) proposed that between individual differences in personality results from a mechanism of niche construction. Specialization in some foraging strategy does not necessarily reflect difference in energetic requirement but may be a strategy to escape intra-specific competition.

Fifth Chapter

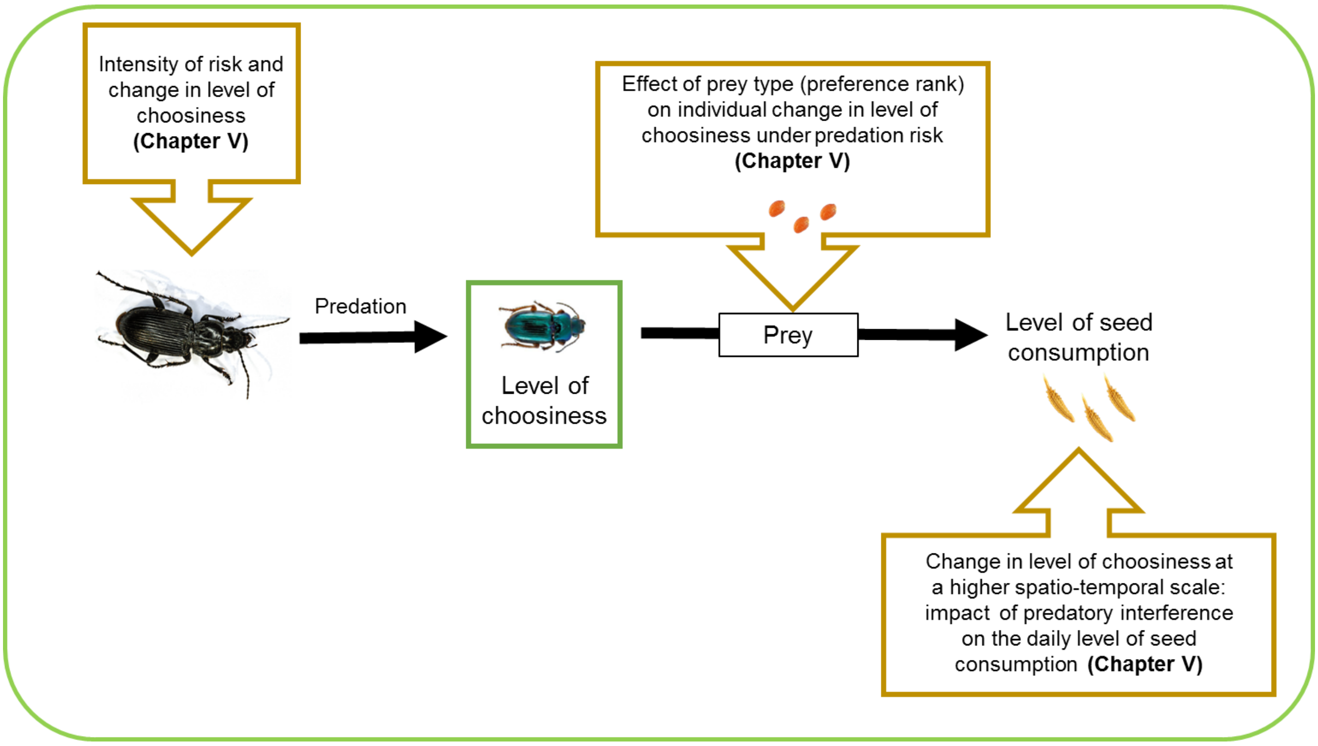
Consistency of the behavioural adjustment to predation risk in more complex, and potentially realistic, spatiotemporal conditions - the effect of the intensity of the risk and seed preference on individual level of choosiness

1) Introduction to chapter V

In Chapter II, I found that *H. affinis* individuals would lower their choosiness when exposed to odour cues from *P. melanarius* individuals, which were used to simulate a risk of predation. This reduction in choosiness led to an increase in the total amount of seed eaten by an individual during the one hour of testing. This result suggests three questions: i) does this reduction in choosiness, observed under predation risk, really induce an overall increase in the total number of seeds eaten by a given individual over a longer time span; ii) will this change in choosiness be observed when individuals are provided with more highly preferred seed species than *T. officinale*; and, iii) will a higher intensity of predation risk, via an actual encounter with *P. melanarius* individuals, produce similar changes in *H. affinis* choosiness?

Overestimating a predation risk will likely be costly for individuals (Abrams, 1994). Individuals might therefore be expected to adjust their behaviour according to the intensity of the risk (Abrams, 1994; Sánchez-González et al., 2017). Olfactory cues are typically considered to provide a lower signal of risk than actual encounter with the predator (Tapia-Lewin and Pardo, 2014), with higher behavioural responses being expected with higher risk intensities (Sánchez-González et al., 2017). Presenting carabid foragers with a higher intensity of the risk, through actual encounters with *P. melanarius* predators, might therefore impact the behavioural adjustment observed in the foraging behaviour of *H. affinis* individuals provoking a different response than was observed with olfactory cues in Chapter II. My hypothesis is that as *both olfactory cues and actual encounters might be used as predation risk cues by H. affinis individuals in the wild but will differ on their impact on individual levels of changes in choosiness.*

Finally, if *H. affinis* level of choosiness is also lowered when exposed to actual encounter with *P. melanarius* individuals, the feeding rate of different seed species should became ever more similar, regardless of their initial relative preference rank. Conversely if choosiness is increased under higher predation risk, only preferred seeds species should be consumed.



This chapter is in preparation for submission to Journal of Pest Science

2) Article 4

Predation risk can increase weed seed consumption by carabid beetles

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In preparation for submission in journal of pest science

ABSTRACT

Carabids beetles are receiving attention as biocontrol agents of weeds that can reduce crop yield by up to 34%. Predicting weed regulation by carabids remains difficult, as laboratory assessments and field measurements of their weed seed diet often do not match. In a previous study, the model carabid granivore, *Harpalus affinis*, was shown to reduce the effort or energy invested in assessing the seeds of *Taraxacum officinale* (choosiness) and eating more seeds in the presence of simulated odour cues from a predator carabid, *Pterostichus melanarius*, in an experiment of limited spatio-temporal scale. Our hypothesis is that the foraging behaviour of carabids will therefore differ with carabid community diversity, potentially explain the difficulty in linking laboratory and field experimental results. Here we test our expectations that *H. affinis* will: i) similarly reduce choosiness in an experiment of larger dimension, and running over several days; ii) respond to the presence of live *P. melanarius* and not just its odour cues; and, iii) show modified choosiness that depends upon its preferences for different species of weed seeds. Our results show that *H. affinis* always ate more seeds of *T. officinale* than *V. arvensis*, thus demonstrating a preference. Choosiness for *V. arvensis* was lowered by direct predator interference interactions, but these effects were limited to females. Our explanation for these results are that: *H. affinis* already have levels of choosiness for *T. officinale* that cannot be lowered further, even under predation; and, that to produce eggs females must foraging even under predation, and so will likely reduce even more markedly their choosiness than males in similar situations of predation. The findings suggest that community composition and diversity can act to modify carabid feeding choosiness and the function of predation rate at larger spatio-temporal scales that more closely mimic the field.

KEYWORDS

Carabids; Weeds regulation; biocontrol; ecosystem service; foraging behaviour, feeding absolute preference, trophic interactions

A. INTRODUCTION

Carabids beetles are receiving ever growing attention as biocontrol agents of agricultural weeds. The ecosystem service of weed seed regulation is particularly important as weeds are responsible for great potential loss in arable crop, with reductions of up to 34% being observed (Oerke, 2006). Although in-field weed seed predation estimates have been related to the abundance of seed-eating carabids, predicting weed regulation effects remains difficult in practice.

The observed variation in in-field predation rates stems in part from marked differences in carabid feeding preferences between different species of weeds, which have been reported from laboratory choice-test studies (Honek et al., 2011, 2007, 2006, 2003; Petit et al., 2014). However, specific associations between carabid and weed species are only partially documented, and the estimates of preference derived from choice tests rarely match the realised choices of carabids observed (Petit et al., 2014). To date, it has been difficult to infer the level of weed seed predation, and consequently the service of weed regulation, which can be delivered by the in-field community of carabid beetles.

Predation interference interactions occur widely within carabid communities in arable fields (Blubaugh et al., 2017; Currie et al., 1996; Kamenova et al., 2015; Wyatt Hoback et al., 2001), but beyond the simple trophic effect of predation, the wider ecological consequences of these interactions have rarely been examined. Predator interference could affect the rates of consumption by foraging individuals (Blubaugh et al., 2017; Sivy et al., 2011; Wyatt Hoback et al., 2001), modifying the selection and consumption of particular food resources (Blubaugh et al., 2017; Ibrahim and Huntingford, 1989; Metcalfe et al., 1987b; Sih, 1980). These findings would suggest that the foraging behaviour of a carabid individual, and thus the level of weed consumption observed, might also be determined by the predation interference it experiences, and thus the composition of the carabid community in which it resides.

In a previous study, we reported on the foraging behaviour of the granivore carabid *Harpalus affinis* (Schrank, 1781), measured under a predation risk, simulated using chemical cues from a predator, at a fine-temporal scale in experimental arenas of 16 cm diameter arenas over one hour (see Chapter II). We observed that both males and females *H. affinis* not only reduced the effort they invested in assessing seeds of *Taraxacum officinale* (Weber) as food resources (choosiness, *sensu* Jennions and Petrie 1997) in the presence of odours of a predatory carabid species, *Pterostichus melanarius,* but also consumed more seeds. This suggested both that mixed communities of carabids, containing foragers and their predators, will lead to changes in foraging patterns and that this could serve as a mechanism of biodiversity-ecosystem functioning whereby increases in the diversity of the carabid community leads to increases in the ecosystem function of total seeds consumed.

The limited, laboratory scale of these findings poses a series of questions that we address in this paper. Specifically, we report on expectations that: i) the reduction in the choosiness for *T. officinale* recorded for *H. affinis* at very fine spatial and temporal scale will be observed in an experimental setting of larger dimension and over the course of several days; ii) the behavioural adjustment observed in response to chemical cue can be observed with the use of live predators, in place of simulating predation risk using odours, and that this is more intense because an actual encounter with a potential predator will induce a more acute perception of risk than chemical cues alone (Tapia-Lewin and Pardo, 2014); and, iii) weed seed preference impacts individual willingness to accept risks of predation and therefore choosiness between species of weed seeds that have different preference values.

We also hypothesise that the sex status of an individual will modulate the behavioural adjustment to the predation risk (Herberholz and Marquart, 2012). Female *H. affinis* have already been observed eating more weed seeds than males in studies, in a manner that is consistent with an expectation of higher energetic requirements (see Chapter II). Any reductions in energetic inputs could therefore have a strong impact on individual fitness as it would decrease the number of eggs produced and reduce the survival time of larvae (Jorgensen and Toft, 1997; Saska, 2005; Saska and Jarošík, 2001; Wallin et al., 1992). Females *H. affinis* might therefore react quite differently to predation risks than males, potentially adopting even lower levels of choosiness in their foraging behaviour. We thus expect to see differences in individual response, between the sexes and that the response will co-vary the weed seed species offered in test.

B. METHODS

a. Study systems

Both species of carabids used in test were collected using pitfalls traps at the INRA Experimental Farm (Dijon, France; 47°14’11.4”N 05°05’53.4”E) between April and June 2017. Carabids were identified and sorted by species into plastic boxes (34 x 19 x 11 cm for granivorous species and 80 x 55,9 x 15,5 cm for carnivorous species) where they were maintained in a climate-controlled chamber under temperature- and light-controlled conditions (18 ± 1 °C, 60% humidity,14:10h light:dark cycle). Species where held in different boxes to prevent interspecific predation (Currie et al., 1996) and in different rooms to prevent exposition to chemical signatures for at least 2 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. The *H. affinis* individuals were fed with seeds, in an equal mixture of four weed species: *V. arvensis* (0.9mg, 1.36mm), *T. officinale* (0.7 mg, 2.67mm), *Senecio vulgaris* L. (0.2 mg, 1.75 mm), *Capsella bursa-pastoris* (L.) Medik. (0.1 mg, 0.8mm). The *P. melanarius* individuals were fed with frozen mealworms (*Tenebrio molitor*) and pre-moistened dry cat food.

62 hours prior to the experiments, individual *H. affinis* were isolated in round plastic containers (9 cm diameter) and deprived food to standardize 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.*

b. Behavioural experiment

To test our hypothesis, 120 individuals of *H. affinis* were tested under four different treatments: i) *H. affinis* foraging for seeds of *V. arvensis* in the presence of *P. melanarius* (n= 30, sexes evenly distributed); ii) *H. affinis* foraging for seeds of *T. officinale* in the presence of *P. melanarius* (n= 30, sexes evenly distributed); iii) *H. affinis* foraging alone with seeds of *V. arvensis* (n= 30, sexes evenly distributed); and, iv) *H. affinis* foraging alone with seeds of *T. officinale* (n= 30, sexes evenly distributed).

Tests were conducted in plastic trays of 80 x 60 x 15 cm divided by plastic exclusion barriers to form 3 different compartments: 2 external compartments of about 20 cm width and an internal compartment of about 40 cm width (Fig. 1). Based on preliminary measurements made on individual *H. affinis*, holes of 4 mm in diameter, made in the barriers every 2 cm, would allow only *H. affinis* (10-12 mm) to pass freely through the barriers and have access to the whole arena. The larger individuals of *P. melanarius* (12-19 mm) 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 (about 1.5 Kg), that had been passed through a 400 µm. The sand was used to more closely simulate the porous substrates of field soils from which carabids were captured. The thin layer of sand that we use reduced the amount of seeds that were lost due to burial. Six Eppendorf tubes filled with water and sealed with cotton wool were placed, two in each area, to provide an *ad libitum* water supply for the carabids. Trays were sprayed with water twice a day (morning and late afternoon) to prevent the sand from drying out.

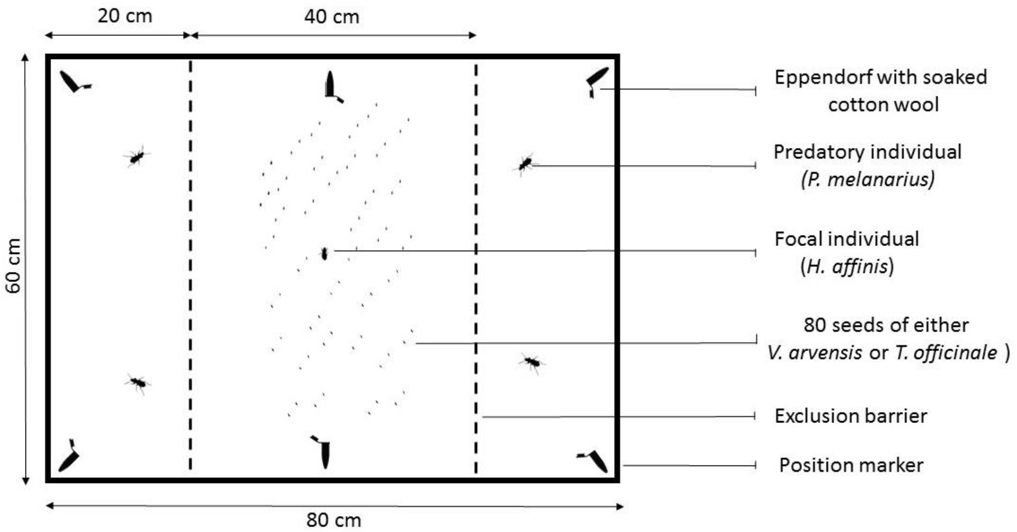

Figure 1: Diagrammatical representation of the test arena. Arena was divided into three areas using plastic 'Exclusion' barriers. *P. melanarius*, was only excluded from the central area. The plastic barriers were drilled with holes of 4mm in order to allow free movement of *H. affinis* individuals but prevent *P. melanarius* from crossing. 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

80 seeds of the test weed species, depending on treatment, were randomly distributed in the central area of the tray (Fig. 1). This number of seeds was obtained from pre-experiment assessment made in order to provide individuals with a high enough number of seeds and avoid total seed depletion during experiment duration. Two *P. melanarius* individuals were then placed in the two outside areas of the tray where they could not have access to the seeds in the central area (Fig. 1), giving a total of 4 live predators per tray. The number of *P. melanarius* used in test was based on the study of Guy et al. (2008), who showed that perception of conspecifics by carabid individuals does not appear to increase above a threshold of four individuals. Temperature and humidity were recorded and treatments were randomized to avoid any effects of position in the room on the trays.

Seed consumption was scored every hour during the first 7 hours and then at 24, 48 and 72 hours. The impact of live *P. melanarius* individuals on the foraging behaviour of *H. affinis* individuals was assessed by evaluating the amount of seeds consumed by *H. affinis* and the use of the arena (space used) during the first 7 hours of the test (i.e. space use). Space use was measured as the proportion of time an individual was observed in areas with *P. melanarius* and the proportion of time spent in the central area without *P. melanarius* (Fig. 1). The time at which an individual ate the first seed was scored as a proxy of its latency to first seed acceptance.

