A theory of the use of information by enemies in the predator-prey space race

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Running title: Information use by prey and predators

Abstract

A comprehensive theory about when and how behaviourally responsive predators and prey should use the information they acquire about the environment and each other's presence while engaged in what is viewed as a space race is currently lacking. This limits our understanding of the role of behaviour in trophic relationships and our ability to predict predator and prey distributions. Here we combined a simulation model with a genetic algorithm to predict how predators and prey behaving optimally should use information in environments with different levels of heterogeneity in prey forage distribution and prey vulnerability. Our results demonstrate the key role of unpredictability in successful movement strategies for both predators and prey, supporting the 'shell-game' hypothesis. We reveal striking differences between predators and prey in the magnitude of this unpredictability and its relationship with environmental heterogeneities, and in how past and recent information about encounters or prey forage availability are used.

Introduction.

Predators and prey can be viewed as engaged in a space race (Sih 1984). Prey move across the landscape, selecting patches offering a favourable balance between foraging opportunities and predation risk (here defined as the probability of being killed) (Gilliam and Fraser 1987; Abrahams and Dill 1989). Simultaneously, predators search for patches where they have the greatest chance of capturing prey (Kacelnik et al. 1992; Kennedy and Gray 1993). Not only prey and predators are most often on the move, but prey and predators generally live in environments where resources are heterogeneously distributed and they get depleted and renewed. To succeed in such dynamic environments, both prey and predators should have evolved cognitive abilities to perceive, memorize and later use information about the environment and the distribution of the other player of the space race.

Simple models have shown that the use of past information can greatly improve foraging success of individuals in heterogeneous environments by reducing their search time and improving the timing of their visits to patches, even when competition decreases resource predictability (Riotte-Lambert et al. 2015, 2017; see also Merkle et al. 2017 for an empirical demonstration). There should thus be strong selection pressure for the evolution of mnesic capacity, and memory-driven space use is increasingly demonstrated, even over large time scales (Fagan et al. 2013; Merkle et al. 2019). In the context of predator-prey interactions the use of memory could make predators and prey more predictable, allowing prey to develop some spatial avoidance strategies and the predator to search more efficiently. For instance, a prey foraging on a limited set of rich resource patches and traveling between them in virtually the same order (‘traplining’, Riotte-Lambert et al. 2016) may become highly predictable by its predator. Even if prey move less deterministically, only avoiding patches with little resources, predators could perceive the intrinsic quality of the patches for the prey, memorize the location of food-rich patches, and focus their search among them (creating a leap-frog effect, Sih 1998; see also Williams and Flaxman 2012). Meanwhile prey could also learn about this now predictable distribution of predators, and start avoiding the resource-rich, but risky, patches. Predators would thus be unlikely to persist with such a strategy. Generally, predators and prey face the dilemma that, while the use of information could apparently be beneficial to them, its use could also make them more predictable, thereby providing some benefits to their opponent in the predator-prey space race.

Under these conditions, the predator-prey race could rather be viewed as a ‘shell game’ in which “predators search for elusive prey, and prey stay on the move to remain elusive” (Mitchell and Lima 2002). Such view emphasizes that randomness could be an integral part of optimal

predator and prey movement strategies (Mitchell and Lima 2002; Mitchell 2009; Laundré 2010). Randomness may, however, loosen the link between an individual and its resources, reducing the benefits of memory use. Mitchell and Lima (2002) and Mitchell (2009)'s models however showed that it can ultimately be beneficial for prey to move randomly, and thus be unpredictable, when the predator can memorize the locations of past encounters. In such situation, the predator would be able to concentrate its search on prey-rich patches if those prey only focused on forage-rich patches and move predictably.

In these models, however, the prey had no memory, and their movement strategies were compared only across various types of random movement. Using a different model, Bracis et al. (2018) showed that prey would benefit from using memory under predation risk, especially when predation risk is decoupled from resource distribution as prey can thus avoid predators while foraging in resource-rich areas. In this model, predators could not adjust to prey distribution however. As for prey, it has been argued that predators would gain from being unpredictable (Roth & Lima 2007; Valeix et al. 2011; Berger-Tal & Bar-David 2015), although this would involve them searching areas where prey are rarer. We are not aware of models predicting the conditions under which randomness in predator movements would benefit them. Empirical demonstrations of the shell game are only emerging (Simon et al. 2019), and the optimal level of randomness that prey and predators should optimally use remains unknown. No theory integrating the co-evolution of prey and predator movement strategies have been proposed yet. As most animals are involved in a predator-prey interaction, we argue this is a fundamental gap in our ability to understand and predict the movement of individuals.

Using a simulation model associated with a genetic algorithm, we develop theoretical expectations for the optimal use, by behaviourally responsive predators and prey evolving in response to one another, of randomness and current and past information about prey forage availability and encounters. We study whether these expectations vary with the abundance and spatial heterogeneity of prey forage resources and prey vulnerability across patches.

Overall, we address the following 3 general questions, for both predators and prey:

(1) How important is the information about prey forage availability compared to the information about encounters with its opponent?

(2) How important is recent compared to long-term information on both forage availability and opponent encounters?

(3) Is it beneficial to introduce some level of randomness in the movement among patches, and if so how much is optimal?

Methods

We combined a simulation model and a genetic algorithm (GA) to find the optimal movement strategies of both predators and prey. The model, GA and analyses were implemented in R version 3.5.2 (R Core Team, 2018), using the Rcpp package (Eddelbuettel and Balamuta 2017).

