Counter-intuitive prey strategies against predators with finite budget in a search game: protection heterogeneity among sites matters more than their number.

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June 17, 2023

1 Abstract

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Combining the search and pursuit aspects of predator-prey interactions into a single game, where the payoff to the Searcher (predator) is the probability of finding and capturing the Hider (prey) within a fixed number of searches was proposed by Gal and Casas (2014). Subsequent models allowed the predator to continue his search (in another 'round') if the prey was found but escaped the chase. However it is unrealistic to allow this pattern of prey relocation to go on forever, so here we introduce a limit of the total number of searches, in all 'rounds', that the predator can carry out. We show how habitat structural complexity affects the mean time until capture: the quality of the location with the lowest capture probability matters more than the number of hiding locations. Moreover, we observed that the parameter space defined by the capture probabilities in each location and the budget of the predator can be divided into distinct domains, defining whether the prey ought to play with pure or mixed hiding strategies.

2 Introduction

Predator-prey interactions often have two distinct phases, and game theory has been widely used to model these encounters separately [Bro13] First, the predator searches for the prey (a search game). Then the predator pursues the prey (a differential game of pursuit evasion). In two recent papers, [GC14] and [GAC15], these two phases of the interaction were combined into a single constant-sum game. In both models, the prey/hider can locate in any of a set of n heterogeneous

Γ_m Game	a multi-stage game where each prey successful evasion decreases predator budget m Formally, it should be noted $\Gamma_m^{n,\{p_i,1\leq i\leq n\}}$
k/m	budget of the predator m refers to the current paper while k refers to the total budget over all periods in previous papers
n	total number of locations
$v(m)$	value of the Γ_m game
p_i	probability of prey capture if found at location i. $p_1 < \cdots < p_n$
b and c	For n=2 locations, p_1=b and p_2=c
h_i	(Prey strategy) probability of prey hiding at location i
s_x	(Predator strategy) probability of predator using the permutation x of the locations
x^i	Rank of the location i in the permutation x chosen by the predator
s^*/s_{NASH}	s^* is the optimal strategy of the prey. When the prey is also optimizing, $s^* = s_{NASH}$, computed at a Nash-equilibrium
P_m	indicates that Γ_m has a pure strategy set
M_m	indicates that Γ_m has a mixed strategy set such that $\forall i > 1, h_i = 0$ and $h_1 = 1$
B_m	indicates that Γ_m has a mixed strategy set such that $h_n = 0$ but $h_1 \neq 1$

Table 1: List of common notations.

locations, where each has a distinct probability that the prey will be captured if found in that location. The first paper is a single round model, where the predator/searcher can look into any

k of the locations. The predator 'wins' the game if it finds the prey and successfully pursues it. The Hider wins if it is not found by the k'th search or if it is found but escapes the pursuit. The second paper is a repeated game version of the first, in which an escaping prey can relocate and play the same game in another round. This model is more realistic but still allows unrealistic indefinite time and unlimited stamina for the predator. To remedy this problem, we introduce here a bound m on the total number of searches available to the predator, summed over all rounds. Unlike the per round search limit k of the earlier papers, our total bound m can be larger than the number of locations. We call this game the recursive game $\Gamma(m)$, because it can end either with a successful pursuit or lead to a reduced game $\Gamma(m')$, $m' < m$. In particular, if the prey escapes the pursuit on the t'th search of the game $\Gamma(m)$, the Searcher and the Hider then play the smaller game $\Gamma(m-t)$, as t of the m available searches have been used up. The biological interpretation of the total search bound m is varied: patience, motivation, energy budget, number of matured eggs in a female parasitoid wasp all of which is usually mixed under the term "giving-up time" in ecology. We start this paper by a state-of-the-art on search problems with finite budget, and the interpretation of the "budget" m in ecology. Then, we introduce the main results of Gal and Casas [GC14] in order to formalize the recursive Γ_m game. For every given m, we then completely solve the game for the sub-cases $n = 2$,$n = 3$ locations, and the case with 1 good location and n-1 identical bad locations. Based on these results, we propose conjectures concerning the general case $n \geq 4$ locations. We discuss the influence of the nature of the hiding locations ("structural complexity") on the overall probability of capture, and explain the unexpected optimal hiding and searching strategies.