All combinations of treatments were tested simultaneously each week in order to avoid any effect of the date. Each focal *H. affinis* individual was randomly assigned to a treatment (n=30 per treatment), and tested alone and only once. The two sexes of the carabids were tested separately to avoid confounding olfactory cues in the test room that might induce mating related behaviours that distract from foraging. This was done by one sex being tested one week and the other sex the next week, in sequence.

c. Statistical Analysis

All statistical analyses were done in R 3.1.3 (R Core Team, 2017). Latency to first seed acceptance and comparison between the four different test situations were analysed by means of the Cox proportional hazard models (Dechaume-Moncharmont et al., 2005) in the 'cox.ph' function from the package 'survival' (Therneau, 2015). For each Cox regression model fit, the proportional hazards assumption was assessed using the 'cox.zph' function. Total seed consumption of each species of weed and effect of the treatment on mean seed consumption were analysed using a generalized linear model, assuming the negative binomial distribution. Space use by individual foragers was modelled as a generalized linear model assuming a binomial distribution. The effects of treatment, sex of individual, seed species and all interactions were tested in both models.

C. RESULTS

a. Effect of weed species on seed consumption

At the end of the 72 hour test, the total consumption of seeds differed between the two weed species (Fig.2b, Table S1). *H. affinis* individuals, of both sexes, consumed more seeds of *T. officinale* than seeds of *V. arvensis* in the controls (Fig.2b, Table S1). This significant difference was already observed after the 24th and 48th hours (Fig.2b, Table S1). There was no effect of sex or of any of the interactions of sex at any of the sample time points (Table S1). Similar results were observed in the predation treatments, in presence of live *P. melanarius*, with more seeds of *T. officinale* being consumed than seeds of *V. arvensis* after 72 hours

(Fig.2d, Table S1). There was no effect of *H. affinis* sex or of any of the interactions of sex in the predation treatments (Table S1).

b. Effect of the biotic interaction on the seeds consumption

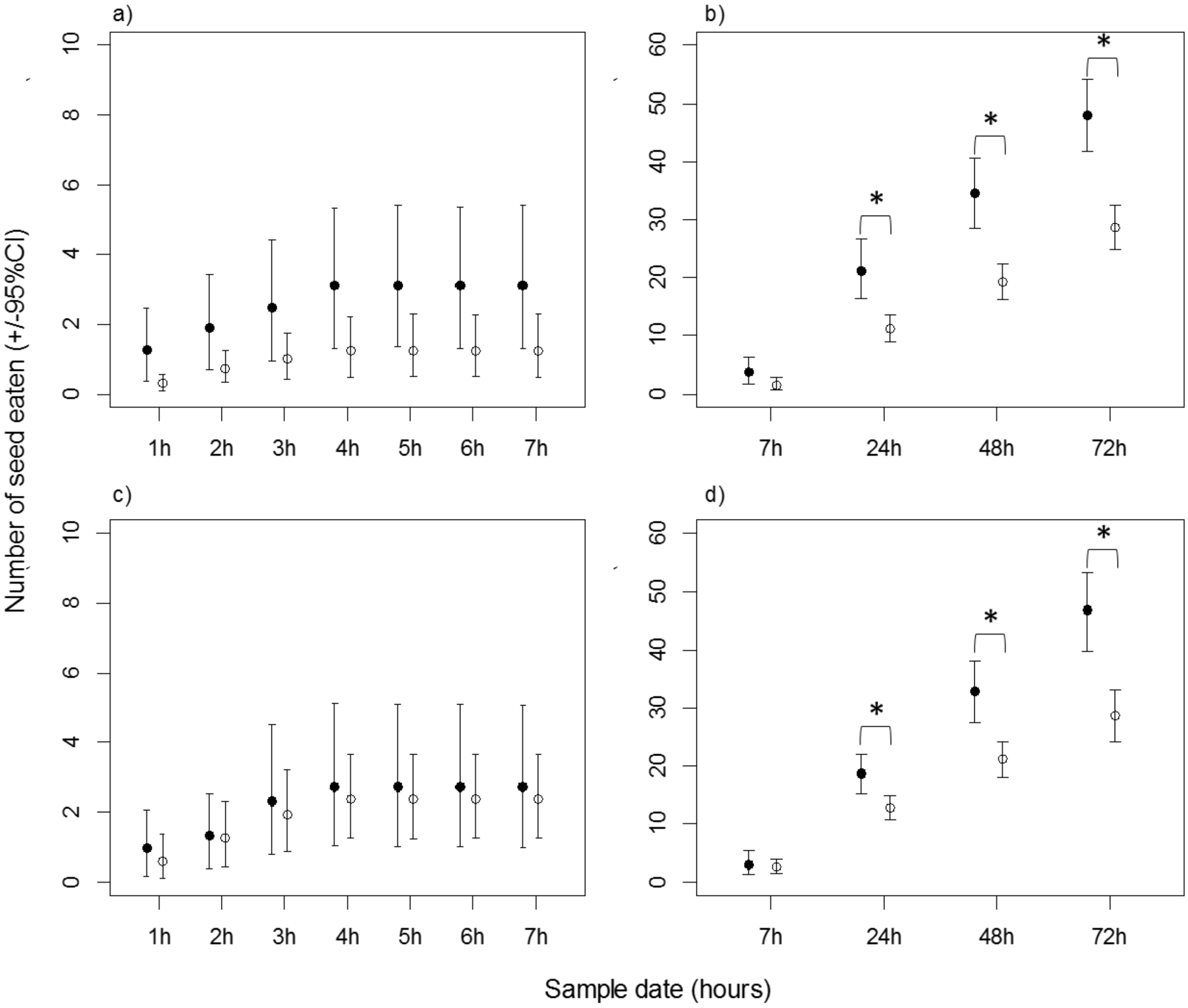

Figure 2: Cumulative number of seed eaten (boostrapped +/- 95%CI) of *T. officinale* (●) and of *V. arvensis* (○) in a-b) the control situation and c-d) in the predation treatment.

The latency to first seed acceptance did not differ between seed species in the control (χ^2_1= 0.65, P = 0.42), with no effect of sex, (χ^2_1=1.89, P=0.17) or interaction between sex and seed species (χ^2_1= 0.47, 0.49). In the predation treatment, latency to first seed acceptance did not differ between seed species (χ^2_1= 0.35, P = 0.55) and there was no effect of sex (χ^2_1=3.23, P=0.07) or sex by seed species interaction (χ^2_1= 2.60, 0.11). Latency to first acceptance among females did not differ between treatments for seeds of either *V. arvensis* (χ^2_1=1.58, P=0.21, hazard ratio = [1.61, 95%CI [0.77, 3.36]) or *T. officinale* (χ_1^2=1.37, P=0.24, hazard ratio = [0.64, 95%CI [0.30, 1.35]). Latency to first acceptance in males did not differ between the treatments for seeds of either *V. arvensis* (χ_1^2=0.06, P=0.79, hazard ratio = [1.09, 95%CI [0.53, 2.25]) or *T. officinale* (χ_1^2=0.58, P=0.44, hazard ratio = [1.33, 95%CI [0.64, 2.779]).

After the first four hours of the test, *H. affinis* females had consumed more seeds of *V. arvensis* in the live *P. melanarius* predation treatment than in the control (Fig. 3a, Table S2).

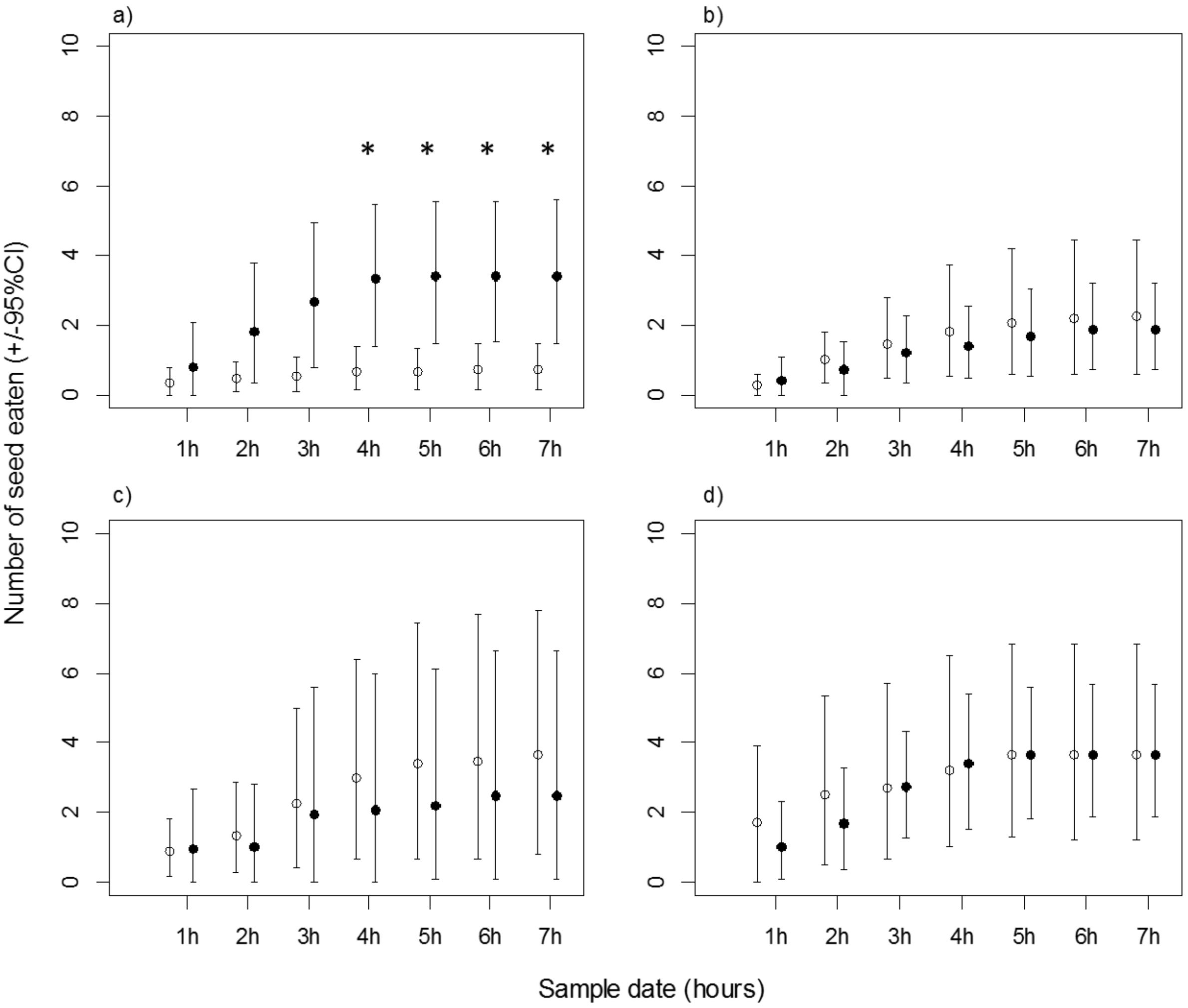

Figure 3: Cumulative number of seed eaten (boostrapped +/- 95%CI) during 7 hours in the control situation (○) or in the predation treatment (●) for a) females with seeds of *V. arvensis*, b) males with seeds of *V. arvensis*, c) females with seeds of *T. officinale*, d) males with seeds of *T. officinale*.

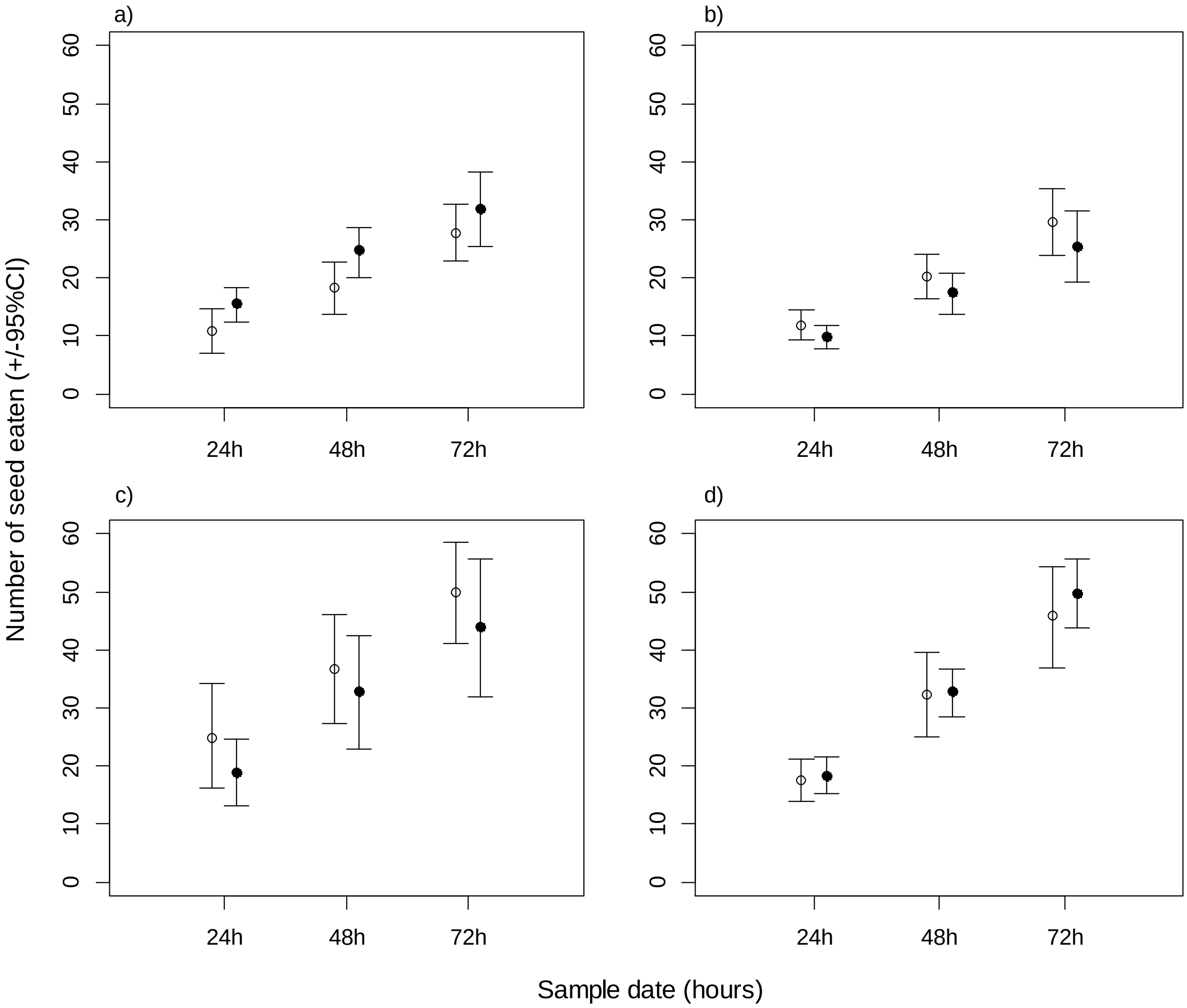

Figure 3bis: Cumulative number of seed eaten (boostrapped +/- 95%CI) during the last three sampledates (24h,48h and 72h) in the control situation (○) or in the predation treatment (●) for a) females with seeds of *V. arvensis*, b) males with seeds of *V. arvensis*, c) females with seeds of *T. officinale*, d) males with seeds of *T. officinale*.

The significant difference in *V. arvensis* seed consumption by females observed early in the trial was no longer significant after 24 hours (Fig. 3bis-a, Table S2). There was no significant difference between treatments in the number of *T. officinale* seeds eaten by females (Fig. 3bis-c, Table S2). Seed consumption of *T. officinale* or *V. arvensis* by males did not significantly differ between treatments (Fig. 3bis-b & 3bis-d, Table S2).

c. Space use of individuals

In the control situation, the proportion of time foragers spent in the central area of the arena (space use) did not differ between seed species (χ^2_1=3.59, P = 0.06, Fig. 3). There was no effect of the sex on space use (χ^2_1= 0.12, P = 0.73, Fig. 3) and no sex and seed species interaction (χ^2_1= 0.03, P = 0.86, Fig. 3). In the predation treatments, there was no effect of the seed species on individuals space use (χ_1^2= 0.65, P = 0.42, Fig. 3). There was a significant effect of the sex on space use, with females spending more time in the central area than males ((females 67% of time [0.59, 0.74], males 58% of time [0.50, 0.67], χ_1^2= 4.20, P = 0.04, Fig. 3). There was no sex and seed species interaction (χ_1^2= 0.89, P = 0.34, Fig. 3).

Table 1: Space use across treatments, as the proportion of time (bootstrapped 95%CI) in the central area of the arena, for the co-variates of seed species and *H. affinis* sex

T. officinale		
	Control	Predation
Males	0.54 [0.38, 0.71]	0.62 [0.53, 0.72]
Females	0.55 [0.38, 0.71]	0.67 [0.56, 0.76]
V. arvensis		
	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]

Irrespective of sex, *H. affinis* individuals spent more time in the central area of the arena in the predation treatments, exposed to live *P. melanarius* individuals, than in the control treatment (females: χ_1^2 =14.25, P < 0.001; males: χ_1^2=4.30, P= 0.04, Fig. 3). There was no effect of the seed species on space use (females: χ_1^2 =0.64, P = 0.42; males: χ_1^2=3.64, P= 0.06, Fig. 3) and no seed species and treatment interactions (females: χ_1^2= 0.86, P= 0.35; males: χ_1^2= 0.021, P= 0.88, Fig. 3).

