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A theory of the use of information

by enemies in the predator-prey space race

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Data accessibility statement: All data were simulated.

27 **Abstract**

28 We currently lack a comprehensive theory about how behaviourally responsive predators and prey
29 use the information they acquire about the environment and each other's presence while engaged in
30 the 'space race'. This limits our understanding of the role of behaviour in trophic relationships and
31 our ability to predict predators and prey distributions. Here we combined a simulation model with a
32 genetic algorithm to discover how predators and prey behaving optimally should use information in
33 environments with different levels of heterogeneity in prey forage distribution and prey vulnerability.
34 Our results demonstrate the key role of movement unpredictability in successful strategies for both
35 predators and prey, supporting the 'shell-game' hypothesis. We however reveal striking differences
36 between predators and prey in the magnitude of this unpredictability, and in how it varies with the
37 environment. Our work offers a robust theoretical framework to better understand predator-prey
38 space use and interpret empirical studies.

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46 **Introduction**

47 Predators and prey can be viewed as engaged in a ‘space race’ (Sih 1984). Prey select patches
48 offering a favourable balance between foraging opportunities and predation risk (Gilliam & Fraser
49 1987; Brown & Kotler 2004), while predators search for patches where they have the greatest chance
50 of capturing prey (Kacelnik et al. 1992; Hopcraft et al. 2005). Not only prey and predators are most
51 often on the move, but prey and predators generally live in environments where resources are
52 heterogeneously distributed as they get locally depleted, and renew. To succeed in such dynamic
53 environments, both prey and predators should have evolved cognitive abilities to perceive, memorize
54 and later use information about the environment and the distribution of their enemies in the space
55 race.

56 Simple models have shown that the use of past information can greatly improve foraging
57 success of individuals in heterogeneous environments by reducing their search time and improving
58 the timing of their visits to patches, even when competition decreases resource predictability (Riotte-
59 Lambert et al. 2015, 2017)(see also (Merkle et al. 2014) for an empirical demonstration). Selection
60 pressure for the evolution of mnesic capacity is likely strong and, accordingly, memory-driven space
61 use is increasingly demonstrated (Fagan et al. 2013; Merkle et al. 2019). The use of memory could
62 however make predators and prey more predictable, allowing prey to develop spatial avoidance
63 strategies, and predators to search more efficiently. For instance, a prey foraging on a limited set of
64 rich resource patches and traveling between them in virtually the same order (‘traplining’, Riotte-
65 Lambert et al. 2016) may become highly predictable by its predator. Even if prey move less
66 deterministically, only avoiding patches with little resources, predators could perceive the intrinsic
67 quality of the patches for the prey, memorize the location of food-rich patches, and focus their search
68 among them (‘leap-frogging’, Sih 1998). Meanwhile, prey could also learn about this now predictable
69 distribution of predators, and start avoiding the resource-rich, but risky, patches. Predators would thus
70 be unlikely to persist with such a strategy. Generally, predators and prey face the dilemma that, while
71 the use of information could apparently be beneficial to them, its use could also make them more
72 predictable, thereby providing some benefits to their enemies in the predator-prey space race.

73 Under these conditions, the predator-prey race could rather be viewed as a ‘shell game’ in
74 which “predators search for elusive prey, and prey stay on the move to remain elusive” (Mitchell &
75 Lima 2002). Such view emphasizes that randomness could be an integral part of optimal predator and
76 prey movement strategies (Mitchell & Lima 2002; Mitchell 2009). Randomness may, however,
77 loosen the link between an individual and its resources, reducing the benefits of memory use.
78 Mitchell & Lima (2002) and Mitchell (2009)’s models however showed that it can ultimately be
79 beneficial for prey to move randomly, and thus be unpredictable, when the predator can memorize the
80 locations of past encounters. In such situation, the predator would be able to concentrate its search on
81 prey-rich patches if those prey only focused on forage-rich patches and move predictably.
82 In these models, however, the prey had no memory, and their movement strategies were compared
83 only across various types of random movement. Using a different model, Bracis et al. (2018) showed
84 that prey would benefit from using memory under predation risk, especially when predation risk is
85 decoupled from resource distribution as prey can thus avoid predators while foraging in resource-rich
86 areas. In this model, predators could however not adjust to prey distribution. As for prey, it has been
87 argued that predators would gain from being unpredictable (Roth & Lima 2007; Valeix et al. 2011),
88 although this would involve them searching areas where prey are rarer. We are not aware of models
89 predicting the conditions under which randomness in predator movements would benefit them.
90 Empirical demonstrations of the shell game are only emerging (Simon et al. 2019)(but see Laundré
91 2010), and the optimal level of randomness that prey and predators should optimally use remains
92 unknown. No theory integrating the co-evolution of prey and predator movement strategies has been
93 proposed yet, and we argue this is a fundamental gap in our ability to understand and predict the
94 movement of animals.

95 Here, we develop theoretical expectations for the optimal use, by behaviourally responsive
96 predators and prey, of randomness and current and past information about prey forage availability and
97 encounters. We study whether these expectations vary with the abundance and spatial heterogeneity
98 of prey forage resources and prey vulnerability across patches.

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

100 (1) How important is the information about prey forage availability compared to the information
101 about encounters with enemies?

102 (2) How important is recent vs. older information on both forage availability and encounters with
103 enemies?

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

106

107 **Methods**

108 We combined a simulation model and a genetic algorithm to find the optimal movement strategies of
109 both predators and prey. The implementation was done in R (R Core Team 2018) using the Rcpp
110 package (Eddelbuettel & Balamuta 2018).