Model outline

The model is summarized here and described fully in the subsequent section. The model simulates the movement of a fixed number of predators and prey between a set of patches. Patches are characterized by (i) the current amount of forage available to the prey (hereafter simply referred to as ‘forage’), which increases logistically over time but decreases with prey consumption, (ii) the maximum amount of forage that can exist in the patch and (iii) the vulnerability (i.e. the likelihood of dying) of prey when attacked by a predator or, equivalently, the success rate of attacks of the predators. At each time step prey forage and accumulate resources. When a predator and a prey are in the same patch, the predator has a probability of encountering a prey that increases with prey density. A predator attacks only once per time step. The success of the attack depends on prey vulnerability, which as indicated above, depends on patch characteristics. The prey’s fitness is determined by the resources consumed weighted by its survival probability, given all encounters during a simulation. The predator’s fitness is determined by the estimated number of prey consumed, i.e. the number of encounters weighted by the attack success of each encounter.

Past experiences within patches are used by both the prey and the predators to assign weights to each patch. Weights represent the assessment of patch quality from experience, and are therefore re-evaluated following each patch visit. Patches with more forage are given greater weights by the prey, as well as by the predators. Prey give more weight to patches where they encountered the predator less frequently. Conversely, predators give more weight to patches where they encountered prey more frequently. Predators and prey could give more or less weight to recent vs. older information. The contributions of randomness and of the weights given to patches in determining movement between patches could vary.

In each run of the model predator and prey are assigned a strategy controlling how weights are computed and how patches are chosen. A strategy is defined by the values of 4 parameters (Table S1-1 in appendix 1, and see 'Model formulation' section) that determine whether forage or encounters, and recent or old information for each, are contributing more to the weighting of the patches, and whether weights contribute little or largely to the actual choice of forage patches used.

Model Formulation

Each predator and prey store estimates of the quality of each patch as weights.

The current weight of patch *i* is noted:

For prey: $w_i = \frac{f_i}{e_i}$(equation 1)

For predator: $w_i = \phi_i \times e_i$(equation 2)

where f_i and ϕ_i are state variables indexing the perceived quality of patch *i* with regard to forage intake, respectively for the prey and the predator, and e_i a state variable indexing the perceived probability of a deadly encounter with a predator (for the prey) or a successful capture of a prey (for the predator) (see below).

At t_0, the beginning of the simulation, predators and prey are randomly distributed among patches in which the amount of forage is set to the maximum value. We assumed that predators and prey know all patches, and weights w_i are initialized with identical values for all patches. e_i are set to 1 for both predator and prey. For prey, f_i are set to the mean forage intake among patches at t_0. For predator, ϕ_i is set to the mean forage availability among patches at t_0. The model consists in a sequence of time steps, with updating of state variables within consecutive substeps.

Substep 1: Calculating forage consumption by the prey and forage renewal

This substep takes place for all patches at each time step. Prey forage intake follows a type II functional response, providing there is enough forage in the patch to feed all prey present. Else forage is equitably shared among all prey present in the patch. Thus, prey intake in patch i is calculated as follows:

$$intake_i = \frac{aR_i}{1 + ahR_i} \text{ if } R_i > n_{prey,i} \times intake_i,$$

$$intake_i = \frac{R_i}{n_{prey,i}} \text{ else. (equation 3)}$$

with a the attack rate on forage, e_i the handling time, R_i the current amount of forage, and $n_{prey,i}$ is the total number of prey in the patch.

Total consumption of forage by prey, C_i is then:

$$C_i = intake_i \times n_{prey,i} \text{(equation 4)}$$

Growth of forage in patches follow a logistic growth with a constant growth rate e_i, but a forage carrying capacity that can change among patches, f_i. The amount of forage is then updated as follow:

$$R_i' = R_i + rR_i\left(1 - \frac{R_i}{K_i}\right) - C_i$$ (equation 5)

We imposed that a minimum amount of forage K_{min} was always left in patches, so that no patch could stay without forage during the simulation. Visual representation of forage consumption and forage growth may be found in appendix 1, fig. S1-1.

Substep 2: Estimating encounters

This substep takes place for each predator present in a patch where prey are also present. Each predator search for prey, and encounters each prey sequentially with a constant probability (E), until an encounter actually occurs. Then, the predator stops searching during this time step. A prey can however encounter several predators. Formally, the probability that a predator encounters a prey increases with the number of prey present in the patch $n_{prey,i}$:

$$Pr(encounter) = \sum_{j=1}^{n_{prey,i}} E(1-E)^j = 1-(1-E)^{n_{prey,i}}$$ (equation 6)

The mean number of predator n_e encountered by a prey is thus:

$$n_e = n_{pred,i}\frac{\left(1-(1-E)^{n_{prey,i}}\right)}{n_{prey,i}}$$ (equation 7)

with $n_{pred,i}$ and $n_{prey,i}$ the number of predators and prey, respectively, present in the patch.

Visual representations of those functions may be found in appendix 1, fig. S1-2 and S1-3.

Substep 3: Updating prey patch weights

For each prey, we update the weight given to the patch being currently occupied. Weights given to the other patches are not updated. The state variable indexing the perceived quality, forage-wise, of patch i, f_i, is updated to f_i' by integrating the information about the current intake:

$$f_i' = \mu f_i + (1-\mu) intake_i$$ (equation 8)

with μ a parameter ranging from 0.01 to 0.99 and determining the relative contribution of recent vs. older information: as the value of μ increases, the relative contribution of old information to f_i' increases, and f_i' becomes mostly related to the long-term average intake at the patch, rather than to its recent state.

The state variable indexing the probability of a deadly encounter with a predator e_i is updated to e_i' by integrating the information about the number n_e of encounters with predators during this time step and the vulnerability v_i (probability of prey death given an encounter) in patch i.

If $n_e > 0$, $e_i' = e_i + n_e \beta \frac{v_i}{v_{max}}$ (equation 9)

If $n_e = 0$, $e_i' = e_i - \frac{\beta}{\delta}$ (equation 10)

Note that e_i is bound between 1 and 100. β represents the importance of information about encounters in determining space use. Prey with large values of β reduce heavily the probability of selecting the current patch after an encounter. δ represents the relative contribution of recent vs. older information in determining e_i. More specifically after an encounter, $\delta \frac{v_i}{v_{max}}$ time steps without encounters in the same patch are required for its effect on patch selection to disappear. Prey with large δ values give high importance to old encounters when using a patch while those with low δ values rely mostly on recent encounters. See fig. S1-4 in appendix 1 for an example of how β and δ determine the dynamic of e_i.