3 State of the art

We divide our literature survey into two parts. The first part covers problems in predator search and pursuit of prey. The second covers search games.

3.1 Predators' limited resources for foraging

The upper bound m can be interpreted as a time or resource budget, but also as something which reflects the motivation of the predator, i.e. its willingness to forage (patience), level of hunger, and so on: an hungry predator could be modelled as an agent with a higher m than a satiated one, when m represents the willingness to forage. The number of hours or resources spent inspecting are often not reset to its original value like in the repeated game [GAC15], but decreases over time. Diurnal predators stop indeed searching at sunset (correlation between light intensity and foraging period, [KB01]), some animals have a very short lifespan impacting their foraging decision [Waj+06], and egg load of a female parasitoid wasp cannot be restored to its original number at the fast behavioral scale (*e.g.* around 36 eggs in a 1-d-old parasitoid wasp, [MM02]). The variable m can describe a budget inherent to the physiology of an animal, such as muscle state, body temperature, aging, condition ... as described in Houston and MacNamara [HKE80]. Many animals with low Surface-Volume ratios are under severe budget constraints and need to make enough energy reserves to survive fatal climatic conditions (e.g. predatory Etruscan shrews are on negative energy budget during winter [Bre+11]). Some aerial predators, such as marine birds or sea mammals dive in the water to forage, and their foraging sessions are limited by the amount of oxygen they have in reserve.

Moreover, the parameter m is reminiscent of the ecological concept of Giving-Up Time (GUT) concept as the time interval between the last item (e.g. prey capture) encountered and the moment when the forager leaves a patch [KRC74]. Based on dynamic programming, Green [Gre84] proposed the assessment rule, a rule for deciding when to leave a patch, which is only based on the number of prey caught at a given time whatever the exact timing of the captures. Waage [Waa79] proposed a model to predict patch leaving time based on a motivation level, a tendency to stay in a patch which decays from an initial motivation level to zero at a constant rate every time a forager fails to find a prey, because of habituation, and leaves a patch when the motivation falls below zero. The GUT depends also on the general quality of the environment. If patches are scarce in the environment, or if travelling costs between patches are high, the predator is expected to spend more time in a patch, thus m would be higher [SK78]. In this paper, we propose a model which is reminiscent of GUT models: a predator with a decremental budget and a given degree of persistence. However, contrary to most GUT models in which the harvested resources are described as passive behaviorally inert resources, we use a game theory approach to model the active avoidance of the prey.

3.2 The Search Game Literature

The problem of minimizing the expected number of searches required to find an object which is hidden among a number of discrete locations (often called boxes) goes back a long way. Usually, the locations are assumed to be heterogeneous in the *detection probability* q_i that the object will be found if its location is searched, with a corresponding *overlook probability* $1 - q_i$. Sometimes this problem is formulated as a game (two person zero-sum) where the object is a hider who wants to maximize the number of searches required to find him. The classical optimization problem of the searcher was solved by Blackwell (see Matula [Mat64]) and was extended to game theoretic versions by many authors. A recent problem with multiple hidden objects was solved in [Lid13]. A version of the problem, where the searcher wishes to maximize the probability of finding the object within a given number of searchers, is solved in [LS16]. The possibility of combining the predator's problems of searching for and successfully pursuing the prey was introduced in [GC14] and [GAC15], with the predator modeled as searcher and the prey as hider. These have already been described in the Introduction and the first one will be examined in more detail in the next Section. The capture probability p_i , that the prey is subsequently captured in the chase at location i is related to the detection probability q_i (or the overlook probability). The main difference is that if the object is overlooked, the search continues uninterrupted whereas if the prey/hider is found but not captured, the searcher knows this and the stage game ends. In some models, the prey can only be found if its location is searched and also if it is in a period of vulnerability. Such models are called patrolling games [AMP11]. If the prey is mobile, the predator has an additional option, not consider here, of remaining stationary in the hope of ambushing a prey that might come to it. This type of search is considered in [ZFZ11] and [Alp+11]. Other applications of search theory to predator-prey interactions are given in [Pit13] and [Bro13]. See also [BR22] for more far-reaching analysis. Our model has costs for predator travelling (moving between locations as measured by searches), but not for pursuit. For something in this direction, see [BK15]. A variation of the original problem by Gal and Casas where each location takes a certain amount to inspect by a

Searcher with a total time budget k (not necessarily an integer) was proposed in [AL20].