D. DISCUSSION

Our results show that *H. affinis* accepts more seeds of *T. officinale* than *V. arvensis* in all treatments. The threshold for seed acceptance (choosiness) was lower in females presented with seeds of *V. arvensis* in the presence of predatory interference, via encountering live *P. melanarius* individuals. The predation rate of *V. arvensis* seeds by *H. affinis* females was higher in the predation treatment than in the control. These results have potentially important implications for weed regulation, as it suggests that predatory interference can modify the selection and consumption of food resources by *H. affinis*. This result is consistent with other, recent studies showing that cues of predation risk can induce a reduction in levels of choosiness for seeds (see Chapter II, Blubaugh et al. 2017).

Such reductions in choosiness, when exposed to predatory interference by carabids in laboratory conditions (see Chapter II) or by vertebrates in the field (Blubaugh et al., 2017)) led to an observable increase in the total number of seeds accepted by the foraging carabid individuals. Consequently, this finding would support our belief that feeding patterns could differ between carabid communities, changing between those where *H. affinis* does or does not encounter predators for example.

Our results showed evidence of a behavioural adjustment in female carabids, but only for seeds of *V. arvensis*. Charalabidis et al. (see Chapter II), in comparison, found a behavioural adjustment in both sexes when offered seeds of *T. officinale*. The absence of observed change in the feeding behaviour of males in this experiment might arise from differences in their experience of predation risk between the experiments (Tapia-Lewin and Pardo, 2014). Here, foraging *H. affinis* were exposed to live *P. melanarius*, but were also provided with a safe patch (i.e. the central zone of the arena). In Charalabidis et al (see Chapter II), the predation risk was simulated *P. melanarius* odours and a safe area did not exist. The availability of the safe area in this experiment might therefore have reduced the overall perception of predation risk (Lima and Bednekoff 1999; Unck et al. 2009; Nersesian et al. 2012).

In Charalabidis et al. (see Chapter II), females did eat more seeds than males when exposed to predator cues. This consistent behavioural difference between the sexes can be explained as an effect of investment by females in the energy-expensive process of egg production (Lorenz, 2003). Fecundity in female carabids is related to adult diet (Fawki and Toft, 2005; Jorgensen and Toft, 1997; Kulkarni et al., 2015b; Wallin et al., 1992). The seed diet of carabids has been shown to affect their survival, overall growth and the subsequent developmental rate of the offspring (Saska, 2005; Saska and Jarošík, 2001). Physiological differences between the sexes also plays a role in consumption. *H. affinis* females were found to have more hemocytes as a component of their immune systems and were larger than males, both of which could lead directly to higher energetic requirements (Juliano 1985, see *Chapter III*) that might be satisfied by eating more seeds than males.

The females in this experiment might have sacrificed potential feeding preference for safety by lowering their level of choosiness and foraging in the area with the highest perceived safety (i.e. the central part of the arena in this experiment), irrespective of the prey available (Altendorf et al., 2001; Blubaugh et al., 2017; Lima and Dill, 1990; Pilakouta, 2009). Both sexes spent more time in the central area of the arena in the predation treatment than in the control. The difference in patch quality, between the safer central and hazardous border area in the predation treatments changed the balance between safety and absolute feeding preference and hence, impacted the foraging decisions of females in our experiment (Brown, 1988; Pilakouta, 2009; Pyke, 1984).

The lack of significant differences in seed consumption after 24 hours between the treatments for could have arisen due a threshold of satiety in individuals foraging under predation risk. Given that their consumption of seeds increased in the seven first hour of the test, in comparison to the control, these foragers under predation risk may have eaten enough seeds to reach satiety before the end of the 24 hours (Mols, 1988). Future experiments should address the kinetics of consumption over 24 hours in treatments with and without predators present, concentrating particularly on satiation, to disentangle this question.

High and unchanged consumption between treatments for seeds of *T. officinale* demonstrates that the interest for this species was higher than for *V. arvensis*. This finding is consistent with individuals consuming more seeds of *T. officinale* in total than seeds of *V. arvensis*. However, this contradicts results previously reported where *H. affinis* individuals consumed *V. arvensis* seeds preferentially to seeds of *T. officinale* (Honek et al., 2007, 2006; Petit et al., 2014). This difference may be explained by the type of setup used in our experiment. These previous studies have used cafeteria-type experiments in which multiple alternative seed species are simultaneously offered to foragers. The presence of many resources, that are not presented independently of one another (Murray et al., 2010; Raffa et al., 2002; Underwood et al., 2004), will affect the choices made by an individual (Murray et al., 2010) and only establish the relative preference for each weed seed species. The no-choice paradigm that we adopt for our study can, by contrast, be used to evaluate absolute preference of individuals because each prey item seed is presented in turn and independently (Reinhold and Schielzeth, 2015; Rodríguez and Greenfield, 2003; Rothbart and Hennig, 2012).

These results suggest that predator choosiness can be modified by predatory interference at scales that spatio-temporally greater than typically used in the laboratory, suggesting the finding might apply to the in-field situation. Should this prove to be the case, it would indicate that the composition of the community of carabids in a field may have marked impact on the forager behaviour. The presence of a risk of predation, via by the presence within the community of predator species, can change the observed predation rate of each species of weed and potentially being a mechanism for a biodiversity-ecosystem function relationship. For comparisons to be made between studies in the field it would therefore be necessary to evaluate the community of carabids present in each experimental situation. The lack of this information, and of the understanding of those species in which predation rick modifies foraging behaviour, may explain why still fail to relate predation rates in field with laboratory experimental results (Petit et al., 2014).

E. ACKNOWLEDGEMENTS

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F. SUPPLEMENTARY MATERIAL

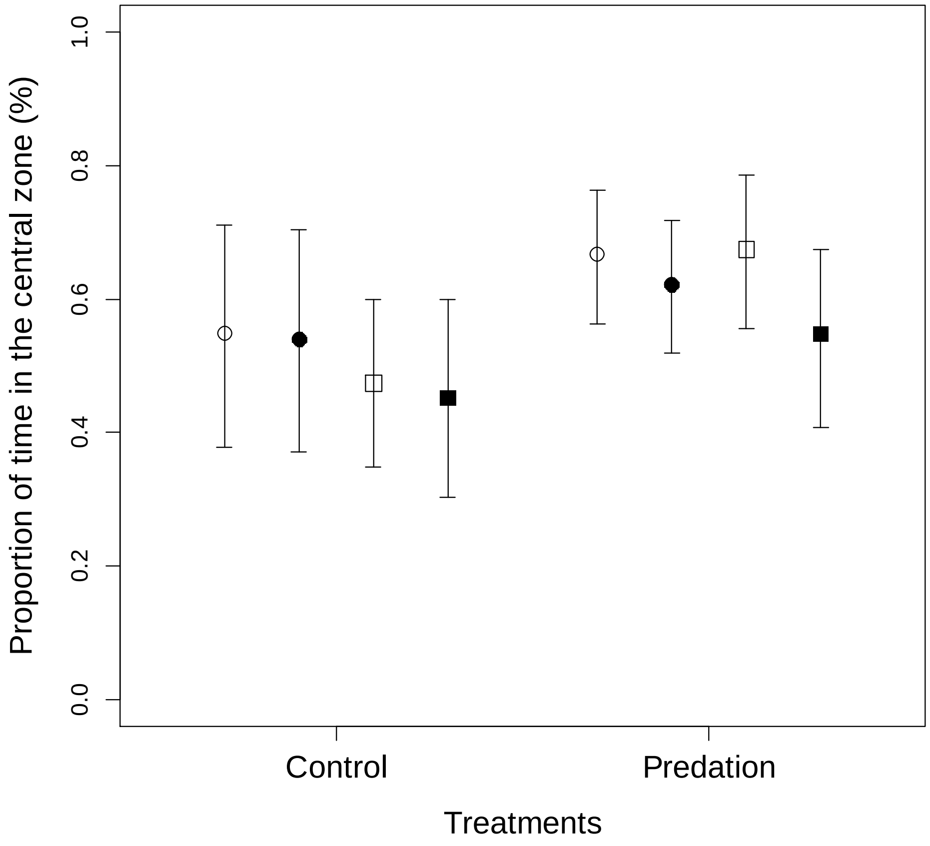

Figure S1: Space use across treatments, as the proportion of time (bootstrapped 95%CI) in the central area of the arena, for the co-variates of seed species (circles for *V. affinis*, squares for *T. officinale*) and *H. affinis* sex (filled for males and empty for females).

Table S1: 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.

Control								
	T. officinale	*V. arvensis*	Seed consumption		Effect of sex		Sex and seed species interactions	
1h	1.27, [0.38, 2.41]	0.30, [0.10, 0.57]	$\chi^2_1 = 3.09$	P = 0.078	$\chi^2_1 = 0.15$	P = 0.70	$\chi^2_1 = 0.37$	P = 0.55
2h	1.89, [0.69, 3.48]	0.73, [0.33, 1.23]	$\chi^2_1 = 2.89$	P = 0.089	$\chi^2_1 = 1.48$	P = 0.22	$\chi^2_1 = 0.14$	P = 0.91
3h	2.48, [0.96, 4.45]	1.00, [0.40, 1.77]	$\chi^2_1 = 2.86$	P = 0.09	$\chi^2_1 = 1.48$	P = 0.22	$\chi^2_1 = 0.52$	P = 0.47
4h	3.10, [1.31, 5.34]	1.23, [0.50, 2.27]	$\chi^2_1 = 3.15$	P = 0.076	$\chi^2_1 = 0.80$	P = 0.37	$\chi^2_1 = 0.70$	P = 0.40
5h	3.52, [1.48, 6.00]	1.37, [0.53, 2.53]	$\chi^2_1 = 3.29$	P = 0.070	$\chi^2_1 = 0.97$	P = 0.32	$\chi^2_1 = 0.89$	P = 0.35
6h	3.55, [1.52, 6.07]	1.47, [0.57, 2.70]	$\chi^2_1 = 2.89$	P = 0.089	$\chi^2_1 = 0.89$	P = 0.34	$\chi^2_1 = 0.86$	P = 0.35
7h	3.65, [1.65, 6.31]	1.50, [0.60, 2.70]	$\chi^2_1 = 3.13$	P = 0.077	$\chi^2_1 = 0.89$	P = 0.34	$\chi^2_1 = 1.08$	P = 0.30
24h	21.3, [16.3, 26.5]	11.3, [3.03, 13.6]	$\chi^2_1 = 11.09$	P < 0.001	$\chi^2_1 = 0.61$	P = 0.43	$\chi^2_1 = 1.43$	P = 0.23
48h	34.5, [28.5, 40.6]	19.2, [16.2, 22.2]	$\chi^2_1 = 14.59$	P < 0.001	$\chi^2_1 = 0.014$	P = 0.90	$\chi^2_1 = 0.62$	P = 0.43
72h	48, [41.6, 54.0]	28.7, [25.8, 31.6]	$\chi^2_1 = 21.40$	P < 0.001	$\chi^2_1 = 0.02$	P = 0.90	$\chi^2_1 = 0.56$	P = 0.45
Predation								
	T. officinale	*V. arvensis*	Seed consumption					
1h	0.97, [0.13, 2.10]	0.6, [0.10, 1.33]	$\chi^2_1 = 3.13$	P = 0.077	$\chi^2_1 = 0.10$	P = 0.74	$\chi^2_1 = 0.18$	P = 0.67
2h	1.33, [0.37, 2.57]	1.27, [0.43, 2.33]	$\chi^2_1 = 0.02$	P =0.88	$\chi^2_1 = 0.058$	P = 0.81	$\chi^2_1 = 0.91$	P = 0.34
3h	2.33, [0.80, 4.47]	1.93, [0.83, 3.17]	$\chi^2_1 = 0.15$	P =0.69	$\chi^2_1 = 0.12$	P = 0.72	$\chi^2_1 = 0.93$	P = 0.34
4h	2.73, [1.00,5.00]	2.37, [1.23,3.67]	$\chi^2_1 = 0.12$	P =0.72	$\chi^2_1 = 0.09$	P = 0.75	$\chi^2_1 = 1.64$	P = 0.20
5h	2.93, [1.20, 5.27]	2.53, [1.37, 3.87]	$\chi^2_1 = 0.12$	P =0.72	$\chi^2_1 = 0.038$	P = 0.85	$\chi^2_1 = 1.73$	P = 0.19
6h	3.07, [1.30, 5.37]	2.63, [1.47, 4.00]	$\chi^2_1 = 0.14$	P =0.71	$\chi^2_1 = 0.043$	P = 0.84	$\chi^2_1 = 1.22$	P = 0.27
7h	3.07, [1.33, 5.40]	2.63, [1.49, 3.97]	$\chi^2_1 = 0.14$	P =0.71	$\chi^2_1 = 0.043$	P = 0.84	$\chi^2_1 = 1.22$	P = 0.27
24h	18.67, [15.4, 21.9]	12.77, [10.7, 14.8]	$\chi^2_1 = 6.25$	P =0.012	$\chi^2_1 = 2.62$	P = 0.16	$\chi^2_1 = 2.33$	P = 0.13
48h	32.87, [27.6, 38.1]	21.10, [18.0, 24.0]	$\chi^2_1 = 8.16$	P = 0.004	$\chi^2_1 = 1.34$	P = 0.25	$\chi^2_1 = 1.39$	P = 0.24
72h	46.8 [39.8, 53.4]	28.7 [24.0, 33.1]	$\chi^2_1 = 10.81$	P = 0.001	$\chi^2_1 = 0.11$	P = 0.73	$\chi^2_1 = 1.55$	P = 0.21

Table S2: **Means cumulative number** (bootsrapped +/- 95%CI) **of seed consumed** by both sexes of *H. affinis* in each of the 4 treatments and at each sample date

	Control	**Predation**			**Control**	**Predation**		
Females with *T. officinale*					**Males with *T. officinale***			
1h	0.87, [0.1; 1.8]	0.93, [0.0; 2.7]	χ^2_1 =0.004	P= 0.954	1.71 [0.0; 3.9]	1 [0.7; 2.3]	χ^2_1 =0.22	P= 0.64
2h	1.33, [0.3; 2.9]	1, [0.0; 2.8]	χ^2_1 =0.09	P= 0.76	2.5 [0.4; 5.4]	1.67 [0.3; 3.2]	χ^2_1 =0.19	P= 0.66
3h	2.27, [0.4; 4.9]	1.93, [0.0; 5.6]	χ^2_1 =0.021	P= 0.88	2.71 [0.6; 5.6]	2.73 [1.2; 4.3]	χ^2_1 =0.0001	P= 0.99
4h	3, [0.7; 6.3]	2.07, [0.0; 6.0]	χ^2_1 =6.53	P= 0.71	3.21 [1; 6.5]	3.4 [1.5; 5.4]	χ^2_1 =0.007	P= 0.93
5h	3.4, [0.7; 7.5]	2.2, [0.1; 6.1]	χ^2_1 =0.17	P= 0.68	3.64 [1.2; 6,9]	3.67 [1.9; 5.6]	χ^2_1 =0.0001	P= 0.99
6h	3.47, [0.7; 7.6]	2.47, [0.1; 6.7]	χ^2_1 =0.10	P= 0.74	3.64 [1.3; 7.07]	3.67 [1.8; 5.7]	χ^2_1 =0.0001	P= 0.99
7h	3.67, [0.9; 7.7]	2.47, [0.1; 6.6]	χ^2_1 =0.17	P= 0.68	3.64 [1.2; 6.9]	3.67 [1.9; 5.7]	χ^2_1 =0.0001	P= 0.99
24h	24.8, [16.1; 34.1]	18.93, [13.2; 24.5]	$F_{1,28}$ =1.09	P= 0.3	17.5, [14; 21.2]	18.4, [15.3; 21.6]	$F_{1,28}$ =0.13	P= 0.72
48h	36.67, [27.3; 45.8]	32.93, [23.07; 42.5]	$F_{1,28}$ =0.27	P= 0.60	32.29, [25.1; 39.4]	32.8, [28.4; 36.7]	$F_{1,28}$ =1.01	P= 0.91
72h	50, [41.07, 58.6]	43.93, [31.5; 55.9]	$F_{1,28}$ =0.59	P= 0.45	45.85, [37.07; 54.3]	49.67, [43.7; 55.5]	$F_{1,28}$ =0.48	P= 0.49
Females with *V. arvensis*					**Males with *V. arvensis***			
1h	0.33, [0.0; 0.8]	0.80, [0.0; 2.1]	χ^2_1 =0.61	P= 0.43	0.27, [0.0; 0.6]	0.40 [0.0; 1.07]	χ^2_1 =0.14	P= 0.70
2h	0.47, [0.1; 0.9]	1.80, [0.3; 3.8]	χ^2_1 =2.11	P= 0.14	1.00, [0.3; 1.8]	0.73 [0.0; 1.5]	χ^2_1 =0.14	P= 0.70
3h	0.53, [0.1; 1.1]	2.67, [0.7; 4.9]	χ^2_1 =3.13	P= 0.08	1.47, [0.4; 2.8]	1.2 [0.3; 2.3]	χ^2_1 =0.08	P= 0.77
4h	0.67, [0.1; 1.3]	3.33, [1.5; 5.5]	χ^2_1 =4.86	P= 0.03	1.8, [0.5; 3.7]	1.4 [0.5; 2.5]	χ^2_1 =0.15	P= 0.70
5h	0.67, [0.1; 1.3]	3.4, [1.5; 5.6]	χ^2_1 =4.97	P= 0.03	2.07, [0.6; 4.1]	1.67, [0.5; 3.07]	χ^2_1 =0.11	P= 0.74
6h	0.73, [0.1; 1.5]	3.4, [1.5; 5.6]	χ^2_1 =4.49	P= 0.03	2.2, [0.6; 4.5]	1.87, [0.7; 3.2]	χ^2_1 =.07	P= 0.79
7h	0.73, [0.1; 1.4]	3.4, [1.5; 5.6]	χ^2_1 =4.49	P= 0.03	2.27, [0.6; 4.6]	1.87, [0.7; 3.2]	χ^2_1 =0.10	P= 0.75
24h	10.87, [7.1; 14.7]	15.67, [12.5; 18.5]	$F_{1,28}$ =3.55	P= 0.07	11.73, [9.4; 14.3]	9.87, [7.8; 11.8]	$F_{1,28}$ =1.21	P= 0.28
48h	18.27, [13.7; 22.8]	24.73, [20.07; 28.8]	$F_{1,28}$ =3.77	P= 0.06	20.13, [16.3; 24.07]	17.47, [13.9; 20.7]	$F_{1,28}$ =0.94	P= 0.34
72h	27.73, [23.0; 32.7]	31.93, [25.5; 37.9]	$F_{1,28}$ =1.02	P= 0.32	29.6, [23.9; 35.3]	25.47, [19.5; 31.6]	$F_{1,28}$ =0.88	P= 0.36

3) Chapter conclusion

The results we find in this more complex spatio-temporal experiment are consistent with those of Chapter II. Here, the individuals of *H. affinis* reduced their choosiness when foraging under predation risk. Surprisingly, this reduction in choosiness was confined to female *H. affinis* and to seeds of *V. arvensis* as prey items. As previously discussed in Chapter IV, behavioural adjustment among females can be explained by difference in physiological needs between sexes.