Finally, the updated weight w_i' is calculated following equation 2:
$w_i' = \frac{f_i'}{e_i'}$ (equation 11)

Substep 4: Updating predator patch weights

For each predator, we update the weight given to the patch being currently occupied. This substep is similar to substep 3 and here we only highlight what differs. Firstly, the state variable indexing prey forage availability ϕ_i is based on the amount of forage available in patch R_i, rather than on prey forage intake, and for updating ϕ_i we replace equation 6 by:

$\phi_i' = \mu \phi_i + (1 - \mu) R_i$ (equation 12)

Secondly, e_i' is calculated using equation 7, as for the prey, except that the predator cannot encounter more than one prey during a time step. Thirdly, in opposition to prey, predator with large values of β heavily increase their selection of a patch after an encounter. Finally, once ϕ_i' and e_i' are obtained, the updated weights w_i' are calculated following equation 2 instead of equation 1:
$w_i' = \phi_i' e_i'$ (equation 13).

Substep 5: Selecting target patches for predators and prey

At this stage, all patch weights w_i have been updated and can be used to determine in which patches will predators and prey move to. This substep is therefore repeated for each predator and each prey. The probability of selecting patch i at the next time step is given by:

$$Pr(i) = \frac{w_i^{\alpha}}{\sum_{j=1}^{p} w_j^{\alpha}}$$ (equation 14)

with α a parameter determining to what extent the choice of patches depends on the weights given to patches. If $\alpha \approx 0$, the individual chooses the next patch virtually at random, independently of the weights. If $\alpha = 1$, the probability for the individual of choosing a specific patch is proportional to the patch weight. If $\alpha = 8$, the highest value we used here, the individual has a very high probability of choosing the patch with the highest weight.

Fitness calculations

At the end of the simulation the fitness of each predator and each prey is calculated as follows:

For each prey the fitness F_{prey} is the product of the total intake and the survival probability:

$$F_{prey} = \left(\sum_{t=1}^{T} intake_t\right) \times \prod_{j=1}^{J} \left(1 - v_j\right) \text{ (equation 15)}$$

With $intake_t$ being the forage intake of the prey at time t, and v_j the prey vulnerability in the patch of the jth encounter, T the total number of time steps and J the total number of predator encounters.

For each predator the fitness F_{pred} is the mean number of prey consumed:

$$F_{pred} = \sum_{j=1}^{J} v_j \text{ (equation 16)}$$

with J the total number of prey encountered and the prey vulnerability in the patch of the jth prey encounter.

Note that encounters only affect fitness and no prey are ever removed from the simulation, as we are interested in calculating optimal strategies for a given population size. A prey can however have a very low probability of survival at the end of the simulation.

Finding optimal strategies

To find the optimal strategies for both predator and prey, we built a genetic algorithm (GA) on top of the model (Hamblin 2013). This well-established approach is especially valuable when brute-force optimization using gradient of parameter values for all parameters across all combinations is not computationally feasible, which was the case for our model. GA relies on a balance between exploration through the generation of new strategies and exploitation through the selection of the best strategies (Hamblin, 2013). As such, it can be viewed as mimicking the process of natural selection.

The GA is initialized with a random set of strategies. For a given number of generations, we iterate the same operation: (i) the fitness of the set of strategies investigated is evaluated by running the model, (ii) strategies experiences selection and mutation, leading to a new set of strategies. First, strategies that will persist (possibly with mutations) are selected. Selection is elitist, so the strategies leading to the 10% highest fitness values are always kept. The other strategies are selected using the k-tournament method, with k = 2 (Hamblin, 2013). The k-tournament is a non-

parametric way of selecting strategies: we generate pairs (if k = 2) of strategies and, for each pair, we keep the strategy leading to the higher fitness. After selection of the strategies, each parameter of the strategies (both from elitist and k-tournament selection) has a 5% chance of being subject to mutation, which could be a recombination (2.5%), a small mutation (1.25%) or a large mutation (1.25%). Recombinations replace the current parameter by the one of another strategy taken at random. Small mutations add a small increment to the current parameter value. Large mutations replace the current parameter by a new random value within the parameter range. On completion of the algorithm, a set of strategies remains and an additional series of generations is ran with selection but without mutation, in order to filter the remaining strategies until a single one remains for both predators and prey (Hamblin, 2013). Even after a long running time, a GA may fail to find optimal solutions because of continuous mutations, local optima or equivalence of strategies (Hamblin 2013). In our case, each one of the 720 simulations ran in a few days so it was difficult to improve convergence by increasing significantly the population size or the length of the run. In order to check the convergence of the algorithm and the robustness of our results we replicated each simulation 3 times. In cases, some parameters values differed between replicates. This was for instance often the case when strategies with low alpha values (near-random movement) were efficient, as other parameters therefore did not affect the actual movement of individuals and were thus subject to mutation-driven drift. Main text figures present results for one replicate and those for the 2 others are shown in appendix 2.

Analyses

We compared optimal strategies of predators and prey in environments with 20 prey, 5 predators and 20 patches, 15 of which being standard patches. Strategies were optimized simultaneously over 20 environment, corresponding to a total population for the genetic algorithm of 400 prey and 100 predators. Environments differed in (1) vulnerability in standard patch, with 4 values: 0.001, 0.003, 0.006, 0.01; (2) vulnerability contrast between standard and riskier patches, with 5 values: 1, 1.5, 3, 10, 20; (3) maximum forage in standard patch, with 3 values: 2.5, 10, 20; and (4) maximum forage contrast between standard and richer patches, with 4 values: 1, 1.5, 2, 4. We tested all combinations of values, yielding a total of 240 different environments. Here we present the distribution of parameters as a function of those four environmental characteristics, while also providing a comprehensive report of all results on optimal strategy parameters, as well as on the distribution of predators and prey, for all the environments tested and for the 3 replicates, in appendix 3. The distributions showed in S3-1 in appendix 3 guided our choice of parameters, and we fixed values and range of values ensuring that a diversity of distributions would be obtained, from both predator

and prey mostly using the standard patch to them mostly using the richer/riskier patch, and also including predator guarding the richer/riskier patch while prey use mostly the standard patch. We also present strategies of prey optimized without any predator in the environment in order to compare movement predictability and the use of long-term information about forage availability with some control values.