111

112 **Model outline**

113 The model simulates the movement of a fixed number of predators and prey between a set of patches.
114 Patches are characterized by (i) the current amount of forage available to the prey (hereafter referred
115 to as 'forage'), which increases logistically over time but decreases with prey consumption, (ii) the
116 maximum amount of forage that can exist in the patch and (iii) the vulnerability (i.e. the likelihood of
117 dying) of prey when attacked by a predator or, equivalently, the success rate of attacks of the
118 predators. At each time step, prey forage and accumulate resources. Predators have a probability of
119 encountering a prey that increases with prey density in the patch, but attack only once per time step.
120 Both prey and predators assign weights to each patch: weights represent the assessment of patch
121 quality from past experience, and the weight of a patch is therefore re-evaluated following each visit.
122 Both predators and prey have movement strategies, defined by the values of 4 parameters (α , μ , β ,
123 and δ , see 'Model formulation' section below), determining whether forage or encounters, and recent
124 or old information for each, are contributing more to the weighting of the patches, and finally whether
125 weights contribute a lot or little to the actual choice of the patch used at the next time step.

126

127 **Model Formulation**

128 Central to the model is the fact that each predator and prey store estimates of the quality of patches as
129 weights. For any given individual, the current weight given to patch i is:

130 For a prey, $W_i = F_i / E_i$ (equation 1)

131 For a predator, $W_i = F_i \times E_i$ (equation 2)

132 where F_i is a state variable indexing the perceived quality of patch i with regard to prey forage, and E_i
133 a state variable indexing the perceived chance of being predated upon (for a prey) or of successfully
134 capturing a prey (for a predator) in patch i (more details below).

135 The model consists in a sequence of time steps, themselves decomposed into consecutive substeps.

136 Parameter values and initialization values of state variables are presented in Supporting Information
137 (SI) 1.

138

139 **Substep 1: Calculating forage growth and consumption**

140 This substep takes place for all patches at each time step t . The amount of forage levels in patches
141 follows a logistic growth reduced by prey consumption, such as:

142 $R_{t+1,i} = R_{t,i} + r_m \times R_{t,i} \times (1 - R_{t,i} / K_i) - (I_{t,i} \times N_{t,i})$ (equation 3)

143 with $R_{t+1,i}$ and $R_{t,i}$ the amount of forage in patch i at time $t+1$ and t respectively, r_m the maximum
144 forage growth rate (constant among patches), K_i a forage carrying capacity that can vary among
145 patches, $N_{t,i}$ the number of prey in patch i at time t , and $I_{t,i}$ the forage intake of a prey in patch i at time
146 t . Prey forage intake follows a type II functional response, providing there is enough forage in the
147 patch to feed all prey present. If not, forage is equitably shared among all prey present in the patch:

148 If $R_{t,i} > (I_{t,i} \times N_{t,i})$, $I_i = a \times R_{t,i} / (1 + a \times h \times R_{t,i})$ (equation 4.1)

149 else, $I_{t,i} = R_{t,i} / N_{t,i}$ (equation 4.2)

150 with a the attack rate on forage and h the handling time.

151 We assumed that prey consumption could not lead a patch to a stage where it would not regrow, and
152 allowed $R_{t+1,i} = R_{\min}$ (with R_{\min} small, Table S1), if eq. 3 returned $R_{t+1,i} < R_{\min}$.

153

154 **Substep 2: Estimating encounters**

155 This substep takes place for each predator present in a patch where prey are also present. Each
156 predator search for prey, and encounters each prey sequentially with a constant probability p_e , until
157 all prey present in the patch have been tested or an encounter occurs. The predator then stops
158 searching during this time step. A prey can however encounter several predators.

159

160 **Substep 3: Updating prey patch weights**

161 For each prey, the weight given to the patch i currently occupied, and only this one, is updated. The
162 state variable F_i indexing the perceived quality, forage-wise, of patch i , is updated by integrating the
163 information about the current intake:

164 $F_i = \mu \times F_i + (1 - \mu) \times I_{t,i}$ (equation 5)

165 with μ a parameter whose value is within]0-1[and determine the relative contribution of recent vs.
166 older information: as the value of μ increases, the relative contribution of old information to F_i
167 increases, and F_i becomes mostly related to the long-term average intake at the patch, rather than to
168 its recent state.

169 The state variable E_i is updated by integrating the information about predation risk, such as:

170 If $N_{t,e} > 0$, $E_i = E_i + N_{t,e} \times \beta \times (\gamma_i / \gamma_{max})$ (equation 6.1)

171 else, $E_i = E_i - (\beta / \delta)$ (equation 6.2)

172 where $N_{t,e}$ is the number of encounters of the prey with predators during this time step, γ_i the
173 vulnerability (probability of prey death given an encounter) in patch i , and γ_{max} the maximum
174 vulnerability observed among all patches. β represents the importance of information about
175 encounters in determining space use: prey with greater values of β gives lower weights to the patch
176 after an encounter. δ represents the relative contribution of recent vs. older information on encounters
177 in determining E_i . Specifically, $\delta \times (\gamma_i / \gamma_{max})$ time-steps without an encounter in patch i are required
178 for the influence of an encounter on the weight of patch i to disappear. Therefore, prey with greater δ
179 values give higher importance to old encounters when selecting a patch. Finally, the weight W_i is
180 updated following equation 1.

181

182 **Substep 4: Updating predator patch weights**

183 For each predator, the weight given to the patch i currently occupied, and only this one, is updated.

184 This substep is similar to substep 3 and we only highlight what differs. Firstly, for predators, the state
185 variable indexing prey forage availability F_i is updated based on $R_{t,i}$, the amount of forage available in
186 patch i at time t , rather than on prey forage intake ($I_{t,i}$), which would be harder to evaluate for a
187 predator. Therefore,

$$188 F_i = \mu \times F_i + (1 - \mu) \times R_{t,i} \text{ (equation 7)}$$

189 Secondly, as for prey, E_i is updated using equations 6.1 or 6.2, but $N_{t,e}$ equals the number of prey
190 encountered by the predator during this time step, which is 0 or 1 as the predator cannot encounter
191 more than one prey during one time step. Finally, the weight W_i is updated following equation 2.