Perhaps more surprising was the feeding rate observed for seeds of *V. arvensis*. All previous studies assessing *H. affinis* feeding preference in laboratory conditions have concluded that *V. arvensis* was one of the preferred seeds species of *H. affinis* (Honek *et al*, 2006; Honek *et al,* 2007; Petit *et al*., 2014). Our results, however, show that when offered seeds of *V. arvensis* alone *H. affinis* ate them at lower rates than *T. officinale*. This result cannot be explained by a difference in the difficulty of finding seeds of *V. arvensis* and *T. officinale,* because feeding rates on these two seeds species did not differ in the predation treatment. Moreover, time spent by *H. affinis* individuals in the central area also did not differ between either the predation and control treatments or the two seed species. Rather, my explanatory hypothesis for future testing is that that the *T. officinale* seeds induced a higher motivation to feeding in *H. affinis* than the *V. arvensis* seeds. The low choosiness observed for *T. officinale* in the control meant that it was not possible to observe a further reduction of choosiness in the predation treatment.

The difference between the results of previous studies and those found here for the feeding rates on seeds of *V. arvensis* might be due to the different methods used. In experiments using the choice test paradigm, the simultaneous presence of multiple resources can affect the choice of an individual (Murray *et al*., 2010) because the resources are not presented independently of one another (Underwood *et al*., 2004; Murray *et al*., 2010; Raffa *et al*., 2012). The difference might also be due to the type of substrate used. When sand was used as a substrate, in an independent microcosm experiment, *H. affinis* also showed greater seed consumption of *T. officinale* than *V. arvensis* (Carbonne, *in prep.*). In contrast, when paper filter was used as a substrate in Chapter III, *H. affinis* did not show preferences for either *T. officinale* or *V. arvensis*. Arguably, the substrate plays a role in the foraging response, possibly via the relative state of imbibition of the seeds, affecting their consumption. Indeed, Law & Gallagher (2015) showed that level of imbibition of seeds increases consumption by carabids.

In contrast to our initial hypothesis, the perception of risk induced by live carabids in this experiment appears to have been lower in comparison to the simulated risk due to predator odours used in Chapter II. Indeed only females, which potentially have higher energetic requirements and therefore more to lose than males, reduced their choosiness in the present experiment, whereas in Chapter II both sexes reduced their level of choosiness under predation risk. This may be because of the presence of the central area, from which *P. melanarius* individuals were excluded, which might may have served as a safe patch or refuge from predation. In the experiment in Chapter II, individuals had no refugia available and had to forage in a patch flooded with *P. melanarius* olfactory cues.

Sixth Chapter

General discussion

My objective for this PhD was to investigate the decision-making process of carabid beetles foraging for seeds, subject to intraguild interference interactions from both other carabid species and conspecific individuals. The decisions taken by a foraging carabid individuals might be expected to differ between different environmental contexts of food and the carabid community, and between individuals of the same species. In developing my work, it became increasingly clear that we do not understand how beetles make choices for what to eat and when to accept a given prey. It is especially difficult to predict in-field predation rates that are at the core of a robust use of carabids as biocontrol agents. This in part arises from a lack of knowledge on how foraging individuals would react to intraguild interference, such as the risks of predation or of competitive interference, which frequently occurs in arable fields. A better understanding of this decision-making process in carabids would help to improve the predictability of conservation biological control and weed regulation ecosystem services.

My overarching objectives were to assess whether: (i) individual carabids foraging for seeds would change their level of choosiness under intraguild interference in order to reduce associated risks of predation or lost opportunity costs; (ii) the intensity of change in choosiness is linked to individual characteristics, such as trophic guild, sex, size, immune traits and personality; and, (iii) the impact of any change in level of choosiness is related to the level of seed consumption. To do this, I studied the foraging behaviour of one of the most abundant granivorous species in arable fields, *Harpalus affinis*. For this General Discussion, I will discuss the results achieved in response to my objectives and propose future directions.

1. *H. affinis* changes its level of choosiness for seeds of *T. officinale* under intraguild interference from other carabid species

In this work, I was able to demonstrate a clear change in the level of choosiness of *H. affinis* individuals foraging under intraguild interferences (Chapter II). Individuals were found to reduce their level of choosiness when foraging for seeds of *T. officinale*, which differed according to the intraguild cues they were exposed to. *H. affinis* expressed a stronger behavioural adjustment to cues of predation risk than to competition. This reduction in level of choosiness, as the latency to first seed acceptance, led to an overall increase in the total number of seeds eaten by individuals during the test.

These results are potentially important, considering the role of carabids as putative biological control agents (Kromp, 1999; McKemey et al., 2003). Many thousands of carabid individuals exist in farm fields in mixed communities of granivores, omnivores and predatory species, all of which can be cannibalistic and inter-specific predators (McKemey et al., 2003). Reductions in the level of choosiness, in an environment filled with predation cues, might lead to an increase in the number of weed seeds accepted by the granivorous carabids. Counterintuitively, therefore, predation risk might be a mechanism for a biodiversity-ecosystem function relationship (Hines et al., 2015; Reiss et al., 2009) amongst the carabids. Rather than the commonly held expectation that communities formed of granivores alone should have the highest weed seed predation (Petit and Bohan, 2017), a hypothesis formed from these results would predict that the ecological function of weed seed predation would increase with the diversity of the carabid community.

Chemical cues left by walking carabids contain species-specific information

My results demonstrate that *H. affinis* individuals change their level of choosiness for seeds when foraging under exposure to chemical cues from two other carabid species. Moreover, the results show that all three carabid species tested in our experiment, i.e. *P. melanarius*, *H. affinis* and *Pseudoophonus rufipes*, leave chemical cues behind while walking on filter papers and that these cues provide specific information to a foraging *H. affinis* individual. Results previously obtained by Armsworth et al. (2005) and Guy et al. (2008) showed that walking carabids release chemical cues along their path of movement and that these cues can be perceived by other passing individuals. In their studies, Armsworth et al. (2005) and Guy et al. (2008) only used *P. melanarius* individuals to provide the odour cues. They demonstrated that these *P. melanarius* cues, identified as a non-volatile cuticular hydrocarbon (see Armsworth et al. 2005), could be used as information both by slug prey and by conspecifics to avoid areas previously visited. Whether or not these chemical cues, left by walking carabids, can be perceived and differentiated according to carabid species, has not yet been investigated. Considering that all carabid species will likely leave specific cues while walking this ‘information signal’ might be used by other co-occurring animal species, including carabid species, to reduce competitive or predatory interference.

I found that foraging *H. affinis* individuals did respond differently to the different cues they were exposed to. *H. affinis* showed greater change in choosiness when exposed to cues of *P. melanarius* than when exposed to cues of *P. rufipes* or to those of conspecifics. One might argue that no actual difference exists in the chemical cues left by the three carabid species I tested, and that the lower reaction to cues of *P. rufipes* and *H. affinis* cues in comparison to *P.*

melanarius observed in our results was not due to specific signal between carabid species but rather to a difference in the level of intensity or amount of a common "carabid cue". The behavioural response of the tested *H. affinis* individuals would suggest otherwise. While measurement of the rate of acceptance (i.e. level of choosiness) showed no significant differences between the two competition treatments, in contrast to the predation treatment, the proportion of space used by the searching individuals did change significantly between our two competition treatments. Individuals lowered their space use in the intraspecific competition treatment, by comparison with the interspecific competition treatment. Moreover, while the change in level of choosiness was not significantly different in either of the two competition treatments and the control, the competition effect sizes were consistent and high. This would indicate that individuals did lower their level of choosiness when exposed to cues of potential feeding competitors in comparison to the control (Nakagawa and Cuthill, 2007), but that not all appropriate co-variates were measured during the experiment. My simplest explanation for these results is that competition cues from conspecifics are perceived differently by *H. affinis* individuals than either competition cues from *P. rufipes* (i.e. interspecific competition) or predation cues of *P. melanarius* suggesting that the cues from particular species impart species-specific information to foraging *H. affinis*. Future studies should address how these specific cues could be used by foraging carabids, as information.

Although results of the trajectometry metrics obtained in chapter II & III for all treatments did not differ from the control, suggesting no link between intraguild interferences cues and carabids movement, I rather think that this should not be generalized. Guy et al., (2008) showed avoidance behaviour in *P. melanarius* exposed to cues of conspecific and thus change in space use. I therefore expect that some species-specific cues might lead to avoidance behaviour and hence potentially impact carabid dispersal. It would therefore be interesting to assess, in future studies, whether this chemical communication among carabids, which I have shown can lead to reductions in choosiness, might also be used in the field. To achieve this work it would firstly, be necessary to test if the cues differ in their chemical composition according to the carabid species they belong to and second, to test behaviourally whether these specific carabids cues in turn induce specific carabids behaviours.

2. Factors affecting change in level of choosiness in carabids

The results I have presented thus far were based on studies of one focal carabid species forager exposed to simulated risk, as chemical cues, from two other species of carabid. Decisions taken by a foraging individual carabid might be expected to differ between contexts and between individuals. While Chapter II of this thesis was aimed at unravelling the process of decision-making in *H. affinis*, Chapter III, IV and V were aimed at improving understanding of the factors that impact variation in level of choosiness and the impact of such variation on the carabids decision-making process.

2.1. *Adjustment of level of choosiness with carabid species*

To improve our understanding of factors that could induce variation in an individual's level of choosiness, I reran the experiment of Chapter II using another carabid species as the forager. I hypothesised that the generality of the findings of Chapter II would depend on the relative importance of seeds in the diet of a carabid species. I therefore choose to use a test species that had a different trophic relationship with seeds, as a food source, being both a more omnivorous species and highly abundant in arable fields: the omnivorous carabid beetle *P. cupreus.*

Omnivore carabids, in contrast to granivorous species like *H. affinis*, rely on both animal and plant prey to meet their energetic requirements. They may, therefore, be more willing to reject a seed when foraging under predation risk than granivorous individuals. For this reason I expected *P. cupreus* individuals to increase their choosiness for seeds when foraging under predation risk and thus only to accept seeds considered as good enough to compensate for the risk of foraging under predation risk. The results confirmed that change in level of choosiness of carabids foraging under intraguild interference could indeed depend on the carabid species tested. *P. cupreus* did not change their level of choosiness when foraging under any intraguild interference tested (Chapter III). However, as already discussed in Chapter III, it may be that the strong interest of *P. cupreus* for seeds of *T. officinale* might have led to such a low level of choosiness that it could not be further reduced under intraguild interference. This explanation is underscored by the observed feeding rates of *P. cupreus* on seeds of *T. officinale* in Chapter III. Omnivorous *P. cupreus* individuals ate more seeds of *T. officinale* than the granivorous *H. affinis,* which would suggest a high interest of *P. cupreus* individuals for seeds of *T. officinale*. The use of *T. officinale,* in Chapter III, came from a desire to compare choosiness in *H. affinis* to that of *P. cupreus,* using a common method. In the future, experiments should be done to assess whether lack of response in *P. cupreus* was due to the species of seed offered or to other factors that might affect decision-making. These other factors might include effects such as: (i) competitive interference amongst individuals of a cannibalistic species that might have been perceived as predatory interferences; and, (ii) an intensity of risk not high enough to induce a change in level of choosiness (as suggested in Chapter V).

Chapter III addressed the question of whether my results were general and would work for other carabid species having different foraging requirements. The results showed that both *H. affinis* and *P. cupreus* did differ in their behavioural adjustment to risks. Moreover, differences were also apparent in the foraging strategies of these two carabid species. *H. affinis* appeared much slower to adopt seed consumption behaviours than *P. cupreus*, in both experiments of Chapter III. Such differences in behavioural adjustment between carabid species might suggest that omnivorous and granivorous carabids might have complementary roles in their contribution to weed seed predation. Linking this variation in behaviour to an effect of carabid guild remain problematic, as I only tested one species from each guild, and only against intraguild cues from two other species. This is not sufficient to extrapolate reliably my results to a full community. In order to conclude there is an effect of carabid guild on variation in choosiness, it would be necessary to test alternative combination of carabids species from all carabid guilds.

Conducting such research would demonstrate how choosiness might change in a given carabid population, placed in a particular community. The purpose of Chapter V was to move towards this complexity by enriching the initial experimental protocol and redoing the experimental tests in Chapter II under these more realistic conditions. Initially, the aim of Chapter V was to expose individuals to 4 different combinations of risk of either: (i) predation risk; (ii) competition risk; (iii) competition mixed with predation risk; and, (iv) a control. These combinations proved impractical, however, as the maintenance necessary to keep enough *P. rufipes* individuals alive on the sand substrate proved impractical.

Combining predation and competition risk within the same treatment level would have been a formal test for potential interactions between these two risks. Individual carabids are likely to experience both risks simultaneously, in field, and any interaction might have an important effect. To complement the planned experiment, my aim was also to analyse of the patterns of predator avoidance between *H. affinis* and the predator *P. melanarius* using sample data from the Farm Scale Evaluation project ([FSE] Champion *et al*., 2003; Bohan *et al*., 2005).

I wanted to test whether the behavioural results from the laboratory could be used to predict seed depletion levels in arable fields from the observed community of species of carabids present in 256 arable fields.

2.2. Adjustment of level of choosiness according to the seed species

Chapter V demonstrated that choosiness can vary between seed species. Female *H. affinis* ate similar amount of seeds of *T. officinale* irrespective of the treatment conditions, whereas seeds of *V. arvensis* were only eaten when *H. affinis* females were exposed to predation risk. The results of Chapter II showed that predation risk could induce a reduction in choosiness in *H. affinis*. This might suggest that the level of choosiness for the two seeds species differed, given that it could decrease for *V. arvensis* but did not change for seeds of *T. officinale*. These results might suggest that weed seed predation would not be uniform for all weed species, and moreover that predation of a particular weed seed species can be modified by biotic interactions between carabid species. The quantification of individual levels of choosiness demonstrates that the two carabid species tested in this thesis, *H. affinis* and *P. cupreus*, differed in their seed diet breadth. *P. cupreus* appeared to have levels of choosiness that changed with each encountered species of weeds, which might be explained by physiological limits, while *H. affinis* could consume all seeds presented and showed no difference in relative level of choosiness for any species.

My results suggest that biological control would be enhanced if some carabid species, such as *H. affinis*, could lower their choosiness for seeds when exposed to predation risk, further widening the range of weed seed consumed. Others species, because of physiological limits, might be limited to particular weed species. Considering that carabid species, such as *P. cupreus*, forage actively and widely, patches of certain species of seeds in arable fields, such as *T. officinale*, would be rapidly found by these carabids and eaten. Seeds of these particular weed species will therefore not be available for other carabids species that have longer latencies to seed attack, such as *H. affinis*. This could lead these “slower” granivorous species to focus on seed species still available to them in the field. Field consumption may therefore not match the preferences observed in cafeteria-tests, as the choice of each carabid foraging individual will be shaped by the overall carabid community composition, potentially explaining the difficulty in extrapolating laboratory results to field situations (Petit et al., 2014).