Results

Movement predictability

In all types of environments, predators are generally much less predictable than prey. Indeed, predators generally have α values below 1 (fig. 1, fig. S2-1 to S2-4 in appendix 2, fig. S3-4 to S3-6 in appendix 3), suggesting significant randomness in their patch choices. Prey movements are much more driven by the information that is integrated into patch weights (greater α)(fig. 1, fig. S2-1 to S2-4, fig. S3-4 to S3-6). In absence of predators, however, prey would be much more predictable, virtually always choosing the best patches ($\alpha \sim 8$, fig. 1, fig. S2-1 to S2-4).
Predator movement strategy involves greater randomness for higher vulnerability in standard patches (fig 1a), higher maximum forage in standard patches (fig 1c) and very high forage contrast between standard and riskier patches (fig 1d). Predator movement predictability is minimum for intermediate contrast of vulnerability between standard and riskier patches (fig 1b). Prey movement strategy involves greater randomness as vulnerability in standard patches increases (fig 1a, fig. S2-1), vulnerability contrast between standard and riskier patches increases (except for highest value, fig 1b, fig. S2-2), maximum forage in standard patches decreases (fig 1c, fig. S2-3), and forage contrast between standard and riskier patches increases (fig 1c, fig. S2-4). Irrespectively of the environment, prey were always highly predictable in absence of predators (fig. 1a,c,d).

Importance of information about encounters.

Keeping in mind that predators use past information less than prey to decide where to move (see above), information about encounters has a greater importance (greater values of β , fig 2, fig. S2-5 to S2-8, in appendix 2, fig. S3-7 to S3-9 in appendix 3) for predators' assessment of patch quality than for prey. Predators grant very high importance to information about encounters in all environments except when the contrast of prey vulnerability is very low between standard and riskier patches (fig 2, fig. S2-5 to S2-8). Prey generally give little importance to information about encounters, but this information becomes slightly more important as vulnerability in the standard

patches (i.e. the safest patches) increase (fig 2a, fig. S2-5), vulnerability contrast between standard and riskier patches increases (fig 2b, fig. S2-6), and forage contrast between standard and riskier patches increases (fig. S2-8).

Relative importance of recent vs. older information about encounters

Generally, predators and prey differ little in how they integrate recent and older encounters when determining patch weights (fig 3, fig. S2-9 to S2- 12 in appendix 2, fig. S3-10 to S3-12 in appendix 3). Both predators and prey grant greater importance to old encounters as vulnerability in standard patches increases (fig 3a, fig. S2-9), and as vulnerability contrast between standard and riskier patches increases (fig. 3b, fig. S2-10). When this vulnerability contrast becomes very large, then prey use information about old encounters more than predators (fig 3b, fig. S2-10). Forage availability has a rather limited effect on prey and predators' relative use of information about recent and old encounters (fig. 3c, 3d, fig. S2-11, S2-12).

Relative importance of recent vs. older information about forage availability

When determining patch weights, and despite the large variability observed in the results, prey tend to use recent information on forage availability (smaller f_i than predators, fig. 4, fig. S2-13 to S2-16 in appendix 2, fig. S3-13 to S3-15 in appendix 3), although predators rely less on information about forage availability than prey to determine where to move (see Results sub-sections above). For predators, the importance of recent vs older information on forage availability increases as vulnerability in standard patches decreases (fig 4a, fig. S2-13), when vulnerability differs greatly between standard and riskier patches (fig 4b, fig. S2-14), and as forage contrast between standard and riskier patches increases (fig 4d, fig. S2-16). For prey, the importance of recent vs older information on forage availability increases as vulnerability in standard patches decreases (fig 4a, fig. S2-13), vulnerability contrast between standard and riskier patches decreases (fig 4b, fig. S2-14). Forage in standard patches (fig 4c, fig. S2-15) and forage contrast between standard and riskier patches (fig. 4d, fig. S2-16) possibly also affect how recent information is used by prey, but results varied largely between simulations. It is clear, however, that the absence of predators should often lead prey to value recent information even more (fig. 4).

Discussion

We developed, to our knowledge, the first model predicting how both optimal predators and prey should use information about prey forage availability and encounters with their opponent. The model revealed general differences in the optimal use of information between predators and prey, as well as the influence of key environmental characteristics such as contrasts in forage availability

and vulnerability between patches on the strategies. The study offers a theoretical framework to interpret previous studies and generalize their predictions. In particular, our model provides three clear predictions that apply to the realistic situation of competitive prey foraging under predation risk: (1) predators and prey play a shell game in which each player is trying to keep its location unpredictable. Predators remain however much more unpredictable than prey; (2) what makes a good patch for a predator is more linked to successful encounters with prey than high prey forage availability; the opposite is true for prey; (3) prey and predators used recent and old information about encounters rather similarly, and gave more weight to recent encounters. In contrast, the relative importance of recent and old information about forage availability was highly variable, differing between prey and predators and depending on environmental characteristics. We now discuss these predictions further, in the light of existing and future possible studies.