3.3 The One Stage game: a stepping stone towards our new model

The current paper can be seen as a generalisation of the single stage game G_k^{2014} of [GC14] mentioned earlier. As this is our point of departure, we describe that model in detail here. A (stationary) Hider locates in one of n locations $i \in \mathcal{N} = \{1, 2, ..., n\}$ while the Searcher inspects (searches) k of these, where n and k are parameters of the game. The order of inspection is not important there, though in our extended version order it will be. If the Searcher inspects the location i chosen by the Hider, we say that the the Hider is *found*; in this case it is *captured*, with a probability p_i that depends on the location i. For convenience we rank the hiding locations in decreasing order of attractiveness to the Hider so that $p_1 \leq p_2 \leq ... \leq p_n$,. The Searcher wins the game if it finds and then captures the Hider. The Hider wins if it is not found in the k searches or if it is found but not captured. The game has constant sum. The payoff matrix is a matrix where the rows are the $\binom{n}{k}$ k-subsets S_k of $\mathcal{N}$ and the columns are the n hiding locations, whose entries are the probability that the Searcher (row player) wins by finding and capturing the Hider:

$$a(S_k, i) = \begin{cases} p_i & \text{if } i \in S_k, \\ 0 & \text{if } i \notin S_k. \end{cases}$$

A mixed Hiding strategy is a probability vector of hiding probabilities $h = (h_1, h_2, ..., h_n)$ where h_i is the probability that the Hider hides at location i. A mixed strategy for the Searcher is a probability distribution over k-subsets of $\mathcal{N}$. Clearly there is a probability r_i that location i is inspected ($i \in S$) to every such mixed search strategy. Conversely, if we know all the probabilities r_i, we can determine the mixed search strategy. Thus, we define the mixed search strategy as a vector of probabilities $r = (r_1, r_2, ..., r_n)$ where r_i is the probability that the Searcher visits location i during the k rounds, satisfying

$$\sum_1^n r_i = k, \text{ for all } i \in \mathcal{N}.$$

In this constant sum game, the value v is the overall probability P of capture, with best play on both sides. Note that if the Searcher inspects location i when the Hider uses the mixed strategy h, the Searcher wins with probability $h_i\ p_i$, the probability that the Hider is found multiplied by the probability it is then captured. We will often consider the equalizing mixed hiding strategy called h^* which makes all these probabilities the same, that is,

$$h_i p_i = \lambda, \text{for all } i \in \mathcal{N}$$

for some constant λ. We say that h^* is the Hider strategy which makes all locations *equally attractive* for the Searcher. The above equations have a unique solution given by

$$\lambda = \frac{1}{\sum_1^n \frac{1}{p_i}}, \text{ and}$$

$$h_i^* = \lambda/p, \ i \in \mathcal{N}.$$

It follows from the formula for λ and the assumption that the p_i are increasing in i that $1 \leq p_1/\lambda \leq n$.

The solution of the game is easy to see in the two extreme cases where $k = 1$ and where $k = n$. When k is 1 this is a standard hide-seek game, sometimes called a diagonal game. The value of this game is λ. The Hider should adopt h^* to make all locations equally attractive, and the Searcher should inspect locations with probabilities proportional to their capture probabilities p_i. On the other hand, when $k = n$ and all locations are inspected, only the Hider has a strategic choice. The strategies 'Hiding in location $i \geq 2$' are dominated by the strategy 'Hiding in location 1 so clearly location $i = 1$ is best for him, with a value of p_1. The surprising finding of [GC14] is that for small k the solution is like that for $k = 1$ and for large k the solution is like that of $k = n$. The threshold of k is given by p_1/λ. This result is stated below.