192 Note that, in contrast to prey and because of the difference between equations 1 and 2, predators with
193 greater values of β give greater (not lower) weight to the patch after an encounter. β however still
194 index the importance of encounters vs. prey forage in driving patch choice.

195

196 **Substep 5: Selecting target patches for predators and prey**

197 This substep is repeated for each predator and each prey. The probability of selecting, at the next time
198 step, patch i among patches 1, ..., p , is given by:

$$199 P_{t+1,i} = (W_i)^\alpha / (\sum_{j=1}^p (W_j)^\alpha) \text{ (equation 8)}$$

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

205

206

207

208 **Fitness calculations**

209 At the end of the simulation, the fitness of each prey is calculated as the product of its total intake and
210 its survival probability. The fitness of each predator is calculated as the number of prey successfully
211 captured.

212

213 **Finding optimal strategies**

214 To find the optimal strategies for both predator and prey, we built a genetic algorithm (GA) on top of
215 the model (Hamblin 2013). This approach is especially valuable when brute-force optimization using
216 gradient of parameter values for all parameters across all combinations is not computationally
217 feasible, which was the case for our model. GA relies on a balance between exploration through the
218 generation of new strategies and exploitation through the selection of the best strategies (Hamblin
219 2013). As such, it can be viewed as mimicking the process of natural selection.

220 The GA is initialized with a random set of strategies, each strategy being defined by a
221 combination of values given to parameters α , μ , β , and δ . For 4000 generations, we iterate the same
222 operation: (i) evaluation of the fitness of strategies investigated by running the model, (ii) selection
223 and mutation of strategies. First, strategies that will persist are selected. Selection is elitist, so the
224 strategies leading to the 10% highest fitness values are always kept. The other strategies are selected
225 using the k-tournament method, with $k = 2$ (see Hamblin 2013). After selection of the strategies, each
226 parameter of the strategies has a 5% chance of being subject to mutation, which could be a
227 recombination (2.5%), a small mutation (1.25%) or a large mutation (1.25%). Recombinations
228 replace the current parameter by the one of another strategy taken at random. Small mutations add a
229 small increment to the current parameter value. Large mutations replace the current parameter by a
230 new random value within the parameter range. On completion of the algorithm, a set of strategies
231 remains and an additional series of generations is ran with selection but without mutation, in order to
232 filter the remaining strategies until a single one remains for both predators and prey (Hamblin 2013).
233 Even after a long run-time, a GA may fail to find optimal solutions because of continuous mutations
234 or local optima. In order to check convergence of the algorithm to strategies that would be repeatedly

235 selected in a given environment, we replicated each simulation 3 times. At times, the final value of
236 some parameters differed between replicates. This was the case when strategies with low α values
237 (near-random movement) were efficient, as other parameters therefore did not affect the actual
238 movement of individuals and were subject to drift. Figures in the main text present results for one
239 replicate and those for the 2 others are shown in SI 2.

240

241 **Analyses**

242 We compared optimal strategies of predators and prey across environments that differed in (1) the
243 vulnerability in standard patches (4 values); (2) the contrast in vulnerability between standard and
244 riskier patches (5 values); (3) the maximum forage in standard patches (3 values); (4) the contrast in
245 maximum forage between standard and riskier patches (4 values, always >1 so that riskier patches
246 were always intrinsically better than standard patches in terms of prey forage). We tested all
247 combinations of values (see Table S1), yielding a total of 240 different environments. In the main
248 text, we present the distribution of values of strategy parameters as a function of those four
249 environmental characteristics, as well as for environments without predators, to compare prey
250 movement strategy with the one observed under predation risk. In SI 2, we provide a comprehensive
251 report of all results on optimal strategy parameters, as well as on the distribution of predators and
252 prey, for all the environments tested and for the 3 replicates.

253

254 **Results**

255 **Movement predictability**

256 In all types of environments, predators are generally much less predictable than prey. Predators
257 generally have α values below 1 (Fig. 1, Fig. S2-1 to S2-5 in SI 2), suggesting significant randomness
258 in their patch choice. Prey movements are much more driven by patch weights (greater α)(Fig. 1, Fig.
259 S2-1 to S2-5). In absence of predators, however, prey would be much more predictable, virtually
260 always choosing the best patches ($\alpha \sim 8$, Fig. 1, Fig. S2-1 to S2-4).

261 Predator strategies involve greater randomness with higher vulnerability in standard patches (Fig. 1a),
262 higher maximum forage in standard patches (Fig. 1c) and very high forage contrast between standard
263 and riskier patches (Fig. 1d). Predator movement predictability is minimum for intermediate contrast
264 of vulnerability between standard and riskier patches (Fig. 1b). Prey movement strategies involve
265 greater randomness as vulnerability in standard patches increases (Fig. 1a), vulnerability contrast
266 between standard and riskier patches increases (except for highest value, Fig. 1b), maximum forage in
267 standard patches decreases (Fig. 1c), and forage contrast between standard and riskier patches
268 increases (Fig. 1c). In absence of predators, prey were always highly predictable (Fig. 1).