Previous theoretical (Mitchell and Lima 2002; Mitchell 2009) and empirical (Roth & Lima 2007; Valeix et al. 2011; Bosiger et al. 2012, Simon et al. 2019) studies have suggested that predators and prey play a shell game in which both the prey and the predator would benefit from moving regularly in an unpredictable manner to prevent the other player to learn and then avoid (for the prey) or focus on (for the predator) places where the other player would be. Theoretical studies have however focused on unpredictability of the prey, as they never allowed predators to move somewhat randomly. Empirical studies never compared movement predictability of predators and prey. Our model fills these gaps from a theoretical standpoint. In the model, predators' movements were often unpredictable. A prey knowing a predator's patch weights would not be able to predict its movement as the predator's movements were only weakly determined by those weights (alpha < 1, fig. 1). Conversely, although prey did not always move towards the best patches, a predator knowing prey patch weights would significantly increase its chances to find prey, as it could restrict the number of patches where to look for, as prey most often selected patches with a probability at least proportional to the patch weight (alpha >> 1, Fig. 1). The comparison of prey strategies in presence or absence of predators however clearly demonstrate that, in absence of predators, prey would be much more predictable, always moving towards the patch perceived as best (see also Riotte-Lambert et al. 2015, 2017 for models leading to highly predictable prey in absence of predation). The general contrast in movement randomness between predators and prey was robust to variations in the levels and contrasts of forage availability and vulnerability in the landscape (see below for a discussion of the effects of these factors).

Differences in movement strategies between predators and prey could be explained by considering the cost and benefits of randomness for both. Regarding benefits, random movement by

predators increases the availability of prey that, if behaviourally responsive to predictable risk, could otherwise increase their antipredator behaviours (Mitchell 2009, Bosiger et al. 2012) or shift location when informed of predator's presence (Courbin et al. 2016). Randomness could thus allow predators to fight behavioural resource depression (sensu Charnov et al. 1976; Kotler 1992). Random movement by prey benefits them as it reduces the searching efficiency of predators that can memorize past encounters and could use this information for later searches (Mitchell 2009). As for costs, even though predators could recognize a good patch, mostly based on past encounters as high forage availability is just a proxy for the potential presence of prey (Flaxman and Lou 2009), the cost of ignoring this information and moving randomly is likely to be lower than for the prey. Predators moving randomly and arriving at a bad patch only suffer from missed opportunity costs (MOCs) of foraging (prey capture). In contrast, prey moving randomly rather than doing an informed choice and arriving on a bad patch could suffer from two costs, lower forage intake (MOC of foraging) and increased predation risk. In our simulations, prey movement was virtually always strongly determined by patch weights, suggesting that in most circumstances the costs associated with randomness largely outweighed its potential benefits. In addition, as predators evolve to be unpredictable, information about past encounters becomes less and less relevant to the prey. Prey therefore end up giving much more weight to information about forage availability than to encounters, focusing their movement towards good foraging patches, with a low, but not negligible, level of unpredictability to extend the predator' area to search, giving prey a chance to avoid encounters. Overall, with our model, we confirm the potential importance of randomness in the predator-prey spatial game, and emphasize and explain why we should expect predators to be unpredictable, and prey not so, but more than in absence of predation.

Our model also provides insights on how prey and predators should use recent and past information about encounters and forage availability. Recent encounters appear to be given more weight than older ones by both prey and predators. This make sense as, generally, information about encounters is poorly used by both: prey because they cannot predict where predators occur and thus mostly use information about forage availability, predators because they move rather randomly and therefore do not use much information, although when they do they favor information about where they met prey rather than about forage availability. It is likely that both prey and predators only used information about recent encounters to try to escape (for the prey) or remain in (for the predator) patches where an encounter occurred. In contrast, and despite strong variability among simulations and environmental contexts, recent and older information about forage availability was used differently by prey and predators. Prey generally gave more weight to recent information about

forage than predators did. This could be explained by the fact that recent information is important for the prey as it allows it to keep foraging in good foraging patches, or move away when foraging in poor patches. For predators, recent forage availability might be a poor predictor of finding prey that could have arrived there by chance, whereas longer-term information about forage availability in patches might be a predictor of the likelihood of prey's presence or density. As discussed before, however, information about forage availability remains weakly used by predators, unless patches do not differ in vulnerability, in which case predators move less randomly and give slightly more weight to information about forage than usual (Fig. 1 and 2). Thus, although our study suggests that leap-frogging, i.e. situation when predators track prey resource rather than prey themselves (Sih 1998; Flaxman and Lou 2009) should be rare, it might be more detectable in environments where prey vulnerability is homogeneous, as in the experimental contexts that have been used to test it (Hammond et al. 2007, Williams and Flaxman, 2012).

Generally, although the level and distribution of risk and prey forage in the environment did not qualitatively alter the observed differences between predators and prey space use strategies, it still did have predictable and noticeable effects. Increasing global risk levels, either by increase the prey vulnerability in all patches, or only in riskier patches, leads prey to give increasing importance to encounters relative to forage availability. As risk increase, prey initially become slightly less predictable, but this effect does not persist, and possibly reverse, in very high risk situations. Simultaneously, prey spend increasingly more time in standard, safer, patches (fig S3.1 in appendix 3), increasingly using long-term information on encounter risk to identify these. Predators become less predictable and use patches increasingly randomly, although this effect appears to be slightly reduced when the vulnerability contrast between standard and riskier patches increases, predators then using long-term information about encounters likely to avoid random movements that would take them to riskiest patches barely ever used by prey. Therefore, our results suggest that lowest levels of movement predictability of prey and predators should be observed at intermediate levels of vulnerability heterogeneity within the landscape. To the best of our knowledge, this theoretical prediction has not been made before, and is amenable to testing. Effects of the levels and heterogeneity of prey forage availability differed from those observed for vulnerability, and in cases affected movement predictability of prey and predators in a contrasted way. While predators become slightly less predictable as forage availability increases in all patches, prey become increasingly predictable, focusing more on standard, safest, patches, using long-term information on forage to identify them. Note how, in absence of predation, prey would in contrast increasingly use the most recent information to find most profitable patches. Prey predictability

however decreases as riskier patches become more profitable. This likely occurs because the costs of not moving to the best patches is increasingly reduced by finding higher forage availability when the prey move to a riskier patch, which they increasing do (see fig S3.1 in appendix 3). Increasing forage availability in all patches, or only in riskier patches, has little effect on the relative importance prey and predators give to forage availability in patches.