Theorem 1 *The solution of the one-stage game [GC14] described above depends on the value of k relative to p_1/λ.*

1. *If $k < p_1/\lambda$ then the optimal hiding strategy is h^*, the optimal search strategy visits each location i with probability $r_i = k\lambda/p_i$ and the value is $k\lambda$.*
2. *If $k \geq p_1/\lambda$ then the value is p_1. The Hider can guarantee paying at most p_1 by always hiding at location 1 and the Searcher can guarantee at least p_1 by choosing $r_1 = 1 < k\lambda/p_1$ and $r_i \geq \min(k\lambda/p_i, 1)$ for all $2 \leq i \leq k$.*

In this game the Hider wins if it is found and then escapes the pursuit. In a subsequent model (a repeated game)[Alp+19], after such an escape by the Hider, it is allowed to relocate to any of the locations and the game continued with again k searches in each such stage game. This repetition could go on indefinitely, though the game ends eventually with probability 1. Such indefinite repetition is unrealistic in a biological setting with limited stamina of both parties, particularly for the predator. So, in the new model, we introduce in the next section, the game does continue after the prey escapes a pursuit, but the predator has a limited total number of searches in all stages of the game.

4 Formalisation of the new Game Γ_m : Limit on Total Searches

We now consider a recursive version Γ_m of the search-pursuit game, where the predator has a limit m on the *total* number of looks in *all* rounds. So, unlike the one-stage game budget k of searches, m can be greater than the number n of locations [GC14]. Unlike the budget of k searches per round of the repeated game [GAC15], here the Searcher can keep looking until a total of m searches have been made. Moreover, the order of the searches now matters because it is better for the searcher to find the Hider early in the round rather than late, as then it will have more searches left in the next round, supposing the Hider escapes. The game can end in one of two ways. If the Searcher finds the Hider (looks in the Hider's location) and successfully pursues and captures him, the Searcher wins and the payoff is 1 If at some point the searcher has only 1 look left and either does not find the hider; or finds him but fails to capture him, then the Hider wins and the payoff is 0.

An example scenario is as follows. Suppose the initial budget (number of looks) is $m = 12$ (say daylight hours) and there are $n = 7$ locations (Fig. 1). In round 1 (beginning of the day) the Searcher finds the Hider on his 5'th look but fails to catch him at that hiding location. Then the Hider relocates and in round 2 the Searcher finds him on his 4th look, but again fails to catch him. In round three, with the Searcher having $12 - 5 - 4 = 3$ remaining looks, it fails to find him on any of the 3. The Hider then wins.

We can describe the above problem as a recursive game Γ_m. The Hider begins by choosing a location $i \in N = \{1, \ldots, n\}$. The Searcher looks at locations, one at a time, until it either runs