2.3. Adjustment of level of choosiness according to risk intensity

Overestimating the risk of predation risk will be costly for individuals (Abrams, 1994). Individuals might therefore be expected to adjust their behaviour according to the intensity of the risk (Abrams, 1994; Sánchez-González et al., 2017). The results from Chapter V and Chapter II might suggest that *H. affinis* individuals are able to adjust the variation in their level of choosiness according to the intensity of the risks they are facing. Reduction of choosiness was observed for females and for seeds of *V. arvensis* alone in Chapter V, whereas it was observed for both females and males and with seeds of *T. officinale* in Chapter II. My working hypothesis, that best explains this difference, centres on a reduced perception of risk by the foragers in Chapter V due to the availability of the 'safe' central area of the arena used in Chapter V. In Chapter II, in contrast, individuals were forced to forage in an area flooded with *P. melanarius* olfactory cues.

Any reduction in the level of choosiness may, in the long run, be detrimental to individuals as it will ultimately lead to the frequent consumption of items of low quality, potentially preventing individuals from attaining all their nutrient requirements (Jensen et al., 2012; Mayntz, 2005). Being able to finely adjust changes in choosiness, with the risk intensity, might therefore be selected for in carabids, especially as intraguild interference interactions, including intraspecific competition, interspecific competition and intraguild predation, will likely occur frequently between carabid individuals and species (Griffith and Poulson, 1993; Guy et al., 2008) given the abundance and diversity of seed-eating carabids in the field.

Such behavioural plasticity in the carabids, with adjustment to the intensity of the risk, was already suggested the results for *H. affinis* individuals showing them able to respond differently to chemical cues released by different carabids species in Chapter II. *H. affinis* expressed a lower response (i.e. lower reduction of choosiness) when exposed to cues of *P. rufipes* and to conspecifics than when exposed to *P. melanarius* cues, suggesting at the ability to adjust the behavioural response to the perceived intensity of the risk (Abrams, 1994). Smaller animals, and particularly invertebrates, have long been considered to have reduce mental faculties (Eberhard, 2011; Kralj-Fišer and Schuett, 2014) and the '*size-limitation hypothesis*' suggest that very small animals will tend to exhibit reduced behavioural capacities and adopt lifestyles that require less behavioural capability (Eberhard, 2011). This idea has begun to be challenged by studies showing strong capabilities and behavioural plasticity in invertebrates (Eberhard, 2011). The ability to finely adjustment foraging, as observed in these carabids, is perhaps not surprising especially considering that the individuals were wild caught from in man-managed agricultural fields where behavioural plasticity would increase the chance of survival in these highly disturbed environments (Snell-Rood, 2013; Sol, Lapiedra, & González-Lagos, 2013). That *P. cupreus* did not reduce its choosiness under predation risk, in Chapter II, might suggest that the intensity of the risk that we used in our experiment was not high enough to induce such a behavioural change. This idea is further emphasized by other studies showing change in feeding rates of other carabid species exposed to predation risk (Blubaugh et al., 2017; Wyatt Hoback et al., 2001). The level of choosiness expressed within a particular situation will therefore likely differ between carabid species, but also with the perceived level of risk within the carabid community, mediated in part by chemical cues.

2.4. *Variation in level of choosiness under predation risk might be dependent on individual characteristics, such as sex, immunity and personality traits.*

Previously, observed changes in choosiness were assessed and interpreted at the scale of the population. Here, my question is whether the overall level of choosiness differs between one foraging context and another. The size of effect obtained in our results, however, suggests at systematic differences between individuals in their variation in choosiness. Thus, the aim of Chapter IV was to assess individual factors that might explain systematic variation in foraging.

Chapter IV showed that changes choosiness in *H. affinis* (Chapter II and V) were better explained by sex than by any of the other tested variables, of immunity, personality and size traits. In Chapter II, IV and V, female *H. affinis* also ate significantly more seeds than males within the same time span, and in chapter-specific contexts. This is consistent with the literature (e.g. Kulkarni, Dosdall, Spence, & Willenborg, 2015; Sasakawa, 2010; Saska, Martinkova, & Honěk, 2010). Moreover, the handling time for seeds of *T. officinale* was also shorter in females than males irrespective of the treatment in which they were foraging (Chapter III). This might suggest that females eat more than males because they have higher feeding requirements. Potentially this could be explained by female size, which is in general bigger than male body size, but no relation between body size and feeding rate were found in our results.

Immune traits could explain the higher feeding rates of females. I found that females have more hemocytes than males, and such higher immune defences have been correlated to increased feeding rates in insects (Ponton et al., 2013). However, I was not able to link feeding rates with immunity score in Chapter IV. This might be explained by the decision to only measure latency to first acceptance as proxy for individual level of choosiness and I therefore did not evaluate the total number of seeds consumed. It is possible that measuring latency to first seed acceptance was not an adequate metric to identify a potential link between individual level of immunity and energetic requirement in carabids. Immunity might have been better explained by the total number of seed eaten by individuals (Ponton et al., 2013). In the future, it would be valuable to assess both how many seeds were be eaten per individual alongside their immunity level, and also whether these values changes through season according with reproductive status (Giglio et al., 2017).

Immunity in insects can be affected by pesticide use (James and Xu, 2012). Linking the immune status and number of seeds eaten by wild caught carabid individuals might help in understanding the observed variability in predation rates observed in man-managed agricultural fields (Saska et al., 2008). The higher seed consumption by females in Chapter IV could be explained as an effect of investment by females in the energy-expensive process of egg production (Lorenz, 2003), as fecundity in female carabids is related to adult diet (Fawki and Toft, 2005; Jorgensen and Toft, 1997; Kulkarni et al., 2015b; Wallin et al., 1992). The seed diet of carabids has also been shown to affect survival, overall growth and the subsequent developmental rate of the offspring (Saska, 2005; Saska and Jarošík, 2001).

While females were observed to eat more than males, overeating was not observed in our results. The hypothesis resulting from Chapter II was that a reduction in level of choosiness would lead to a potential increase in individual overall seed consumption. However, the results of Chapter V showed that where rates of seed predation were higher during the first few hours of the test, the total daily seed consumption ultimately did not differ between treatments. Individuals exposed to predation did not continue feeding at the elevated rate, but seemed to become satiated to the same levels as control individuals, avoiding overeating. While overeating might be a good strategy for an expected long period of fasting, such as hibernation or migratory flight, it also be hazardous when foraging under predation risk. High fat reserves can reduce an individual’s ability to flee when exposed to a predator. A trade-off might therefore exist between an individual fat reserves and predation risk avoidance (Gosler et al., 1995). Foraging individuals might be predicted to avoid overeating when foraging under predation risk, which seems to be supported by our results. A study made on *Pterostichus coerulescens*, showed that foragers would avoid filling their abdomens completely when they had enough stored energy reserves (Mols, 1988). When satiated, individual locomotor activity also dropped almost to zero and the *P. coerulescens* no longer responded to prey items (Mols, 1988). This might suggest that overeating is unlikely in our beetles, and that reductions in choosiness under predation would increase the speed of seed acceptance until a fixed satiety threshold was reached rather than increasing the total seed consumption (Baranovska et al., 2014). Thus, reductions in choosiness under intraguild interference in the field, might lead to changes in seeds due to higher predation rates but not due to overall higher seed consumption foraging carabids in the community.

Chapter IV demonstrated the existence of personality traits in carabids. This was, to my knowledge, the first study working on this question in carabids. While personality traits were not linked to variation in level of choosiness or immunity in our results (Chapter IV), we think that a further study of personality traits in carabids would be interesting. Personality may be closely linked to different expectations of future fitness, leading to contrasted life history strategies (Tremmel and Muller, 2013). A study by Tremmel & Muller (2013), for example, showed that individuals of the mustard leaf beetle, *Phaedon cochleariae* (F.), feeding on low quality food became bolder than individuals fed on high quality food items. As bolder individuals might be more willing to explore new environment (Toscano et al., 2016), understanding links between individuals nutritional states, foraging environment quality and personalities in carabids might help improving our current understanding of carabids distribution, abundance and communities composition in semi-natural environments. However, the behavioural plasticity found in Chapter II & III were obtained at the population scale and individual behavioural plasticity was not examined. The goal of Chapter IV was originally to address between-individual differences in behavioural plasticity in carabids by testing successively the same individual in two different foraging conditions (Dingemanse and Wolf, 2013). The low numbers of individuals observed eating in Chapter IV made it difficult to compare effectively the intensity of variation in level of choosiness between individuals with such a low sample size, however. This “set of behavioural phenotypes that a single individual produces in a given set of environments” is referred to as *behavioural reaction norm* in the behavioural literature (Carter et al., 2012; Dingemanse et al., 2010). Studying such behavioural reaction norms in carabids might be interesting in order to address community resilience in man managed habitats. Populations that support differences in plasticity are more likely to contain individuals that are able to cope with the novel conditions, and thus to be more persistent to rapid environmental change (Dingemanse and Wolf, 2013).

3. Potential issues encountered through our results

3.1. Encountered difficulties raising from using wild caught individuals

There were, however, elements of the experimental design that were not well controlled. Culturing carabids is time consuming, being difficult both to set-up and to execute in the laboratory. Hence, I relied on wild-catches to provide enough individual carabids to run my experiments. Hence, the age of carabids, as an example trait, could not be controlled. Attempts have previously been made to determine carabid age using mandible-wear characteristics and reproductive condition (Houston, 1981; Wallin, 1989). These techniques come with additional problems, as they would have introduced problems of over-handling of our carabids that may have affected our results. I therefore decided that the best approach was to test as large a number of individuals as possible and to randomize the individuals among tests so as to distribute across all treatments any potential impact of individual age. Reproductive condition of the individual carabids were also not controlled for. However, as all individuals were maintained in boxes of mixed sexes, we assumed that most were mated when entering our tests. Anecdotally, the results of Chapter IV showing high level of hemocytes in females would suggest that all were mated (Giglio et al., 2016), and larvae and eggs were frequently observed in the cultures. The history of feeding and feeding experience could also not be fully controlled as these wild caught individuals. To reduce potential differences among individuals, feeding regimes were standardised, at least two weeks prior to the experiments, around a diet made up of the seeds that would be encountered in test. This would also have reduced potential avoidance behaviours, such as food neophobia, during the testing. Previously females carabids fed on unbalanced diets were found to select food items based on their nutrient compositions, presumably in an attempt to balance lipid, carbohydrate and protein intake (Jensen et al., 2012). Standardizing for past feeding experience, by imposing a common feeding regime, was necessary therefore for the appropriate testing of choosiness for feeding items. Despite this, it would still be interesting to understand whether an individual level of choosiness for a feeding items changed with past feeding experience. Adopting the method of Jensen et al. (2012) would allow levels of choosiness to be measured for individual foragers, of known feeding history, when confronted with prey of different quality – containing nutrients that were not present in the previous diet, for example - would assess the effects of food item relative quality on the individual level of choosiness.

3.2. Effect of the season on the data

The greatest uncontrolled effect in my work is probably the effect of seasonality. Chapter II and III, which studied *H. affinis* and *P. cupreus,* were both done across the same season of mid-Summer to early Autumn. Season did not explain the difference behaviour observed between these two species, and both species are active and feeding in the wild at the time of year of experimentation (Roger et al., 2010). In Chapter IV, however, less than 20% of the tested *H. affinis* individuals ate seeds. This finding was initially puzzling, given that in Chapter II more than 60% of individuals ate at least one seed under similar conditions. It is likely that this difference between studies is due to the season in which the individuals were tested. *H. affinis* is a spring breeder and while the tests in Chapter II were obtained between July and early autumn, the results presented in Chapter IV were obtained from experiment that only commenced in early Autumn and finished during Winter. The propensity to eat has been found to decline after July, which might explain the large number of individuals that did not eat in Chapter IV (Honek et al., 2006). It is also possible that the accumulated hand manipulation during culturing and then the experimental manipulation, which these more aged individuals would have experienced, could also have contributed to the observed low consumption rate in Chapter IV. This is emphasized by *H. affinis* spending most of its time in shelter when available (Chapter III). High use of shelter might suggest that this species is highly sensitive to risk.

It would be interesting to do an experiment assessing change in choosiness throughout the Spring to early Winter period to evaluate seasonal changes, should they exist, on individual levels of choosiness, and how this co-varies with seed species with different nutrient value. I would expect that the seeds used as food changed over the seasons, and that this would be due to the individuals preferring seeds containing particular nutrients that they need to complete particular life processes (Jensen et al., 2012; Mayntz, 2005).

4. Conclusion – the impact of changes in *H. affinis* choosiness and foraging behaviour, and its implications for the biocontrol of weeds

My results confirm that the decision-making processes of foraging carabids differs between contexts, between species and between individuals. Some carabid species lower their level of choosiness when foraging under intraguild interferences, hence making choices for food items that do not reflect preferences measured in laboratory studies (Petit et al., 2014). My results also suggest that variation in choosiness in carabids might be hard to control in fields as the intensity of risk and availability of different seeds species modify individual levels of choosiness. The choosiness of individuals would thus vary between communities of carabids with different composition and with to the seed species present in the weed community in field. These findings would explain the high variability in seed predation rates observed between studies conducted in-field, and the differences observed between laboratory studies and fields measurements. Moreover, given that a change in level of choosiness might be linked to intensity of risk and carabids might differ in their sensitivity to risks, it would be difficult to predict how each carabid individuals would vary in their level of choosiness according to the carabid community in which it is foraging. We could, however, postulate that a link should exist between carabid community composition and seed predation rates. In any given carabid community, made up of a mix of different species and guilds of carabids with different foraging strategies, intraguild interference would induce a range of change in choosiness and different predation rates and ranges of weeds consumed across all carabid species present. These changes in choosiness could, in some cases, lead to complementarity between the carabid species. Some species might behave more like *H. affinis*, being highly sensitive to perturbation and lowering their choosiness for seeds more readily. Still other species would act like *P. cupreus* and focus only on certain species of weeds (Chapter III). This idea of complementarity has been emphasized by studies finding link between carabids community composition and seed consumption in arable fields (Kulkarni et al., 2017; Menalled et al., 2007; O'Rourke et al., 2006; Trichard et al., 2013). A better understanding of how carabids predators make prey choices would, for example, help to improve the predictability of conservation biological control and weed regulation ecosystem services, it could be mandatory to extend our knowledge on carabids decision-making process. I think that on way of studying potential link between carabids community composition and predation rates of seeds in fields could be to use database.

My results from this PhD also confirmed that choices made by an individual carabids, experiencing intraguild interference in the field from among a high diversity of alternative food items, might not always reflect its preference, as assessed in laboratory studies (Underwood et al., 2004). Some studies suggest that a better insight into individual preferences and choice would be to test individuals in two-step testing methodology, using a combination of a no-choice test followed by a choice test (e.g. Allison & Cardé, 2008; Dougherty & Shuker, 2014; Murray, Withers, & Mansfield, 2010; Underwood, Chapman, & Crowe, 2004). The no-choice test would assess individual choosiness for a given seed species and improve knowledge of the effect of the prey item on choosiness, given that prey can differ in catchability, handling time and likelihood of inducing a second consumption (as species of prey might differ in the amount of energy that they provide, the consumption of one prey might not always be followed by another consumption). I suggest that in order to improve our knowledge on carabids feeding choices and preferences, seed species should first be tested using a no-choice paradigm and then be tested jointly in choice-tests using the data from the no-choice test as a control (Underwood et al., 2004). Results from such an experiment would help both understanding individual interest for a given seed species and variation of this interest when other alternatives are available.

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Publications and science communication

Accepted papers

1. Charalabidis, A., & Bohan, D. (2015, January, 25). Biodiversité: une solution contre les pesticides? Un petit carabe prometteur. *Bien Public*, p.24.

2. Charalabidis, A., Dechaume-Moncharmont, F.-X., Petit, S., Bohan, A. D. (2017) Risk of predation males foragers less choosy about their food, PLoS One (*in press*)

Submitted articles

1. Charalabidis, A., Dechaume-Moncharmont, F.-X., Bohan, A. D., Petit, S. (2017) Contrasted foraging strategy, predator interference and weed suppression in seed-eating carabids, *Submitted in Biological control*

Articles in preparation

1. Charalabidis, A., Dechaume-Moncharmont, F.-X., Iltis, C., Moreau, J., Balourdet, A., Petit, S., Bohan, A. D. (2017) The variability in foraging strategies is better explained by sex than by immunology or personality traits in carabids (in prep)

2. Charalabidis, A., Mosquera-Munõz, D., Derocles, S., Dechaume-Moncharmont, F.-X., Petit, S., Bohan, A. D. (2017) Predation risk can increase weed seed consumption by carabid beetles (in prep)

Review

Review of an article for publication in Biological control

Oral communications

1. **FJC 2016 :** Charalabidis, A., Petit, S., Dechaume-Moncharmont, F.-X. & Bohan. D., (2016). Journée des doctorants de l'Université de bourgogne 16 juin 2016, Besançon, France. More choosy under a risk of predation or of competition

2. **Ecology & Behaviours 2016:** Charalabidis, A., Petit, S., Dechaume-Moncharmont, F.-X. & Bohan. D., (2016). 12th meeting of Ecology and Behaviour, 27 juin – 1 juillet 2016, Lyon, France. More choosy under a risk of predation or of competition

3. **ISBE 2016 :** Charalabidis, A., Petit, S., Dechaume-Moncharmont, F.-X. & Bohan. D., (2016). 16th congress of the international society for behavioural ecology, 28 juillet-3 aout 2016, Exeter, Angleterre. More choosy under a risk of predation or of competition

4. **SFEcologie 2016 :** Charalabidis, A., Petit, S., Dechaume-Moncharmont, F.-X. & Bohan. D., (2016). International conference on ecological sciences, 24-28 octobre 2016, Marseille, France. Do competition and predation risk affect weed seed selectivity in granivorous carabid beetles?