Our work provides a theoretical framework to predict how prey and predator movement strategies should have evolved in environments of varying forage and vulnerability levels and heterogeneity. To make these predictions useful, we tried to find the right balance between model simplicity and realism, while focusing on improving previous approaches by considering both prey and predators as behaviorally-responsive players of the space game, as observed by empirical studies (Hammond et al. 2007, Williams & Flaxman 2012). These predictions should now be challenged by experimental and observational studies to reveal the extent of our understanding of predator-prey interactions.

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Figures

Figure 1. Optimal values for movement predictability for predator and prey, in function of (a) vulnerability in the standard patch, (b) vulnerability contrast between standard and rich patch, (c) maximum forage in the standard patch and (d) maximum forage contrast between standard and rich patch. Low values correspond to random and unpredictable movement. High values correspond to movement directed towards the best patch, as estimated by the individual. White boxplots show the strategy for prey without predator in patches and are therefore not assigned to vulnerability values.

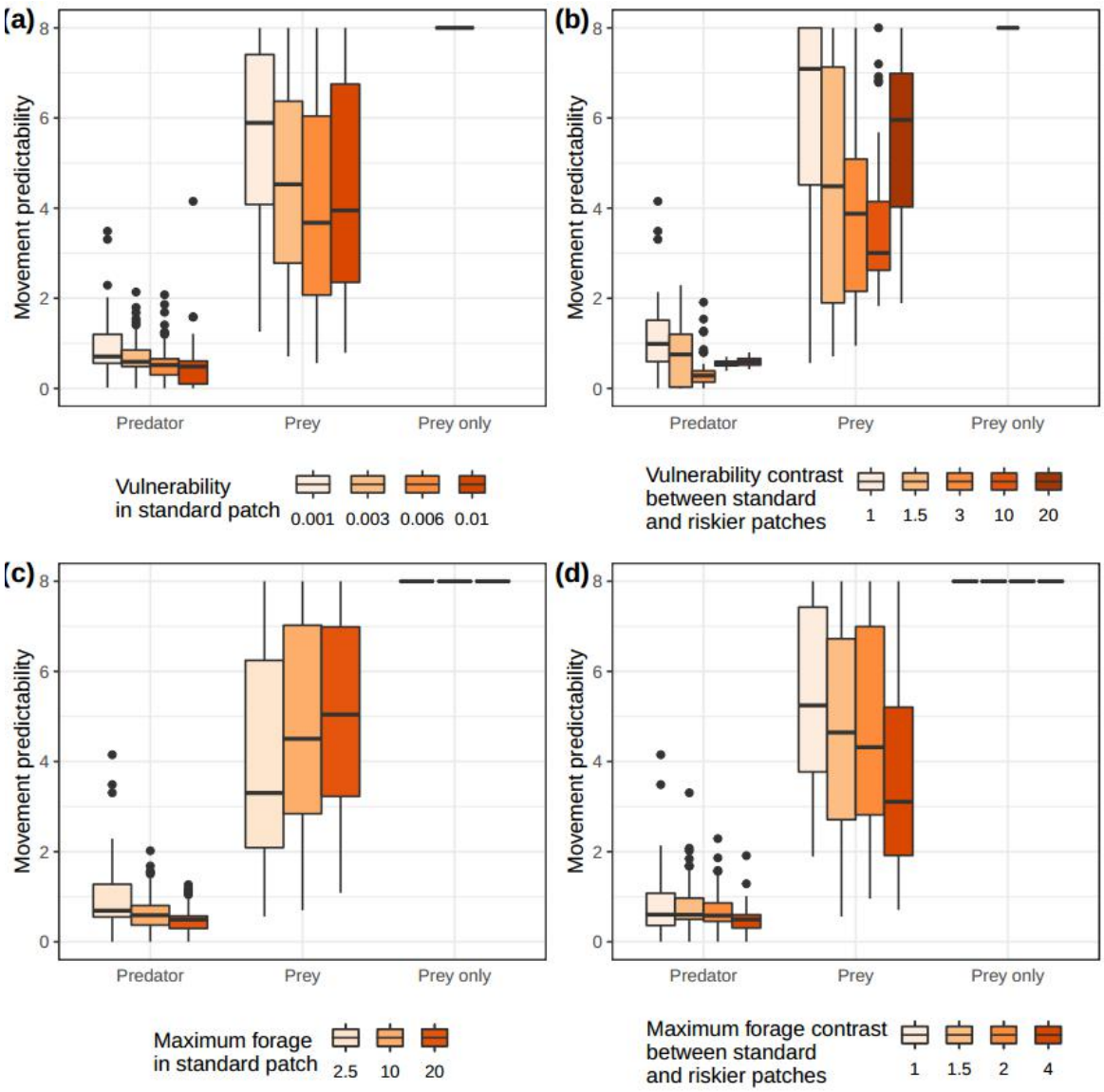

Figure 2. Optimal values for the importance of information about encounters for predator and prey, in function of (a) vulnerability in the standard patch, (b) vulnerability contrast between standard and rich patch, (c) maximum forage in the standard patch and (d) maximum forage contrast between standard and rich patch.