269

270 **Relative importance of information about encounters**

271 Keeping in mind that predators use past information less than prey to decide where to move (see
272 above), encounters have a greater importance (greater values of β , Fig. 2, Fig. S2-6 to S2-10 in SI 2)
273 for predators' assessment of patch quality than for prey. Predators grant very high importance to
274 information about encounters in all environments except when the contrast of prey vulnerability is
275 very low between standard and riskier patches (Fig. 2, Fig. S2-6 to S2-10). Prey generally give little
276 importance to information about encounters, but this information becomes slightly more important as
277 vulnerability in the standard (i.e. safest) patches increase (Fig. 2a, Fig. S2-6), the contrast in
278 vulnerability between standard and riskier patches increases (Fig. 2b, Fig. S2-7), and the contrast in
279 maximum forage between standard and riskier patches increases (Fig. S2-9).

280

281 **Relative importance of recent vs. older information about encounters**

282 Generally, predators and prey differ little in how they integrate information about recent and older
283 encounters when determining patch weights (Fig. 3, Fig. S2-11 to S2-15 in SI 2). Both predators and
284 prey grant greater importance to old encounters as vulnerability in standard patches increases (Fig.
285 3a, Fig. S2-11), and as the vulnerability contrast between standard and riskier patches increases (Fig.
286 3b, Fig. S2-12). When this vulnerability contrast becomes very large, prey use information about old
287 encounters more than predators (Fig. 3b, Fig. S2-12). Prey forage availability has a limited effect on

288 prey and predators' relative use of information about recent and old encounters (Fig. 3c, 3d, Fig. S2-
289 13, S2-14).

290

291 **Relative importance of recent vs. older information about forage availability**

292 Despite the large variability observed in the results, prey appear to use recent information on forage
293 availability more than predators (Fig. 4, Fig. S2-16 to S2-20 in SI 2). Note that predators however
294 rely less on information about forage availability than prey to determine where to move (see above).
295 For predators, the importance of recent vs older information on forage availability increases as
296 vulnerability in standard patches decreases (Fig. 4a, Fig. S2-16), when vulnerability differs greatly
297 between standard and riskier patches (Fig. 4b, Fig. S2-15), and as forage contrast between standard
298 and riskier patches increases (Fig. 4d, Fig. S2-19). For prey, the importance of recent vs older
299 information on forage availability increases as vulnerability in standard patches decreases (Fig. 4a,
300 Fig. S2-16) and the vulnerability contrast between standard and riskier patches decreases (Fig. 4b,
301 Fig. S2-17). Maximum forage in standard patches (Fig. 4c, Fig. S2-18) and contrast in maximum
302 forage between standard and riskier patches (fig. 4d, Fig. S2-19) also affect how recent information is
303 used by prey, but results varied largely between simulations. It is clear, however, that the absence of
304 predators leads prey to mostly value recent information (Fig. 4).

305

306 **Discussion**

307 We developed, to our knowledge, the first model predicting how optimal predators and prey should
308 use information about prey forage availability and encounters with their enemies. The model revealed
309 general differences in the optimal use of information between predators and prey, as well as the
310 influence on patch choice strategies of key environmental characteristics such as contrasts in forage
311 availability and vulnerability between patches. Our study offers a theoretical framework to interpret
312 previous studies and generalize their predictions. In particular, our model provides three clear
313 predictions that apply to the realistic situation of competitive prey foraging under predation risk: (1)
314 predators and prey play a shell game in which each player is trying to keep its location unpredictable.

315 Predators remain however much more unpredictable than prey; (2) what makes a good patch for a
316 predator is more linked to successful encounters with prey than high prey forage availability; the
317 opposite is true for prey; (3) prey and predators used recent and old information about encounters
318 rather similarly, and give more weight to recent encounters. In contrast, the relative importance of
319 recent and old information about forage availability is highly variable, differing between prey and
320 predators and depending on environmental characteristics. We now discuss these predictions further,
321 in the light of existing and possible studies.

322 Previous theoretical (Mitchell & Lima 2002; Mitchell 2009) and empirical (Roth & Lima
323 2007; Valeix et al. 2011; Bosiger et al. 2012; Simon et al. 2019) studies have suggested that predators
324 and prey play a shell game in which both the prey and the predator would benefit from moving
325 regularly in an unpredictable manner to prevent the other player to learn and then avoid (for the prey)
326 or focus on (for the predator) places where the other player would be. Theoretical studies have
327 however focused on unpredictability of the prey, as they never allowed predators to move somewhat
328 randomly. Empirical studies never compared movement predictability of predators and prey. Our
329 model fills these gaps from a theoretical standpoint, and predicts that predators' movements should
330 often be unpredictable. A prey knowing a predator's patch weights would not be able to predict its
331 movement as the predator's movements were only weakly determined by those weights. Conversely,
332 although prey did not always move towards the best patches, a predator knowing prey patch weights
333 would significantly increase its chances to find prey, as it could restrict the number of patches where
334 to look for, as prey most often selected patches with a probability at least proportional to the patch
335 weight. The comparison of prey strategies in presence or absence of predators however clearly
336 demonstrates that, in absence of predators, prey would be much more predictable, always moving
337 towards the patch perceived as best. The general contrast in movement randomness between
338 predators and prey is robust to variations in the levels and contrasts of forage availability and
339 vulnerability in the landscape.