5. **SFECA** 2017 (Gif sur Yvette) – Société française d'étude du comportement animal - Do competition and predation risk affect weed seed selectivity in granivorous carabid beetles?

6. **FJC 2017 :** Charalabidis, A., Petit, S., Dechaume-Moncharmont, F.-X. & Bohan. D., (2017). Un prédateur généraliste peut-il être un bon candidat pour le biocontrôle des adventices. Dijon.

Poster communications

1. **Journée des doctorants INRA 2015:** Charalabidis, A., Bohan, D., Petit, S., & Dechaume-Moncharmont, F.-X. (2015). Journée des doctorants de l'UMR agroécologie, 16 mars 2015, Dijon, France. Ecologie comportementale de la régulation des graines par les carabes.

2. **FJC 2015:** Charalabidis, A., Bohan, D., Petit, S., & Dechaume-Moncharmont, F.-X. (2015). Journée des doctorants de l'Université de bourgogne 18 juin 2015, Dijon, France. Ecologie comportementale de la régulation des graines par les carabes.

3. **EWRS 2015:** Charalabidis, A., Bohan, D., Petit, S., & Dechaume-Moncharmont, F.-X. (2015). 17th European Weed Research Society Symposium: "Weed management in changing environments", 23-26 Juin 2015, Montpellier, France. Feeding preference of an omnivorous carabid beetle.

4. **GIS 2015 :** Petit, S., Charalabidis, A., Labruyere, S., Trichard, A., & Bohan, D., (2015). Rencontres du GIS GC-HP2E et du RMT Florad sur la gestion durable des adventices (15/12/15). La prédation des graines d'adventices par les coléoptères Carabidae.

Teaching and student supervision

1. Monitorat à l'université de bourgogne (2015-2016) en licence et master – 88 hours of lectures given

2. **Internship of Benjamin Carbonne** (6 months-2015): L'interception densité dépendante des graines d'adventices par les coléoptères carabiques

3. **Internship of Diana Mosquera-Munoz** (6 months-2017): Effect of biotic interactions on the foraging behaviour of carabids beetles

Public understanding of science

1. Participation à la journée porte ouverte de l'INRA 2015 et 2016 : Présentation des coléoptères carabiques en lien avec le service écosystémique de lutte contre les adventices (2jours : 1j scolaire/ 1j grand public)

2. Présentation de l'Agroécologie aux étudiants d'Agroparistech à travers l'exemple de la lutte biologique par l'utilisation des carabes.

3. Participation à la journée mondiale des sols (Dijon, Palais des Congrès, 05/12/15) : Tenue d'un atelier sur la prédation des graines d'adventices par les carabes (1j)

4. Participation à l'Expérimentarium (Université de bourgogne) - programme de vulgarisation scientifique (rencontre de scolaires/ grand public)

5. **Radio :** Le microscope et le blouse – Radio Campus

6. **Newspapers :** http://www.infos-dijon.com/news/campus/campus/dijon-les-chercheurs-se-presentent-au-grand-public.html

7. **Cartoon :** http://experimentarium.u-bourgogne.fr/spip.php?page=article_a&id_rubrique=16&id_auteur=336

Résumé de la thèse en français

1) Introduction générale

a) Faire un choix à un cout implicite – cause de variation éventuelle de la sélectivité alimentaire

Faire un choix exige implicitement d'accepter de consacrer du temps à une tache aux dépens d'une autre. Ainsi, consacrer mon après-midi à faire du shopping revient à accepter de ne pas la passer au cinéma. Si ce n'est pas très grave pour ce qu'il s'agit d'activités de loisir, renoncer à une tache peut s'avérer bien plus problématique si son exécution est essentielle pour la survie. Lors que la quête alimentaire, par exemple, les individus investissent leur temps dans la recherche de ressources qui leur permettront de combler leurs besoins énergétiques. Si cette tâche est importante, elle est néanmoins en conflit avec une autre tâche essentielle, celle de surveiller le milieu pour la présence de prédateurs éventuels. Les individus se retrouvent donc face à un compromis entre : continuer à chercher de quoi se nourrir et consacrer leur attention à réduire au maximum les chances d'une rencontre avec un prédateur. Afin de réduire ce compromis de temps, un moyen peut être de réduire sa sélectivité, et donc le nombre de ressources rejetées, en présence d'un prédateur afin de réduire la durée de la quête alimentaire. Être sélectif, et donc long à choisir, peut aussi s'avérer délicat si la quête de nourriture se fait en présence de compétiteurs. En effet, en présence de compétiteurs, rejeter une ressource revient à implicitement accepter de ne jamais pouvoir la récupérer puisqu'elle est alors disponible pour d'autres individus, eux-mêmes en quête de nourriture. Être trop sélectif revient donc à prendre le risque de ne jamais trouver une ressource acceptable et finir, dans les cas extrêmes, par mourir de faim. Si réduire sa sélectivité peut donc s'avérer être une bonne stratégie dans certains contextes, prendre la première ressource rencontrée aléatoirement n'est toutefois pas toujours la meilleure stratégie. Dans un cas où la ressource peut être empoisonnée par exemple, ou cacher un prédateur (comme une araignée cachée dans une fleur), consacrer un minimum de temps à l'évaluation de la ressource avant de l'accepter peut être dangereux. Il existe donc un compromis entre être rapide à faire son choix, et ainsi réduire les risques de prédation ou de compétition, et être précis dans son choix. Un moyen de réduire le temps d'évaluation sans trop réduire le niveau d'exigence est de fixer un seuil d'acceptation. Par exemple, chez l'amphibien *Uperoleia larvigata* les femelles sélectionnent les mâles en prenant comme critère de choix leur poids à elle. Ainsi, une femelle ne prendra pas pour partenaire un mâle faisant plus de 70% de son poids. Ce critère arbitraire permet à la femelle d'éliminer directement de son champ des possibles tous les mâles ne correspondant pas à ce critère. Le choix pour une ressource peut aussi se faire sur son abondance relative : je ne consomme que les ressources les plus abondantes, ou sur sa facilité de capture et de manipulation. Ces règles de décision, si elles diffèrent entre les individus, permettent aussi de diminuer la compétition au sein d'une population. En effet, les femelles basant leur choix sur leur propre poids, elles réduisent les chances de s'intéresser aux mêmes mâles que les autres femelles. Ces règles de décision permettent de définir les préférences des individus.

Toutefois, les préférences ne reflètent pas toujours les choix. Le choix pour une ressource peut se faire par comparaison avec une autre plutôt que par une préférence absolue pour cette ressource. Prenons l'exemple d'un menu de restaurant. Initialement venue pour consommer un poulet au curry, mais ne trouvant pas mon choix préféré sur la carte, mon choix se portera sur l'option qui me semble la meilleure par rapport aux autres. Ce phénomène s'observe chez les guppys où les mâles forment des paires avec des mâles de moins bonne qualité afin de paraître meilleurs aux yeux des femelles qu'ils ne le sont globalement à l'échelle de la population. La manière dont les options sont présentées peut aussi influencer le choix. Par exemple, demandez à un enfant de choisir entre des brocolis et une part de gâteau. Son choix se fera sans doute pour le gâteau. Représentez la même part de gâteau mais face à un sachet de bonbons. Le choix pour la part de gâteau n'est plus si évident.

Le temps qu'un individu va investir avant de trouver une ressource qui lui convient et qu'il va accepter définie, entre autre, sa sélectivité (« choosiness » en anglais). La sélectivité diffère de la préférence en cela qu'elle désigne un seuil d'acceptabilité alors que la préférence illustre l'option choisie face à un choix. Reprenons l'exemple des brocolis et de la part de gâteau. Un enfant refusant de manger le brocoli, dans ce contexte, indique sa préférence pour le gâteau. Un enfant refusant de manger le brocoli, si c'est la seule option qui lui est offerte, est sélectif. La préférence et la sélectivité sont donc deux choses différentes et font parties des nombreuses composantes du choix. Etant deux choses différentes elles sont testées différemment. La sélectivité est fréquemment testée à l'aide de test de non-choix alors que la préférence est testée à l'aide de test de choix (ou « cafeteria »).

Comme expliqué plus haut, être sélectif implique d'investir du temps dans son processus de décision. Ce temps n'est plus disponible pour d'autres taches et cela peut s'avérer problématique dans des situations telles que des situations où le risque de prédation est important ou des situations où la compétition est forte. Ainsi, les individus ont intérêt à faire varier leur sélectivité en fonction de l'intensité du risque dans lequel ils se trouvent. La plupart des études visant à tester cet attendu montrent une augmentation de sélectivité en présence de prédateurs. Cette augmentation de sélectivité s'explique souvent par la présence de refuges permettant aux individus de sélectionner une ressource qui leur permettra de compenser pour le transport jusqu'au refuge. Bien que plus sélectifs, ils réduisent le temps d'exposition en consommant la ressource dans un abri. Dans le cas où aucun abri n'est disponible, cependant, une baisse de sélectivité est parfois observée. La sélectivité des individus peut donc varier en fonction du contexte dans lequel ils se trouvent. En présence de compétiteurs, une baisse de sélectivité est aussi attendue car elle permet de réduire les coûts d'opportunité. En effet, les autres compétiteurs pouvant consommer les ressources mises de côté, abandonner une ressource revient définitivement à la perdre et à subir des « coûts d'opportunité ». Réduire sa sélectivité, et donc son seuil d'acceptation, permet de s'assurer de ne pas finir sans avoir accepté de ressources et avec plus aucune opportunité disponible.

La sélectivité des individus devrait donc varier en fonction du contexte dans lequel ils recherchent leur nourriture. La sélectivité peut aussi varier en fonction des individus. En effet, un individu avec un niveau de satiété plus faible sera plus enclin à baisser son seuil d'acceptation qu'un individu bien nourri. La physiologie des individus ainsi que leur taille ou leur sexe pouvant impacter leurs besoins énergétiques, on s'attend à ce que ces facteurs puissent aussi influencer la sélectivité des individus. Enfin, la personnalité d'un individu pourrait aussi influencer sa propension à s'exposer au risque. Un individu « téméraire » sera plus enclin à prendre un risque qu'un individu « timide ». Leur réponse au contexte, et donc leur variation de sélectivité, ne devrait donc pas être la même entre les différents contextes.

Comment les individus font leur choix et la façon dont leur seuil de décision peut varier en fonction des individus et des contextes en font une question de recherche passionnante mais complexe. Ainsi, cette question est de plus en plus étudiée en écologie comportementale. Toutefois, cette question est souvent négligée en écologie et en agroécologie. Or, étudier les prises de décisions de potentiels auxiliaires de cultures pourrait permettre d'améliorer les potentiels services écosystémiques qui pourraient être rendus par eux.

b) Volonté de généralisation de l’utilisation d’auxiliaires de cultures en milieu agricole

Suite à la Seconde Guerre mondiale et pour pouvoir répondre à un accroissement de la demande, l’agriculture a subi des changements importants. Une spécialisation et une intensification des cultures avec une augmentation de l’utilisation des terres arables, une augmentation de la mécanisation, de l’irrigation et de l'utilisation des intrants chimiques ont ainsi permis de doubler la production mondiale de denrées alimentaires entre 1965 et 1995. Une des actions principales en vue d’augmenter les rendements a été la lutte contre les bioagresseurs. En effet, une étude menée par Oerke (2006) a démontré que les adventices, par exemple, représentaient la nuisance la plus importante pour la plupart des cultures. Bien qu’efficaces pour augmenter les rendements, ces pratiques agricoles intensives ont toutefois eu des effets négatifs tels de l’apparition de résistances aux molécules herbicides rendant le système actuel, basé sur la chimie, de plus en plus fragile. Leur bilan environnemental est aussi préoccupant (pollution des eaux, diminution de la biodiversité). Dans ce contexte, des mesures ont été mises en place afin de réduire l’usage des produits phytosanitaires. Le plan Ecophyto 2 prévoit ainsi leur réduction de 50% avant 2025.

Toutefois, les besoins alimentaires mondiaux nécessitent de maintenir la production à un certain niveau. Des solutions fiables et alternatives aux produits phytosanitaires doivent donc être mises en place afin de pallier à leur diminution. La lutte biologique, définie par l’Organisation Internationale de Lutte Biologique (OILB) comme étant « l’utilisation d’organismes vivants pour prévenir ou réduire les dégâts causés par des ravageurs », fait partie des solutions proposées pour substituer l’utilisation des produits phytosanitaires. Le principe de la lutte biologique est la réduction substantielle d’un organisme ravageur pour « l’amener en dessous d’un seuil de nuisibilité, écologiquement et/ou économiquement acceptable» à l’aide de l’agent de lutte.

Les carabes, des coléoptères de la famille des *Carabidae*, sont, par exemple, un agent de lutte potentiel. Les carabes sont très présents dans les agrosystèmes et on en compte jusqu’à 40 000 espèces dans le monde. Présentant un régime alimentaire polyphage, ils peuvent consommer à la fois du matériel végétal et du matériel animal. Les carabes sont des consommateurs importants des graines d’adventices**.** Se déplaçant essentiellement au sol, ils consomment les graines issues des pluies de semences. On parle donc en majorité, pour les carabes, d’une prédation post dispersion des semences puisque la consommation des graines se fait au sol après dispersion (pluie de semences). Ce type de prédation s'oppose à la prédation des graines pré-dispersion où la consommation se fait directement sur la plante. Après la dispersion, les graines se retrouvent éparpillées en surface sur le sol et sont, durant cette période, particulièrement sensibles à la prédation. Les taux de consommation de semences par les carabes pourraient même influencer la démographie de certaines espèces d'adventices. Des données récoltées en Angleterre ont, par exemple, mis en évidence une régulation à l'échelle nationale des graines issues de la pluie de semences par les *Carabidae* dans des cultures différentes avec des managements différents (maïs, colza de printemps et d'hiver et betteraves). Les carabes détruisant les graines qu'ils consomment, le renouvellement de la banque de graines était corrélé négativement à l'abondance de carabes dans le champ. De plus, d'après l'étude de Frank et al. (2011), les carabes se concentrent dans les zones où les graines sont à plus forte densité. Les carabes consomment essentiellement des graines d'adventices et ne consomment que très rarement des cultures (graines de blé, soja ou maïs). Cela peut probablement s'expliquer par la taille des semences de cultures, souvent bien plus importante que celle des adventices et par des dates de semis qui ne coïncident pas avec les périodes d'activité des principaux *Carabidae*. De plus, les carabes adultes se déplacent essentiellement au sol et creusent peu, ainsi, un enfouissement des semences de culture les rend donc peu disponibles à la prédation en surface.

Les carabes sont des consommateurs importants de proies végétales et animales. Dans le rapport de l'évaluation des écosystèmes pour le millénaire (MEA), les services écosystémiques sont définis comme étant « les bénéfices que les êtres humains tirent des écosystèmes ». Ils sont classés en 4 catégories : services de support, services de régulation, services d'approvisionnement et services culturels. Les carabes pourraient fournir un service de régulation, «services permettant de modérer ou réguler les phénomènes naturels, tel que la gestion des parasites». En effet, une consommation suffisamment importante des ravageurs des cultures (plantes et animaux) par les carabes pourrait permettre de réduire les impacts sur les rendements et l'utilisation de produits chimiques polluants en tant que moyen de lutte.

Toutefois, on observe une forte variabilité dans les taux de prédations dans les données obtenues suite aux expériences réalisées dans les champs. Ainsi, pour une même parcelle, les taux de prédations peuvent varier de 10% à 80% d'une semaine sur l'autre ou varier fortement en fonction des champs testés et de leur localisation. La variabilité observée pour les taux de prédation pourrait s'expliquer par des aspects comportementaux non compris encore. En effet, la majorité des études se sont intéressées aux richesses spécifiques ou à l'abondance de carabes mais peu se sont intéressées aux interactions qui peuvent exister entre les individus et aucune sur l'effet que ces interactions peuvent avoir sur les choix alimentaires des individus.

Ainsi, **l'objectif de cette thèse** est de mieux comprendre la prise de décision et les comportements alimentaires de carabes. Ces connaissances serviraient, à terme, à améliorer le service écosystémique de régulation des graines d'adventices potentiellement offert par les coléoptères carabiques en permettant un service mieux encadré et nécessitant moins d'individus.