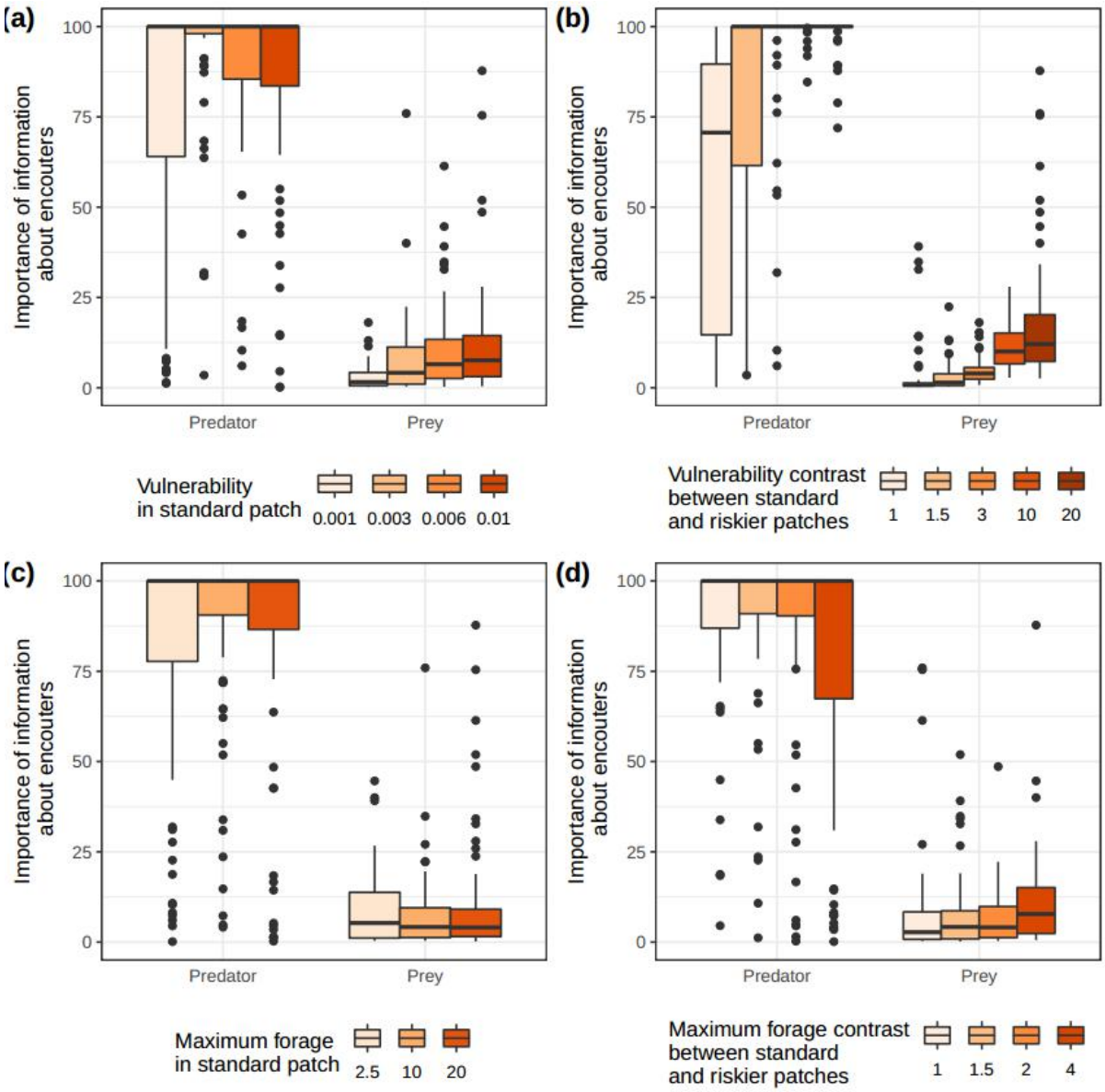

Figure 3. Optimal values for the use of long-term information about encounters for predator and prey, in function of (a) vulnerability in the standard patch, (b) vulnerability contrast between standard and rich patch, (c) maximum forage in the standard patch and (d) maximum forage contrast between standard and rich patch. Low values correspond to the use of recent information.