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

342 predators increases the availability of prey that, if behaviourally responsive to predictable risk, could
343 otherwise avoid places where predators would be likely to be present, leading to behavioural resource
344 depression (sensu Charnov 1976). Random movement by prey benefits them as it reduces the
345 searching efficiency of predators that can memorize past encounters and could use this information
346 for later searches (Mitchell 2009). As for costs, even though predators could recognize a good patch,
347 mostly based on past encounters as high forage availability is just a proxy for the potential presence
348 of prey (Flaxman & Lou 2009), the cost of ignoring this information and moving randomly is likely
349 to be lower than for the prey. Predators moving randomly and arriving at a bad patch only suffer from
350 missed opportunity costs of foraging. In contrast, prey moving randomly rather than doing an
351 informed choice and arriving on a bad patch could suffer from two costs, lower forage intake and
352 increased predation risk. In our simulations, prey movement was virtually always strongly determined
353 by patch weights, suggesting that in most circumstances the costs associated with randomness largely
354 outweighed its potential benefits. In addition, as predators evolve to be unpredictable, information
355 about past encounters becomes less and less relevant to the prey. Prey therefore end up giving much
356 more weight to information about forage availability than to encounters, focusing their movement
357 towards good foraging patches, with a low, but not negligible, level of unpredictability to extend the
358 predator' area to search, giving prey a chance to avoid encounters. Overall, with our model, we
359 confirm the potential importance of randomness in the predator-prey spatial game, and explain why
360 we should expect predators to be unpredictable, and prey not so, but more than in absence of
361 predation.

362 Our model also provides insights on how prey and predators should use recent and
363 past information about encounters and forage availability. Recent encounters appear to be given more
364 weight than older ones by both prey and predators. This make sense as, generally, information about
365 encounters is poorly used by both: prey because they cannot predict where predators occur and thus
366 mostly use information about forage availability, predators because they move rather randomly and
367 therefore do not use much information, although when they do they favor information about where
368 they met prey rather than about prey forage availability. It is likely that prey and predators used

369 information about recent encounters to escape (prey) or remain in (predator) patches where an
370 encounter occurred. It is consistent with observations that prey often leave patches when a predator is
371 detected, and do not return immediately (Courbin et al. 2016). Predators are likely to leave rapidly
372 anyway as patch weight has a low contribution to patch choice. In contrast, and despite strong
373 variability among simulations and environmental contexts, recent and older information about forage
374 availability was used differently by prey and predators. Prey generally gave more weight to recent
375 information about forage than predators did. This could be explained by the fact that recent
376 information is important for the prey as it allows it to keep foraging in good foraging patches, or
377 move away when foraging in poor patches. For predators, recent forage availability might be a poor
378 predictor of finding prey that could have arrived there by chance, whereas longer-term information
379 about forage availability in patches might be a predictor of the likelihood of prey's presence or
380 density. As discussed before, however, information about forage availability remains weakly used by
381 predators, unless patches do not differ in vulnerability, in which case predators move less randomly
382 and give slightly more weight to information about forage than usual (Fig. 1 and 2). Thus, although
383 our study suggests that leap-frogging, i.e. when predators track prey resources rather than prey
384 themselves (Sih 1998; Flaxman & Lou 2009), should be rare, it might be more detectable in
385 environments where prey vulnerability is homogeneous, as in the experimental contexts where it has
386 been tested (Hammond et al. 2007; Williams & Flaxman 2012).

387 Generally, although the level and distribution of risk and prey forage in the environment did
388 not qualitatively alter the observed differences between predators and prey space use strategies, it still
389 had noticeable effects. Increasing global risk levels, by increasing the prey vulnerability in all
390 patches, or only in riskier patches, leads prey to give increasing importance to encounters relative to
391 forage availability. As risk increases, prey initially become slightly less predictable, but this effect
392 does not persist, and possibly reverse, in very risky environments. Simultaneously, prey spend
393 increasingly more time in standard, safer, patches (Fig. S3 in SI 3), increasingly using long-term
394 information on encounter risk to identify these. Predators become less predictable and use patches
395 increasingly randomly, although this effect appears to be slightly reduced when the vulnerability

396 contrast between standard and riskier patches increases, predators then using long-term information
397 about encounters, likely to avoid random movements that would take them to riskiest patches barely
398 ever used by prey. Therefore, our results suggest that lowest levels of movement predictability of prey
399 and predators should be observed at intermediate levels of vulnerability heterogeneity within the
400 landscape. To the best of our knowledge, this theoretical prediction has not been made before, and is
401 amenable to testing. Effects of the levels and heterogeneity of prey forage availability differed from
402 those observed for vulnerability, and in cases affected movement predictability of prey and predators
403 in a contrasted way. While predators become slightly less predictable as prey forage availability
404 increases in all patches, prey become increasingly predictable, focusing more on standard, safest,
405 patches, using long-term information on forage to identify them. Note how, in absence of predation,
406 prey would in contrast increasingly use the most recent information to find most profitable patches.
407 Prey predictability however decreases as riskier patches become more profitable. This occurs because
408 the costs of not moving to the best patches is increasingly reduced by finding higher forage
409 availability when the prey move to a riskier patch, which they increasing do (Fig. S3).

410 Overall, our work provides the most comprehensive theoretical framework to date to predict
411 how prey and predator movement strategies should have evolved in contrasted environments. In
412 particular, we focused on improving previous approaches by considering both prey and predators as
413 behaviorally-responsive players of the space race, as this is now well established empirically (e.g.
414 invertebrates: Hammond et al. 2007; large mammals: Valeix et al. 2011; Courbin et al. 2019). Our
415 predictions should now be challenged by experimental and observational studies to reveal the extent
416 of our understanding of predator-prey interactions. A key insight gained here is that the interplay
417 between memory use and purposeful randomness should be a central focus of future studies.