2) Chapitre II - Influence de la compétition et de la prédation sur la sélectivité alimentaire chez le carabe granivore Harpalus affinis

a) Contexte

L'exploitation d'une ressource limite souvent l'accès simultané à d'autres ressources les laissant ainsi disponibles aux compétiteurs. Lorsqu'il se retrouve face à une potentielle ressource, un individu a donc intérêt, avant de décider ou non de l'utiliser, d'en évaluer la qualité. Ainsi, il peut éviter d'investir du temps et de l'énergie sur une ressource de mauvaise qualité aux dépens d'autres ressources de meilleure qualité. En effet, la qualité des ressources disponibles peut être très variable et certaines ressources peuvent même s'avérer dangereuses. Certaines fleurs, par exemple, peuvent cacher des prédateurs et ainsi, parfois, s'avérer dangereuses pour les pollinisateurs les moins vigilants.

Néanmoins, ce processus d'évaluation de la qualité des ressources est aussi chronophage. Il existe un compromis entre la précision d'évaluation de la qualité d'une ressource et le temps passé à évaluer cette qualité. Or, passer trop de temps à évaluer une ressource rend les individus plus vulnérables aux prédateurs et aux compétiteurs. En effet, l'animal qui se concentre sur une unique denrée alimentaire, par exemple, est moins sensible aux variations de son environnement et risque ainsi ne pas avoir conscience de la présence à proximité d'éventuels prédateurs ou de compétiteurs pour la ressource. Ainsi, pour éviter une surexposition aux prédateurs et aussi éviter des coûts d'opportunité trop importants en présence de prédateurs le temps passé à évaluer la qualité d'une ressource ne doit pas être trop important.

Dans un environnement hostile, un animal peut adopter schématiquement deux types de comportements. Le premier cas de figure est celui dans lequel l'animal ne modifie pas sa sélectivité envers de potentielles sources de nourriture ; l'individu se concentre sur des ressources qui compensent le risque encouru pour leur obtention. Le second, les individus diminue leur sélectivité et accepte plus de ressources, indépendamment de leur qualité, dans un temps total plus court. Cette deuxième option est souvent négligée dans les études cherchant à évaluer la réponse des individus aux risques. Ainsi, la réponse est souvent mesurée uniquement par l'importance de la diminution des ressources acceptées et très peu souvent par la variation du seuil d'acceptabilité alimentaire. Nous pensons que prendre en compte les processus de prise de décision dans ce genre d'études pourrait permettre de mettre en évidence des stratégies de réduction des risques de prédation et de compétition encore négligées.

b) Protocole expérimental

Pour reproduire expérimentalement ce type de situations, nous avons étudié le comportement alimentaire du carabe granivore *Harpalus affinis*, confronté à trois situations de stress : i) une situation de risque de prédation, ii) une situation de risque de compétition par d'autres individus de la même espèce (compétition intraspécifique) et iii) de risque de compétition par des individus d'une autre espèce de carabes (compétition interspécifique).

Nous avons choisi de simuler les risques de prédation et de compétition par des odeurs générées par des carabes au cours de leurs déplacements. En effet, des travaux expérimentaux ont montré que les carabes réagissent aux odeurs laissées par d'autres individus jusqu'à 48 heures après leur passage. Par ailleurs, nous voulions éviter la confrontation directe entre individus qui aurait été la source d'interactions plus complexes (compétition sexuelle, réponse à une déplétion rapide des graines etc.). Conformément aux protocoles d'autres expériences, nous avons utilisé du papier imprégné par l'odeur de 20 individus qui le parcouraient pendant au moins 24 heures avant l'expérience. En fonction du type de risque que l'on cherchait à simuler, les individus qui parcouraient la feuille appartenaient soit à la même espèce pour simuler la compétition intraspécifique, soit à l'autre espèce granivore (*P. rufipes*) pour la compétition interspécifique, soit à l'espèce omnivore (*P. melanarius*) pour simuler le risque de prédation. Afin d'avoir un témoin de la réponse des individus en milieu neutre, nous avons effectué un test contrôle dans lequel les individus étaient exposés à des feuilles de papier vierges (sans odeurs de carabes). Au terme des 24 heures, les feuilles imprégnées étaient utilisées en test. Les individus étaient placés au centre d'un cercle de 20 cm de diamètre, contenant 2 cercles de respectivement 5 et 16 cm de diamètre sur lesquels 20 graines étaient équitablement reparties. Une fois les graines déposées et un temps de 8 minutes nécessaire à l'acclimatation des individus et à une réduction du stress engendré par la manipulation, une arène composée d'un couvercle de boîte de pétri en Pyrex de 20 cm de diamètre était déposée au-dessus de l'arène. Le couvercle permettait de contenir les individus au sein de l'arène de test et d'éviter toute communication chimique entre les individus testés et l'expérimentateur. Une fois le couvercle déposé, le comportement alimentaire des individus ainsi que leur trajectoire étaient enregistrés pendant 1 heure. Toutes les expériences étaient conduites dans un environnement de température, de luminosité et d'humidité contrôlée.

Au cours l'expérience, nous mesurions 4 éléments pour évaluer la sélectivité d'un individu : la date à laquelle le carabe se met en mouvement, la date à laquelle il accepte sa première graine, la durée pendant laquelle il consomme, et le nombre de graines ingérées au cours de l'heure de test. Dans les cas où le carabe est soumis à un environnement de prédation, nous nous attendions à ce qu'il explore moins son environnement ou à ce qu'il se déplace plus rapidement pour éviter un éventuel prédateur. Ce type de déplacement influe sur la probabilité de rencontrer les graines, indépendamment du niveau de sélectivité du carabe (un individu qui explore moins son environnement rencontrerait moins de graines). Nous avons donc couplé aux observations fines de comportement, des mesures de trajectométrie. À l'aide d'une caméra placée au-dessus de l'arène nous avons obtenu des informations sur l'espace parcouru et la vitesse moyenne des carabes dans chacun des traitements de l'expérience. Nous avons également étudié la tendance des carabes à longer les bords de l'arène (thigmotactisme) et à éviter la zone la plus exposée au centre de l'arène (centrophobie). En effet, le thigmotactisme et la centrophobie sont des métriques communes pour évaluer l'anxiété des individus.

Nous avons utilisé des graines de *Taraxacum officinale* en tant que ressources disponibles pour nos expériences. Cette graine ne fait pas partie des graines les plus consommées par *H. affinis*; nous voulions éviter le cas d'une graine « trop tentante » pour ces individus, car nous aurions couru le risque que le carabe consomme cette graine, peu importe le degré de risque auquel il était exposé.

290 carabes *H. affinis* ont été utilisés pour les tests et répartis aléatoirement en 4 groupes de taille similaire et avec une sex-ratio équilibrée. Chaque individu était testé une seule fois, séparément des autres.

c) Résultats et discussion

Dans les cas de prédation et de compétition intraspécifique simulés, les carabes se sont mis en mouvement sensiblement plus rapidement que pour le contrôle ou la compétition interspécifique. Le délai avant acceptation de la première graine, quant à lui, a diminué dans tous les cas de simulation de risque par rapport au groupe contrôle, sans toutefois avoir été statistiquement significatif pour les traitements « compétition intraspecifique» et « compétition interspécifique ». Les individus ont, par contre, accepté leur première graine plus rapidement dans la situation de prédation que dans tous les autres traitements. En ce qui concerne le nombre de graines mangées, les carabes soumis au risque de prédation ont mangé plus de graines que dans tous les autres traitements. La durée totale de manipulation des graines par les carabes n'étant pas significativement différente entre les traitements et le contrôle, nous avons conclu que l'augmentation de consommation totale en situation de prédation était expliquée par une réduction globale de la latence avant 1ère acceptation et donc du seuil d'acceptation des individus. Concernant le nombre de graines consommées, nous avons aussi montré que les femelles ont, en moyenne, consommé plus de graines que les mâles tous groupes confondus. Par ailleurs, les données de trajectométrie ont montré que dans tous les cas, les carabes ont exploré environ 60 à 70% de l'arène sans que leur vitesse moyenne ne diffère sensiblement entre les traitements. Cela nous a permis d'exclure l'hypothèse d'une augmentation de consommation expliquée par une fréquence de rencontre des graines plus importante.

Cette expérience a tout d'abord confirmé que les carabes de l'espèce *Harpalus affinis* perçoivent les odeurs laissées par d'autres carabes. Leur réaction a été différente selon les odeurs des différentes guildes de carabes rencontrés durant l'expérience. Les individus de l'espèce *H. affinis* ont modifié leur comportement plus fortement lorsqu'ils étaient exposés à un risque de prédation qu'à un risque de compétition. Soumis à un risque de prédation, les individus ont significativement réduit leur seuil d'acceptation des graines; ils ont ainsi consommé plus de graines que dans le contrôle ou dans les deux situations de compétitions.

3) Chapitre III –Lien entre l'importance des graines dans le régime alimentaire d'une espèce de carabe et sa sensibilité au risque.

4) Comparaison de la sélectivité alimentaire des carabes en condition de compétition intraguilde selon leur statut granivore ou omnivore

a) Contexte

Les individus avec un régime alimentaire spécialiste sont généralement considérés comme des auxiliaires de cultures plus efficaces que les individus d'espèces généralistes. Si l'on prend l'exemple des carabes et du service écosystémique de régulation des adventices en milieu agricole, une espèce granivore (spécialiste) est censée être plus efficace qu'une espèce généraliste à réguler les graines. Un individu généraliste, puisqu'il peut compter sur d'autres sources de nourriture, devrait, en effet, fournir moins d'efforts pour obtenir une graine qu'un granivore qui, lui, dépend des graines pour sa survie. Cependant, certaines études ont montré que les espèces généralistes pouvaient aussi avoir un rôle non négligeable de régulation des adventices dans les systèmes de cultures, remettant en cause ce paradigme. En observant individuellement des carabes généralistes et spécialistes confrontés à différents types de graines, nous avons voulu tirer des informations susceptibles d'améliorer nos connaissances sur le rôle potentiel de deux espèces de carabes possédant un régime alimentaire différent sur la régulation des adventices.

Lorsqu'un carabe rejette une graine ou diminue sa sélectivité alimentaire dans des conditions de compétition ou de prédation, il prend le risque de ne finir avec rien ou seulement avec des ressources de mauvaise qualité. Cette décision pourra donc impacter plus fortement un individu dont le régime alimentaire repose exclusivement sur des graines, tel que le granivore *H. affinis*, que des individus omnivores pouvant compter sur des proies animales en l'absence de graines. On s'attend ainsi à ce qu'un individu omnivore soit plus tenté de rejeter une graine qu'il rencontre qu'un granivore. Un individu omnivore devrait moins diminuer sa sélectivité alimentaire qu'un individu exclusivement granivore lorsqu'il est soumis à un risque de prédation. D'autre part, il est intéressant d'étudier si les résultats observés de baisse de sélectivité alimentaire chez un carabe dans des conditions de prédation et de compétition se maintiennent lorsqu'on le met en présence de différents types de graines. En effet, on s'attend à ce que la prise de risque soit plus importante pour une graine « de bonne qualité » que pour une graine ne permettant pas de compenser l'effort fourni. Au cours de l'expérience suivante nous étudierons le comportement de *Poecilus cupreus*, le carabe omnivore le plus capturé dans nos pièges, et celui *d'H. affinis,* notre modèle d'étude, vis-à-vis de 4 espèces de graines d'adventices différentes.

b) Protocole expérimental

Dans un premier temps nous avons confronté les deux espèces de carabes, la généraliste et la spécialiste, à 4 espèces de graines différentes. Chaque espèce de graine était proposée séparément et suivant un protocole de test de non-choix. Nous avons mesuré le temps de latence avant 1ère consommation et le nombre total de graines consommées pour chacune des espèces d'adventices et de carabes testées. L'intérêt de cette expérience, durant laquelle nous n'avons pas simulé de risque de prédation ou de compétition, était d'obtenir un témoin et évaluer l'appétence de chacune des différentes espèces de graines en situation de contrôle. Dans un second temps, nous avons réutilisé le protocole du chapitre précédent et mesuré le comportement de *P. cupreus* pour les graines de *T. officinale* lorsqu'il était exposé aux 4 mêmes traitements que précédemment testés sur *H. affinis*. En confrontant les résultats recueillis sur les deux espèces, nous avons comparé les variations de sélectivité alimentaires d'une espèce généraliste avec celles d'une espèce spécialiste.

Pour la première partie de l'expérience, nous avons choisi d'utiliser quatre espèces de graines d'adventice communément rencontrées dans les champs et consommées par nos deux espèces de carabes: *Capsella bursa-pastori*, *Senecio vulgaris*, *Taraxacum officinale* et *Viola arvensis*. Pour cette partie de l'expérience, 80 *Harpalus affinis* ont été répartis équitablement en 4 groupes mixtes de 20 individus et 72 *Poecilus cupreus* ont été répartis en groupes mixtes de 19 individus. Pour chaque type de graines, les individus étaient observés pendant une heure dans une arène circulaire de 9cm de diamètre contenant 20 graines. Au-delà de la première heure, et au cours des 12 heures suivantes, nous avons mesuré toutes les heures le nombre de graines restantes dans l'arène et la position du carabe. Lorsque les carabes se trouvaient sous le papier humide tapissant le fond de l'arène, nous avons considéré qu'ils étaient cachés. Si les individus étaient visibles ou cachés était aussi noté toutes les heures. Enfin, lors de chaque mesure horaire, nous avons retiré les débris des graines consommées et déjà pris en compte pour éviter les comptages doubles.

Pour la seconde partie sur *P. cupreus*, nous avons simulé la compétition interspécifique et la compétition intraguilde avec les mêmes espèces de carabes que lors des expériences menées sur *H. affinis* (*cf* partie précédente), à savoir *P. rufipes* et *P. melanarius* respectivement. Durant la phase pré-test, nous avons ajouté à l'alimentation de *P. cupreus* des larves de ténébrion et du bœuf congelé. 288 *P. cupreus* ont participé à l'expérience (contre 290 *H. affinis* auparavant). Pour garantir la comparabilité des résultats entre eux, le protocole expérimental de cette seconde partie est rigoureusement le même que celui employé avec *H. affinis*.

c) Résultats et discussion

Les individus *P. cupreus* utilisés en test étaient en moyenne plus grands et plus lourds que les individus *H. affinis*.

Les observations faites au cours de la première partie de l'expérience testant la sélectivité des 2 espèces de carabes vis-à-vis de 4 espèces de graines différentes (*Capsella* *bursa-pastori, Senecio vulgaris, Taraxacum officinale* et *Viola arvensis)* ont montré que le comportement de l'espèce de carabe généraliste, *P. cupreus* variait en fonction de l'espèce de graine présentée. En effet *P. cupreus* a montré un intérêt plus important pour les graines de *T. officinale* et *S. vulgaris* que pour les 2 autres espèces de graines testées. Nous pensons que les différences d'intérêt observées entre les espèces de graines testées s'expliquent par des différences de facilité de consommation des graines par *P. cupreus.* Les individus rejettent des espèces de graines trop difficiles à consommer. En ce qui concerne *H. affinis*, nous n'avons pas noté de différences dans la façon de consommer les 4 espèces de graines proposées. Cette capacité de consommer un plus grand nombre d'espèces de graines, indépendamment de leur taille et de leur forme est un atout pour cette espèce granivore dont la survie dépend essentiellement des graines.

Dans la deuxième partie de l'expérience, visant à tester l'effet de la présence éventuelle d'autres espèces de carabes sur le comportement alimentaire de nos espèces modèles, *P. cupreus* n'a pas sensiblement modifié son comportement dans les contextes de prédation et de compétition. Cette absence de modification comportementale observée chez des individus *P. cupreus* soumis à un risque de prédation peut tout premièrement s'expliquer par une odeur utilisée pour simuler la prédation qui n'est en fait peut-être pas perçue comme un risque suffisant pour induire un changement comportemental chez *P. cupreus*. Ce résultat pourrait aussi s'expliquer par un seuil d'acceptabilité globalement plus bas, chez *P. cupreus,* pour les graines de *T. officinale* que pour les 3 autres espèces de graines testées, tel que suggéré par les résultats de l'expérience précédente. Il est possible que le seuil d'acceptabilité, déjà bas pour les graines de *T. officinale,* n'ai pas pu être diminué lors de la seconde phase de l'expérience, ce qui explique pourquoi nous n'avons pas observé de diminution de la sélectivité pour *P. cupreus* exposé à des graines de *T. officinale.*

H. affinis, à l'inverse de *P. cupreus,* a modifié son comportement et réduit sa sélectivité alimentaire en présence d'un risque de prédation. Cette baisse de sélectivité a conduit à un doublement de sa consommation totale de graines. Cette différence entre les deux espèces de carabes pourrait s'expliquer par *P. cupreus* qui ne se base pas autant sur les informations olfactives pour évaluer le danger environnant qu'*H. affinis*. Néanmoins, ces résultats vont dans le sens d'un individu généraliste dont la survie repose sur un plus large panel de ressources et qui n'aurait pas besoin d'ajuster autant sa sélectivité dans un contexte de stress environnemental qu'un individu spécialiste dépendant d'un nombre plus limité de ressources.