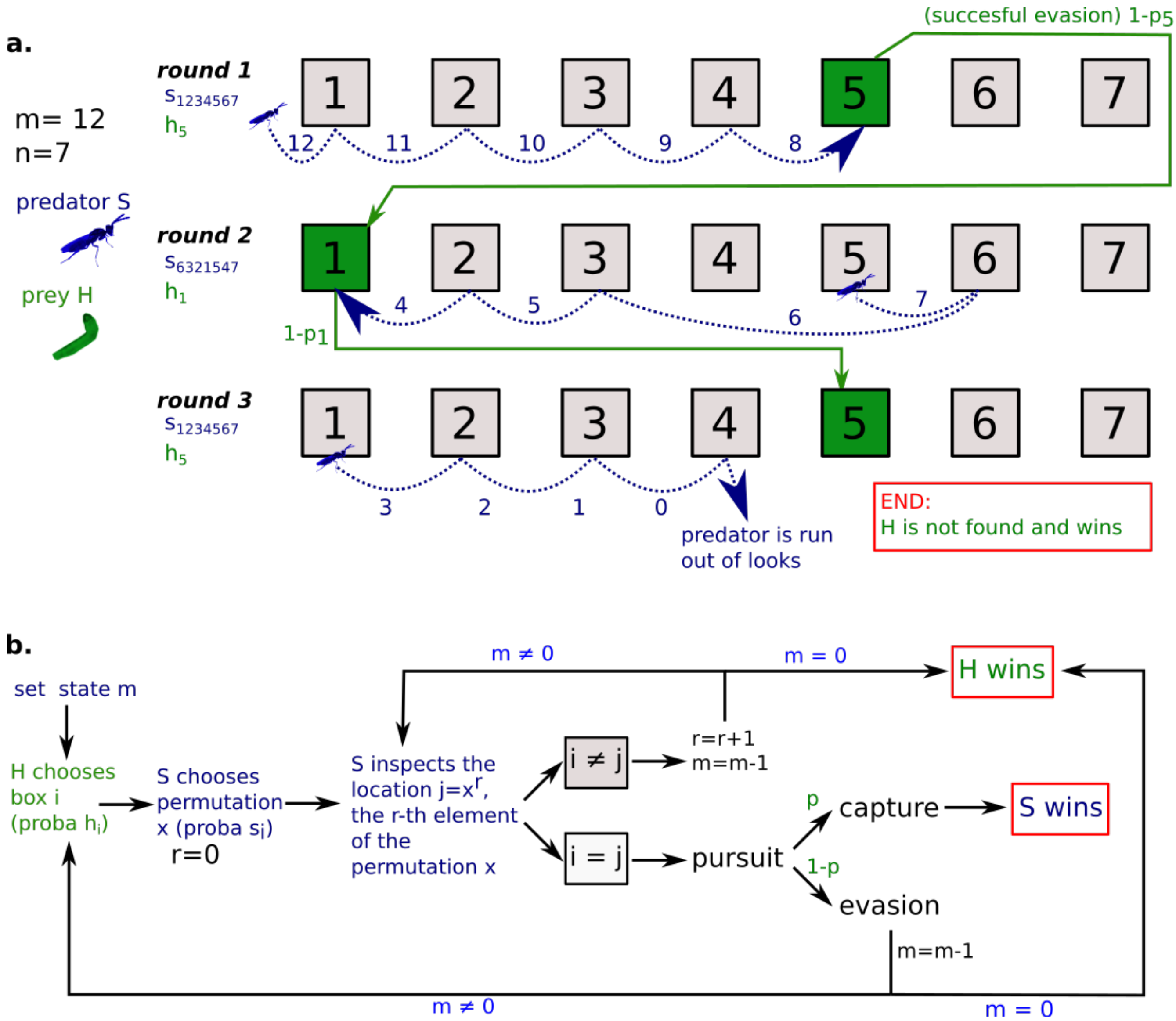

Figure 1: Definition of the Γ_k game. (a) In the Γ_k game, the predator starts with an initial number of looks k (k=12 in this example) and loses one look every time it inspects a location (in dark blue). The prey hiding location is shown in light grey. In this example, the prey successfully relocates to another location whenever it is found, as shown in green. Each successful relocation of the prey indicates the beginning of a new round. The predator eventually loses as it runs out of looks. (b) Extended form of the game Γ_k

out of searches (possible only if $m < n$) or it finds the Hider when it searches location i on the t'th search, $t \leq n$. In the latter case it captures the Hider with probability p_i (winning the game with payoff 1) or fails with complementary probability $1 - p_i$. In the latter case the game continues, but the number of searches is reduced to $m - t$ (that is, the game Γ_{m-t} is played). The Hider wins (payoff 0) if the Searcher runs out of searches while the Searcher wins (payoff 1) if it captures the Hider.

Let's formalize the payoff matrix. A strategy for the Hider is one of the n hiding locations. A strategy for the Searcher is a permutation $s = (x_1, x_2, \ldots, x_n)$ of the locations N, where x_j denotes the location searched in period j , if the Hider has not been found by then. Of course if $m < n$, only the first m locations in x will be relevant (strategies will be equivalent if they agree in the first m places).We denote by x^j the position of location j in the permutation x, for example if $x = (3, 1, 2, 4)$ then $x^1 = 2$. Thus the payoff matrix for the recursive game Γ_m , with row player (Searcher) as maximizer, and the Hider's location denoted by i, is given by $A = \{a_{x,\ i}\}$ where A is the $n!$ by n matrix with entries

$$a_{x,i} = \begin{cases} 0 & \text{if } x^i > m, \\ p_i + (1 - p_i)\ \Gamma_{m-x^i} & \text{if } x^i \leq m. \end{cases} \tag{1}$$