418

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426 **Figures**

427 **Figure 1. Optimal values, for predators and prey, of parameter α , indexing movement**

428 **predictability**, for varying (a) vulnerability in the standard patches, (b) vulnerability contrast between

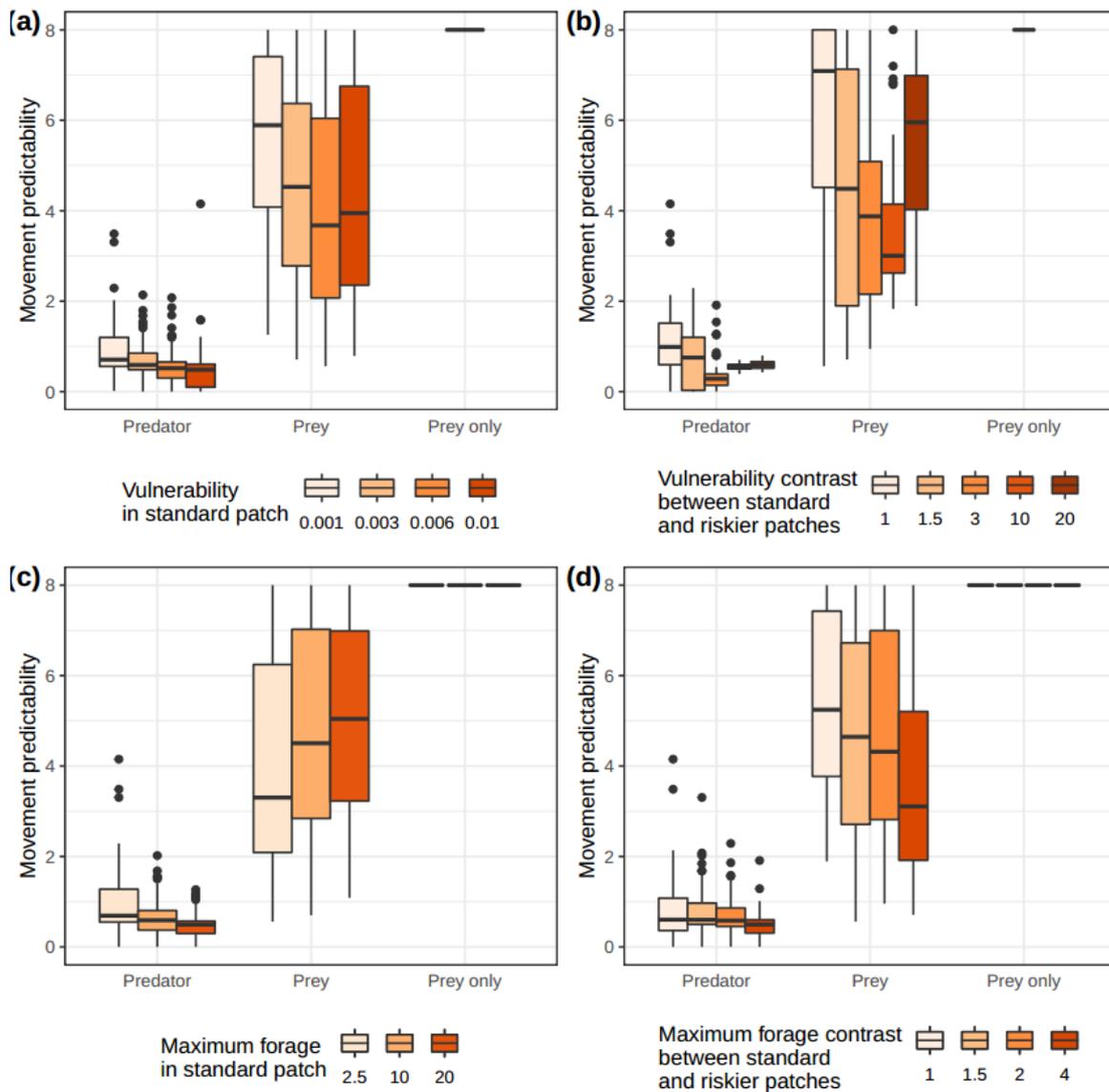
429 standard and rich patches, (c) maximum forage in the standard patches and (d) maximum forage

430 contrast between standard and rich patches. Values for environments without predators are also

431 shown (patches were then not assigned vulnerability levels). Lower values correspond to less

432 informed, i.e. more random, movements.