Si l'on extrapole certains des résultats obtenus dans ces deux expériences, on peut émettre l'idée que : dans les champs de culture, si les individus généralistes présentent bien des préférences pour certaines espèces de graines, potentiellement du fait de l'existence de limites physiologiques à la consommation d'autres espèces, alors ces graines pourraient être moins disponibles pour des individus spécialistes. Ces mêmes individus peuvent alors se retrouver à consommer un certain type de graines ne correspondant pas à leurs préférences. Cela pourrait être l'un des éléments expliquant la discordance entre les expériences réalisées sur le terrain et en laboratoire (avec des tests de choix multiples). Par ailleurs, pendant les 13 heures de la deuxième expérience, *P. cupreus* a consommé en moyenne 11 graines tandis qu'*H. affinis* en a consommé 15 ; on voit ici que pour certaines espèces d'adventices, un individu généraliste peut consommer presque autant de graines qu'un individu spécialiste. Les différences observées entre les deux espèces testées laissent penser que de nombreuses stratégies existent chez les carabes et entre les espèces. Une meilleure connaissance de ces stratégies pourrait permettre d'améliorer l'efficacité du service écosystémique de la régulation des graines par les carabes.

5) Chapitre IV - Influence des traits de personnalité et du système immunitaire sur le niveau de sélectivité alimentaire

a) Contexte

Les individus d'une même espèce peuvent différer dans leurs comportements et donc dans leur manière de chercher de la nourriture. Ces différences comportementales entre les individus qui persistent dans le temps et entre les contextes sont regroupées sous le terme de personnalité dans la littérature. D'autres facteurs individuels peuvent aussi expliquer les différences comportementales observées entre les individus. Certains facteurs d'ordre physiologiques tels que la taille, le sexe et le système immunitaire des individus peuvent aussi, par exemple, influer les comportements de quête de nourriture. Par ailleurs, the « *Pace of Life Syndrome hypothesis* » *(POLS)* postule un lien entre la personnalité et les caractéristiques physiologiques d'un individu. Un individu qui explore plus son environnement que les autres sera confronté à plus d'organismes parasites. Ainsi, son système immunitaire va être plus stimulé que les autres, nécessitant alors de la part de l'individu un apport énergétique supplémentaire, le poussant à chercher plus de nourriture. Afin de savoir si les variations interindividuelles de comportement observées dans nos deux premiers chapitres s'expliquent mieux par des différences de personnalités ou par des différences de physiologie entre les individus, nous avons regardé l'effet de la personnalité et du niveau immunitaire sur la sélectivité alimentaire chez *H. affinis*.

b) Protocole expérimental

Afin de tester l'effet de la personnalité des individus ou de leur niveau immunitaire sur leur comportement alimentaire, nous avons réalisé une série de 3 expériences sur 110 individus testés individuellement. Tout d'abord, pour mettre en évidence l'existence de personnalités différentes entre les individus chez le carabe *H. affinis*, nous avons testé la répétabilité des schémas d'exploration de l'environnement des individus. Pour ce faire nous avons étudié, et répété à six jours d'intervalle, le déplacement des carabes sur de grandes plaques carrées de 160 cm de large. Chaque mesure était précédée d'une phase de privation de nourriture de 24 heures puis chaque individu été placé sur l'arène vide et leur déplacement enregistré au cours des 10 minutes suivantes au moyen d'une caméra placée au-dessus de l'arène. Six jours après, l'expérience était répétée dans les mêmes conditions et sur les mêmes individus afin de tester la répétabilité comportementale des individus et mettre en évidence leur personnalité. Une fois les personnalités identifiées, les mêmes individus étaient testés selon le protocole de simulation de prédation par les odeurs de *P. melanarius* dans des arènes circulaires de 18cm de diamètre. Deux cercles concentriques dans l'arène délimitaient trois zones de surface : une partie intérieure de 5cm de diamètre, une partie intermédiaire de 16 cm de diamètre, et une partie périphérique jusqu'aux bords de l'arène. 20 graines de *Taraxacum officinale* étaient régulièrement réparties le long des deux cercles. L'expérience était limitée à une heure à chaque fois, pendant laquelle nous mesurions le délai d'acceptation de la première graine par le carabe. Comme dans les protocoles détaillés dans les parties précédentes, cette durée reflète la sélectivité alimentaire des carabes au cours d'un test de non-choix. Au terme de cette deuxième expérience qui a duré un mois, nous avons procédé à la troisième, toujours sur les mêmes individus. Cette dernière expérience consistait à prélever l'hémolymphe des carabes et à mesurer 3 paramètres reflétant l'activité de leur système immunitaire : la concentration en cellules immunitaires (les hémocytes), la concentration enzymatique en phenyloxidase (*PO*) et l'activité totale de la *PO* (activité de la phényloxidase et de sa pro-enzyme, la prophenoloxidase, *PPO*). Les mesures de concentration étaient optiques au moyen d'un microscope, tandis que les mesures d'activité étaient réalisées par spectrophotométrie.

c) Résultats et discussion

La première expérience d'exploration de l'environnement a mis en évidence une répétabilité importante de la façon dont chaque carabe explore son environnement, que ce soit en termes de distance totale parcourue ou de pourcentage de surface explorée. Nous n'avons pas observé de lien avec la taille ou le sexe des individus sur leur comportement d'exploration.

Dans la deuxième partie, nous avons retrouvé que les femelles mangeaient significativement plus tôt que les mâles, sans qu'intervienne le paramètre de taille des individus. La dernière expérience de mesures immunologique a montré que la concentration en hémocytes était plus élevée chez les femelles que chez les mâles. En revanche l'activité de la *PO* et de la PPO était comparable chez des individus de taille ou de sexe différents. En comparant les résultats de chaque individu avec ceux des deux expériences précédentes, nous n'avons pas observé de corrélation entre statut immunologique et exploration de l'environnement, pas plus avec la date de première consommation de graine.

Nos résultats ont donc permis de mettre en évidence l'existence de personnalités différentes chez les carabes *H. affinis*. Par ailleurs nos résultats montrent des différences immunitaires entre les sexes pour les niveaux d'hemocytes. Les femelles ont en moyenne plus d'hémocytes que les mâles. Toutefois nos résultats ne permettent pas de conclure sur le rôle d'aucun de ces deux traits sur le comportement alimentaire des individus testés. De plus nous n'avons pas mis en évidence de lien entre la personnalité des individus et leur statut immunologique ; nos resultats ne permettent donc pas de renforcer l'hypothèse du *Pace of Life Syndrome*. Les femelles consomment plus tôt que les mâles mais leur plus haut niveau d'hémocytes ne permet toutefois pas de l'expliquer statistiquement (bien qu'une corrélation forte soit observée). Nos observations selon lesquelles la sélectivité alimentaire des femelles est significativement diminuée lorsqu'elles sont soumises à un risque de prédation pourraient donc être rapportées aux observations par d'autres équipes de recherche selon lesquelles le nombre d'œufs produits est corrélé à la nourriture disponible. La dépendance des femelles envers la nourriture pour assurer leur descendance serait un moteur pour moduler leur sélectivité en situation de stress.

6) Chapitre V - Persistance de l'ajustement de comportement des carabes au risque de prédation dans des conditions plus proches de celles du milieu naturel

a) Contexte

Dans les chapitres précédents, nous avons mis en évidence une modification du comportement alimentaire de *H. affinis* lorsqu'il est soumis à un risque de prédation simulé par des traces olfactives de *P. melanarius*. Lorsqu'ils sont exposés à un risque de prédation, les individus *H. affinis* diminuent leur sélectivité alimentaire et cela se traduit par une augmentation du nombre de graines consommées pendant la durée du test (1h). Dans cette dernière partie de la thèse, nous avons voulu voir si cette modification de comportement se maintenait sur une durée plus longue et si l'augmentation de consommation était réelle ou seulement un artefact de la durée du test. Par ailleurs, les tests précédents étaient effectués seulement sur des graines de *T. officinale*, une graine modérément appréciée par *H. affinis*. Nous avions fait ce choix pour augmenter la sensibilité de nos expériences – une espèce de graine très appréciée aurait induit une prise de risque plus importante qu'une espèce moyennement aimée. A l'inverse une espèce non aimée aurait surement été délaissée quel que soit le contexte ; nous avons donc voulu voir si les modifications dans le comportement des carabes se maintenaient si on leur proposait une graine qu'ils préfèrent et qu'ils trouveraient aussi à disposition dans les champs. Enfin, dans les tests précédents, l'effet d'un risque de prédation sur le comportement alimentaire était testé par simulation à l'aide d'odeurs de prédateurs ; ce faisant nous voulions éviter que des graines soient consommées aussi par des compétiteurs et que la baisse de sélectivité observée soit due à une perception de ressource limitée plutôt qu'à la compétition. Dans cette dernière partie, nous avons complexifié et intensifié ce risque en mettant *H. affinis* directement en présence de *P. melanarius*. Nous avons envisagé deux réactions possibles d'*H. affinis* face à ce risque accru : les individus pourraient se mettre à consommer indifféremment plusieurs types de graines (cas d'une diminution importante de leur sélectivité alimentaire). Ou bien au contraire, dans ce contexte, il faudrait que les graines aient sur *H. affinis* un pouvoir d'attraction suffisant pour le motiver à affronter une telle situation ; cela se traduirait par une consommation plus importante des graines qu'il préfère (augmentation de la sélectivité alimentaire).

b) Protocole expérimental

Pour permettre des rencontres entre *H. affinis* et *P. melanarius* tout en évitant une consommation de graine par *P. melanarius*, les individus ont été testés dans une arène possédant des zones d'exclusions. L'arène complète était composée de grands bacs de 60*80cm découpés en 3 zones : 2 zones rectangulaires de 20* 60 cm placées sur les côtés et une zone centrale de 40*60cm. Les zones étaient séparées par des barrières d'exclusion perforées par des trous de 4mm laissant *H. affinis* passer mais bloquant le passage de *P. melanarius*. Les individus étaient testés soit avec des graines de *T. officinale* soit avec des graines de *V. arvensis*. 80 graines d'une des deux espèces étaient placées au centre de l'arène et le nombre de graines consommées était noté toutes les heures pendant les 7 premières heures puis toutes les 24 heures jusqu'à atteindre une durée totale de 72h (3 jours) de test. Les individus étaient testés sur sable pour simuler un sol plus poreux et donc plus proche du milieu naturel qu'un simple papier (comme dans les chapitres précédents). La position des individus était aussi mesurée afin d'évaluer la proportion de temps que les individus *H. affinis* passaient dans les zones où *P. melanarius* était présent en comparaison de la zone centrale. Cette information permettait de différencier une diminution de sélectivité pour les graines d'une augmentation de consommation due à une surexposition des graines, la taille de l'arène étant perçue comme réduite à la zone centrale en présence de *P. melanarius* dans les bordures de l'arène.

c) Résultats et discussion

Dans cet environnement plus réaliste, la diminution de sélectivité alimentaire d'*H. affinis* ne s'est retrouvée que chez les femelles et seulement pour les graines de *V. arvensis*. L'intérêt des individus *H. affinis* pour les graines de *T. officinale*, quant à lui, n'a pas changé en fonction des traitements. Ce résultat est étonnant compte tenu des résultats précédemment obtenus par d’autres équipes de recherche sur *V. arvensis* et *H. affinis*. *V. arvensis* étant majoritairement décrite comme une espèce très appréciée par *H. affinis* et préférée à *T. officinale*, aucune baisse de sélectivité n’aurait dû être observée et la consommation de *V. arvensis* aurait dû être plus importante que celle de *T. officinale* dans le contrôle. Si l’on suppose que l’attrait pour *T. officinale* est d’emblée maximal, il se peut alors que l’augmentation de risque de prédation n’ait qu’un faible impact sur la sélectivité des individus pour les graines de cette espèce et donc sur la consommation totale de ces graines. Cela serait compatible avec l’idée que pour une graine comme *V. arvensis* présentant un moins grand intérêt pour nos carabes, nous ayons pu détecter la diminution de la sélectivité alimentaire face à une augmentation du risque de prédation. D’autres facteurs peuvent également expliquer pourquoi nous n’avons pas observé la diminution attendue de sélectivité envers les graines de *T. officinale* : par exemple, les résultats des autres études ont été obtenus à l’aide de tests de choix tandis que nous avons choisi des protocoles de non-choix. Ce choix nous a permis de différencier le choix d’un individu de ces préférences relatives. De plus, les tests de non-choix pourraient nous rapprocher plus de la situation d’un carabe dans un champ qui ne trouve qu’une graine à la fois que les tests de choix. De plus, les différences observées entre les études peuvent aussi s’expliquer par les substrats utilisés qui peuvent jouer sur les niveaux d’imbibition des graines.

Le fait que le changement comportemental ne soit observé que chez les femelles dans ce chapitre suggère que la perception du risque était plus faible dans cette expérience que dans celles des chapitres précédents. La rencontre avec *P. melanarius* étant concentré aux bords de l’arène, des zones de refuges étaient disponibles pour nos individus alors que dans nos expériences précédentes l’odeur de *P. melanarius* était repartie homogènement dans l’arène. Cette différence dans la méthode d’exposition au risque a pu induire une perception différente de l’intensité du risque. Le risque peut avoir été perçu plus important avec l’utilisation des odeurs, car omniprésent alors que seulement situé dans les bords de l’arène dans cette dernière expérience. Cette étude montre que les individus sont sensibles à l’intensité du risque et à l’espèce de graine présente lorsqu’ils ajustent leur comportement alimentaire aux risques présents dans le milieu.

7) Chapitre VI – Discussion générale

Dans cette thèse nous avions pour objectif de mesurer l'impact que des interactions entre espèces de carabes pourraient avoir sur le comportement alimentaire des individus. Les carabes vivant dans des milieux où de nombreuses espèces sont présentes simultanément, mieux connaitre les interactions potentielles entre ces espèces et l'effet de ces interactions sur les comportements alimentaires des individus pourrait permettre d'améliorer notre compréhension sur la variabilité des taux de prédation encore observée dans les champs.

Nos résultats ont tout d'abord servi à montrer que les carabes déposent des odeurs sur leur passage qui sont perçues, à la fois par les autres individus de leur espèce et aussi par les individus des autres espèces. Ces odeurs ont, de plus, des impacts différents sur les comportements alimentaires des individus testés en fonction de l'espèce de carabe dont elles sont issues. Les espèces représentant un risque de compétition induisent une réponse moins importante que les espèces représentant un risque de prédation pour *H. affinis.* Lors d'une exposition réelle des individus, et non plus en utilisant des odeurs, ces résultats sont maintenus laissant penser que ces résultats obtenues en laboratoire seraient potentiellement extrapolables aux champs. Bien que des études complémentaires soient nécessaires pour conclure, nos résultats suggèrent néanmoins que la composition d'une communauté de carabe pourrait impacter les comportements alimentaires des espèces qui la composent et ainsi, le service écosystémique que cette communauté peut rendre.

Nos résultats montrent une différence entre les mâles et les femelles sur les taux de consommation. Les femelles consomment en moyenne plus de graines que les mâles. Cette différence n'est pas dépendante de la personnalité des individus, ni de leur taille ou de leur statut immunitaire. Cette différence serait plus surement due à un coût différent des gamètes entre les deux sexes. Les œufs auraient un coût de maintien plus important que les gamètes mâles entrainant des besoins énergétiques plus importants chez les femelles que chez les mâles. Cette hypothèse nécessite, néanmoins, d'être vérifiée à l'aide de tests complémentaires.

Les différences de personnalité observées entre les individus n'ont pas pu être liées à leur comportement alimentaire. Cela peut s'expliquer par un choix de métrique non adapté pour les analyses (« choosiness ») et une étude utilisant le nombre total de graines consommées pourrait éventuellement avoir des résultats différents sur une échelle spatio-temporelle plus importante (telle que celle utilisée dans le chapitre IV de la thèse). Par ailleurs, la personnalité des individus pourrait être liée à d'autres comportements, tels que la dispersion, qui seraient aussi importantes à prendre en compte dans l'étude du service écosystémique de régulation des graines. Si certains individus sont plus enclins à se disperser, cela pourrait expliquer la difficulté existante aujourd'hui pour expliquer la distribution des espèces aux champs.

En résumé, nos résultats confirment qu'il est important de s'intéresser au comportement des individus lors de l'étude d'un potentiel service écosystémique afin de mieux comprendre les variations observées dans les résultats d'études faites au champ. Dans notre cas, les individus confrontés à un risque de prédation étaient moins sélectifs que les autres. Cela indique que la composition de la communauté de carabe pourrait impacter les choix des individus des différentes espèces composant cette communauté. De plus, nos résultats montrent que l'ajustement des individus semble dépendre de l'espèce à laquelle ils appartiennent et potentiellement à leur régime alimentaire. Enfin le sexe des individus semble aussi fortement impacter leur prise de décision en contexte alimentaire. Des études complémentaires visant à tester l'effet de la saison et des périodes de pontes sur ces variations comportementales pourraient donc s'avérer très intéressantes pour mieux comprendre les prises de décisions chez les carabes.