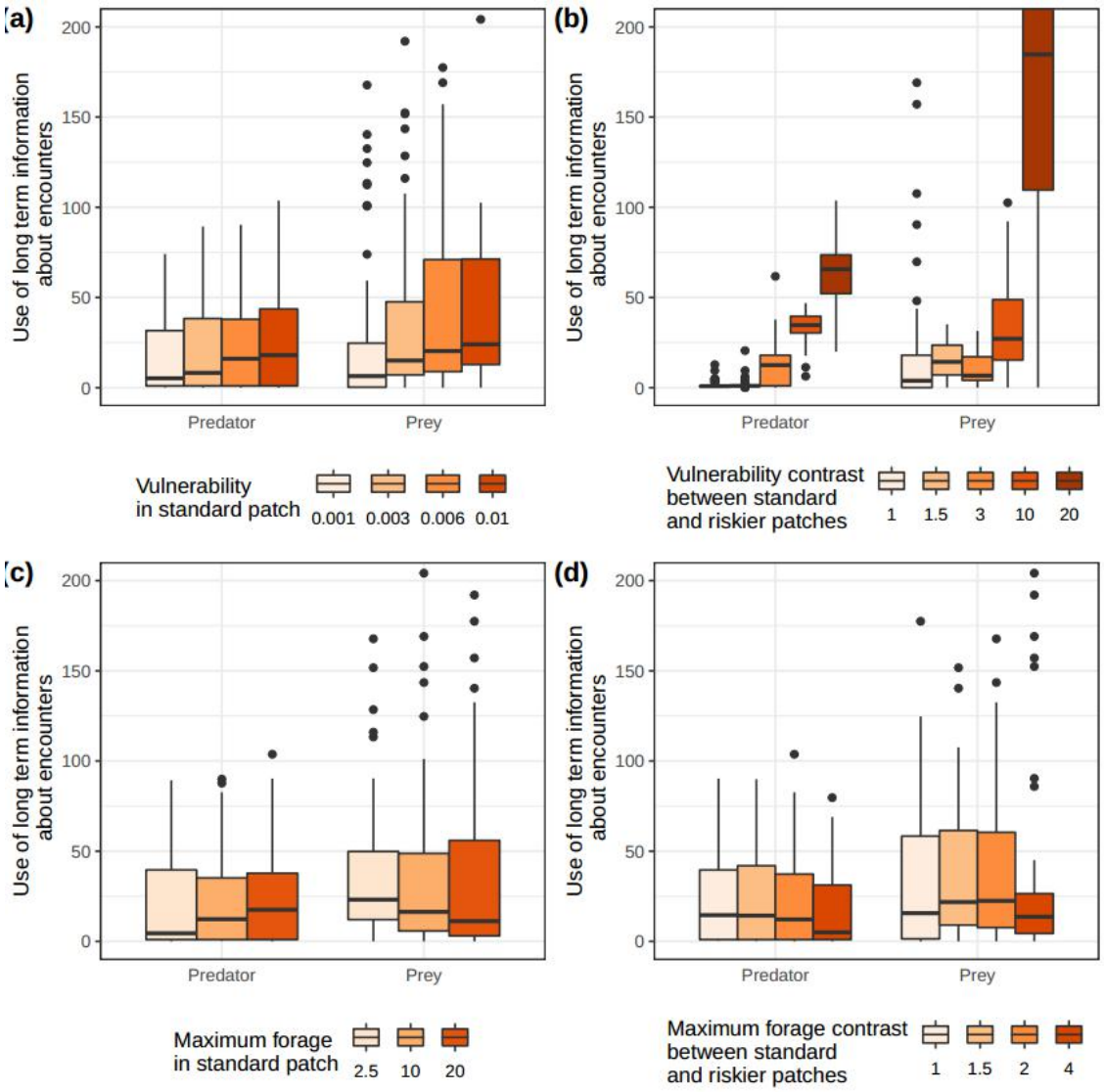
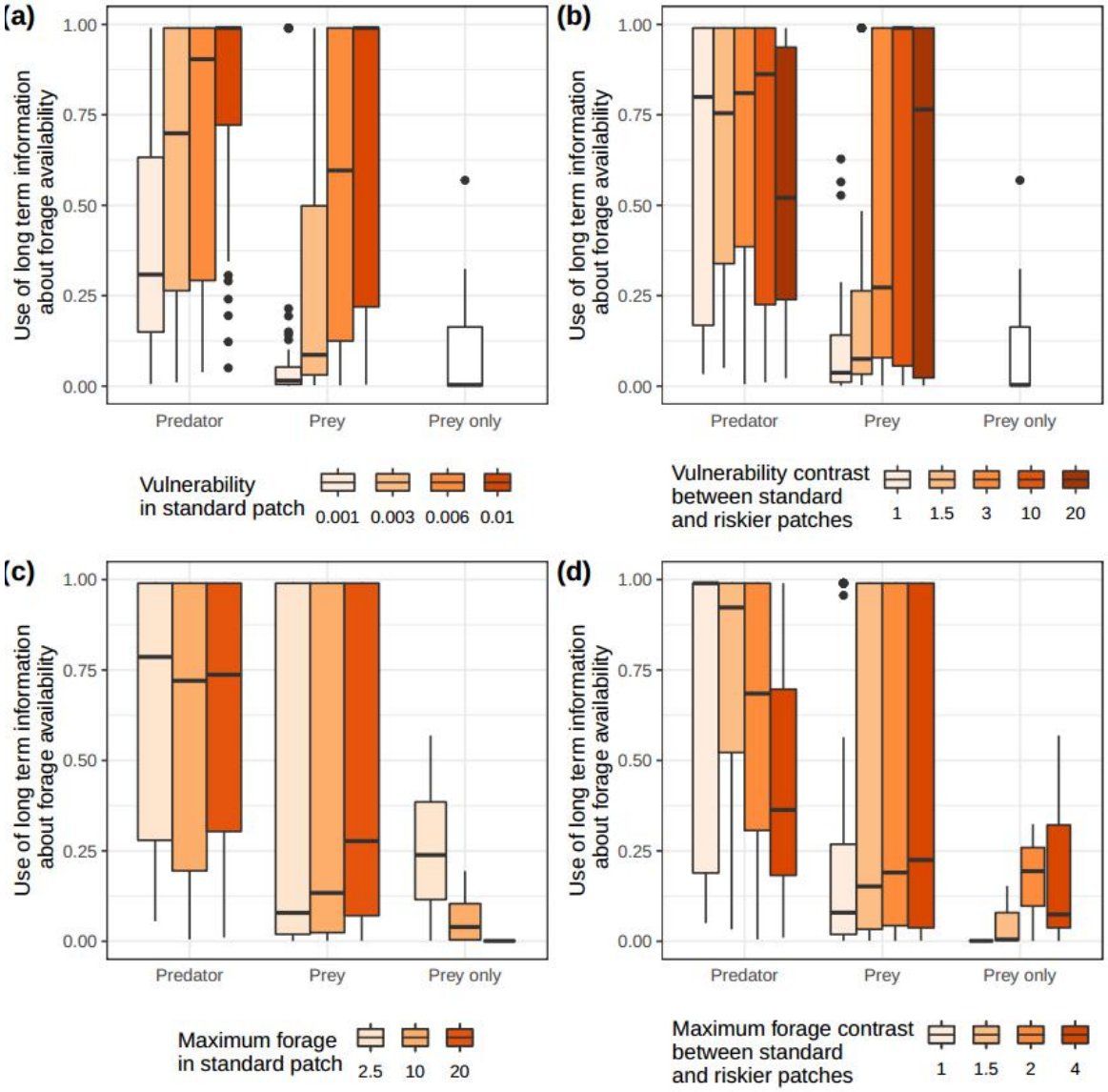
Figure 4. Optimal values for the use of long-term information about forage availability for predator and prey, in function of (a) vulnerability in the standard patch, (b) vulnerability contrast between standard and rich patch, (c) maximum forage in the standard patch and (d) maximum forage contrast between standard and rich patch. White boxplots show the strategy for prey without predator in patches and are therefore not assigned to vulnerability value.