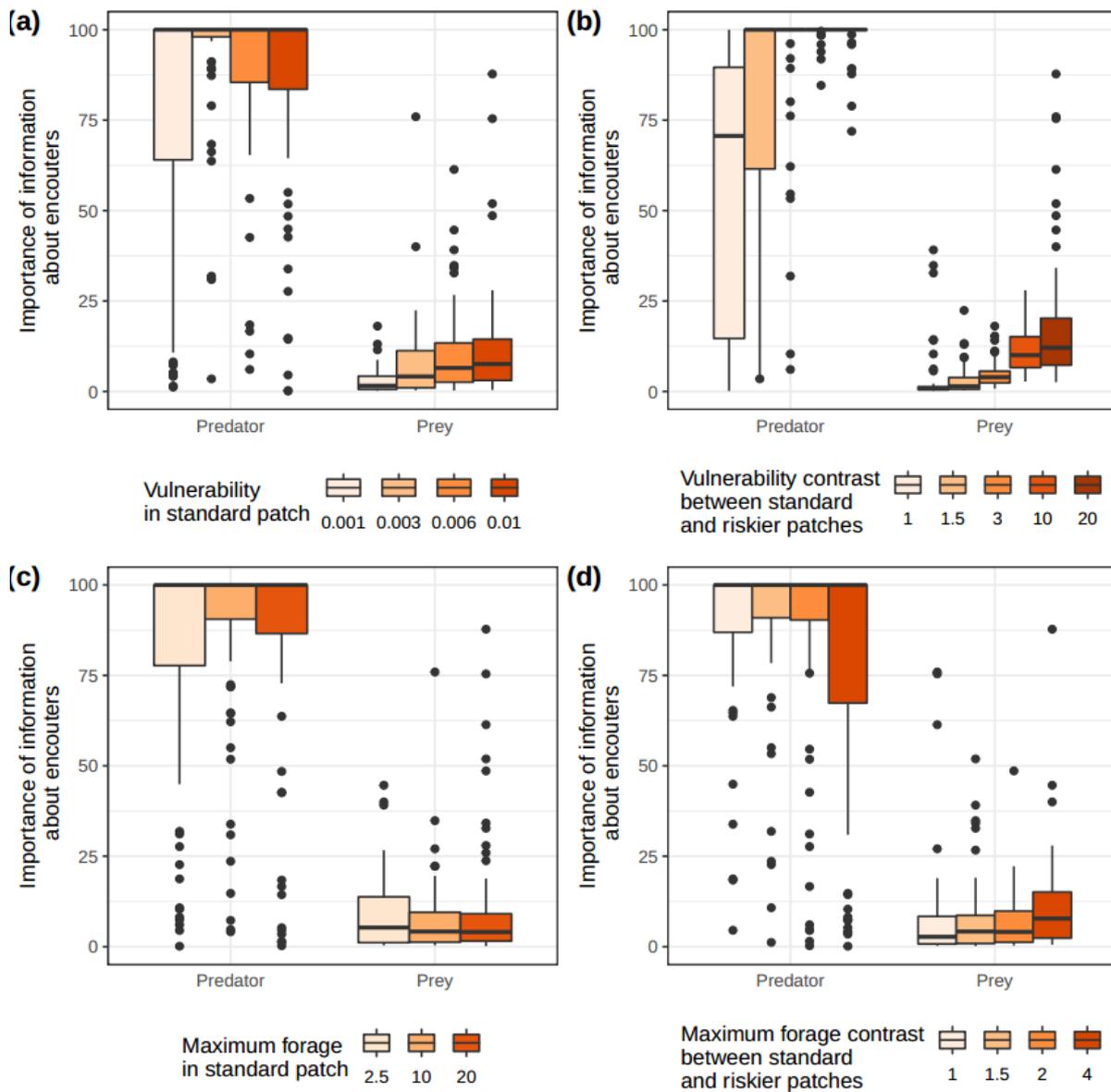
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436 **Figure 2. Optimal values, for predators and prey, of parameter β , indexing the relative**
437 **importance of information about encounters, for varying (a) vulnerability in the standard patches,**
438 **(b) vulnerability contrast between standard and rich patches, (c) maximum forage in the standard**
439 **patches and (d) maximum forage contrast between standard and rich patches. Lower values**
440 **correspond to lower importance given to encounters, relative to prey forage availability.**
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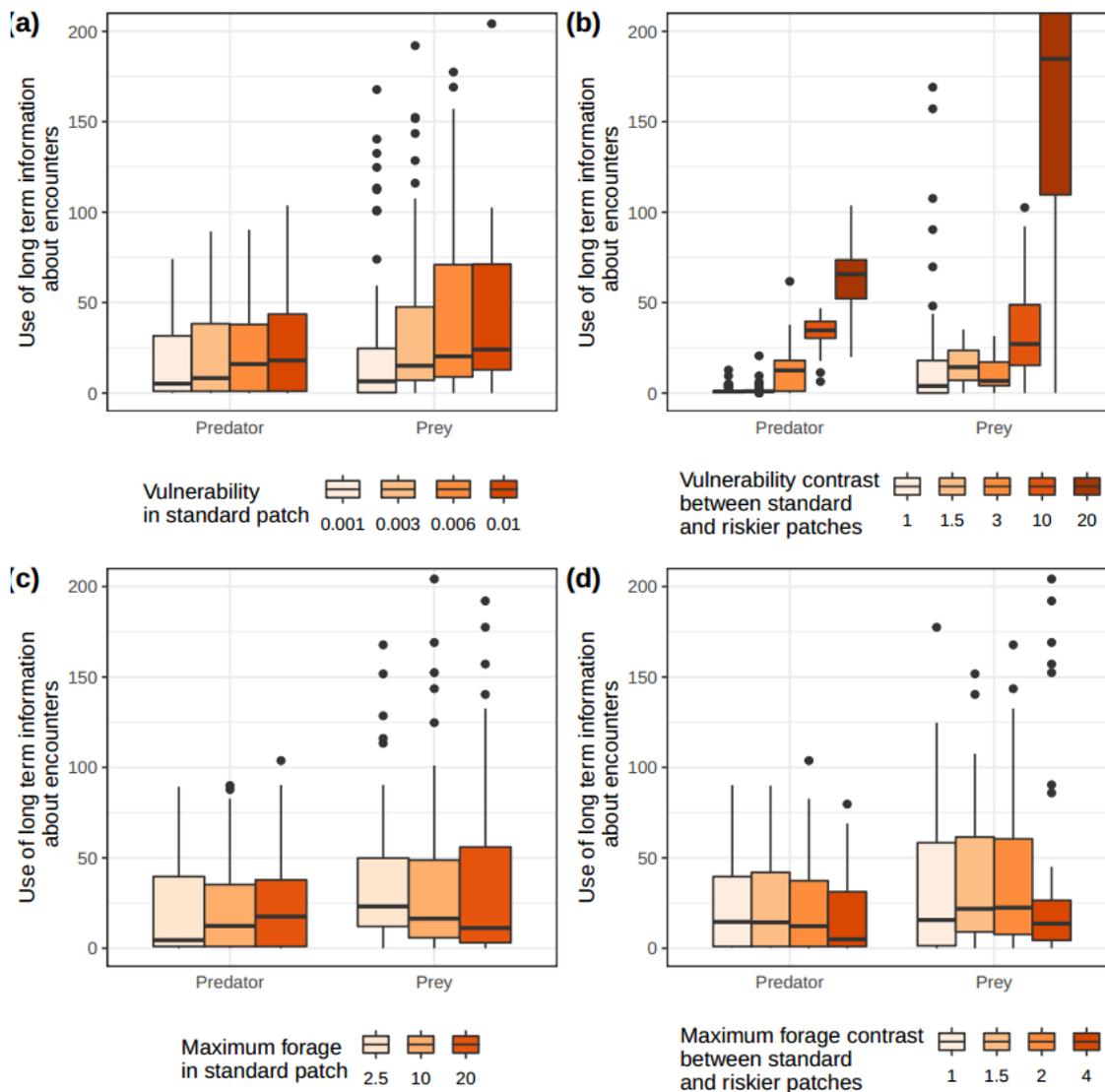
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447 **Figure 3. Optimal values, for predators and prey, of parameter δ , indexing the use of long-term**
448 **information about encounters**, for varying (a) vulnerability in the standard patches, (b) vulnerability
449 contrast between standard and rich patches, (c) maximum forage in the standard patches and (d)
450 maximum forage contrast between standard and rich patches. Lower values correspond to a lower
451 weight given to older information.
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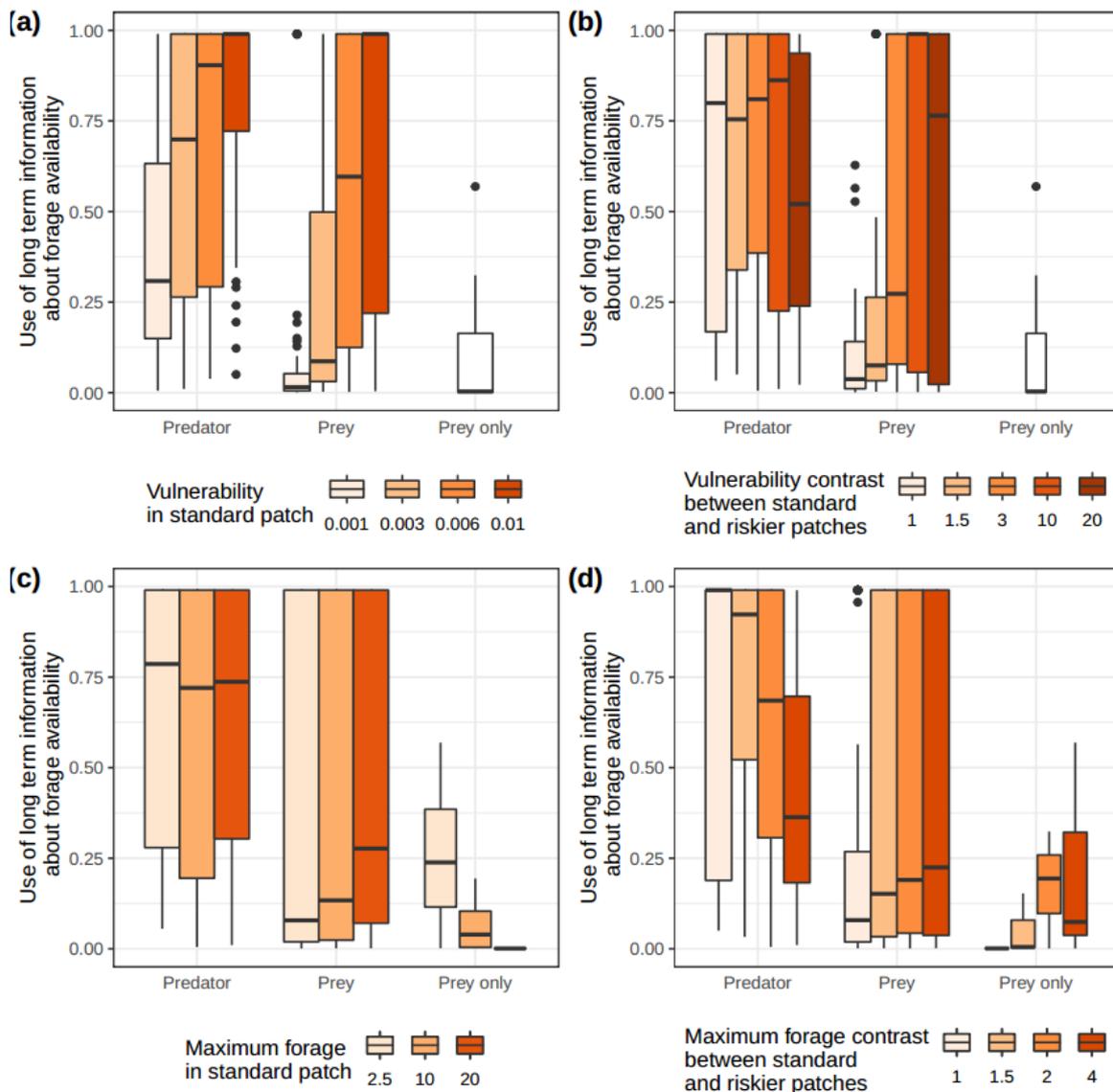
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459 **Figure 4. Optimal values, for predator and prey, of parameter μ , indexing the use of long-term**
 460 **information about forage availability**, for varying (a) vulnerability in the standard patches, (b)
 461 vulnerability contrast between standard and rich patches, (c) maximum forage in the standard patches
 462 and (d) maximum forage contrast between standard and rich patches. Values for environments
 463 without predators are also shown (patches were then not assigned vulnerability levels). Lower values
 464 correspond to a lower weight given to older information.
 465



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