The case $x^i > m$ can only occur if $m < n$, and corresponds to the situation where the Searcher was planning to inspect the Hider's location i at time x^i, but as x^i is larger than his remaining number of looks m, it has run out of time (or looks), and loses the game. The other case is where the Searcher finds the Hider on his x^ith search. It then captures the Hider, and receives payoff 1, with probability p_i. With complementary probability $1 - p_i$ the Hider escapes, leaving the Searcher with only $m - x^i$ searches, so that the smaller game Γ_{m-x^i} is then played. Using the notation $v(j) = value(\Gamma_j)$ and assuming we know the values $v(j)$ for all the smaller games $\Gamma_j,\ j = 0, 1, \ldots, m-1$ we can solve for $v(m)$ recursively, starting from v(0)=0 (the Hider wins if the Searcher has no more looks). We have

$$v(m) = value\left(A\left(v(1), v(2), \ldots, v(m-n)\right)\right). \tag{2}$$

This notation makes explicit the dependence of $v(m)$ on the lower values $v(1)$ to $v(m-n)$, since the smallest possible value of $m - x^i$ is $m - n$. Observe that when $m \geq n$ the top case $x^i > m$ in (1) is not possible, so the game can either continue (to another stage) or conclude with a win for the Searcher. If there is only $m = 1$ look available, it is easy to see that the game Γ_1 has the value

$$v(1) = \lambda(p) = \frac{1}{\sum_{i=1}^{n} 1/p_i}.$$

That is, the game Γ_1 is identical to the game G_1^{2014} of Gal and Casas ([GC14]) (with the same vector p and n).

5 Resolution of the Γ_m game

We have solved particular cases (n=2 locations, n=3 locations, 1 good location and N bad locations) as a stepway to games with many hiding sites.

5.1 The specific case of $n = 2$ locations

5.1.1 Formalisation of the game

In order to get the solution to the recursive game, we start by restricting our attention to the case of n=2 locations, with capture probabilities denoted by $p_1 = b$ and $p_2 = c$, with $0 < b \leq c \leq 1$. As above we have $v(0) = 0$ and $v(1) = \lambda(b,c) = bc/(b+c)$. For $m \geq 2$ the game Γ_m is given by the following matrix.

$x \backslash i$	1	2
1, 2	$b + (1-b)\ \Gamma_{m-1}$	$c + (1-c)\ \Gamma_{m-2}$
2, 1	$b + (1-b)\ \Gamma_{m-2}$	$c + (1-c)\ \Gamma_{m-1}$

There are only two search strategies, depending on which location is searched first. If the Hider is in location 1, it will be found (as $m = 2$ searches are sufficient) and then it will be captured with probability b and will escape with probability $1 - b$. In this case the Searcher has $m - 1$ searches left if it searched location 1 first, and $m - 2$ searches left if it searched 2 first. We know that the values v_m are non-decreasing in m, as more searches can only help the Searcher. Observe that the upper left matrix entry (search 1 first, hide at 1) is a pure saddle point if we have

$$b + (1-b)\ v_{m-1} \leq c + (1-c)\ v_{m-2}, \text{ or equivalently}$$

$$v_{m-1} \leq f(b, c, v_{m-2}), \text{ where} \tag{3}$$

$$f(b,c,x) = \frac{1-c}{1-b}x + \frac{c-b}{1-b}.$$

Since we are still restricting to $n = 2$ locations, the Hider can be found only on the first or second search, so the Searcher's budget m can go down by 2 at most. Hence the recursion that defines v_m depends only on the two previous values, v_{m-1} and v_{m-2}. We can evaluate the value and determine the nature of the games Γ_m (whether there is a solution in pure or mixed strategies) for every $m > 1$ based on the location of the pair (v_{m-1},v_{m-2}) relative to the f line (the saddle point condition (3)) (See Supplementary). This preliminary analysis, made for various (b,c) pairs, suggests the existence of three distinct domains. For $(b,c) = (0.4, 0.5)$, players have mixed strategies in all games $\Gamma_m, m > 1$. For $(b, c) = (0.4, 0.8)$, players have pure strategies in all games $\Gamma_m, m > 1$. For $(b, c) = (0.4, 0.6)$, players have pure strategies if m=2 and mixed strategies otherwise. We have generalized this observation by finding the equations of the boundaries of the three domains.

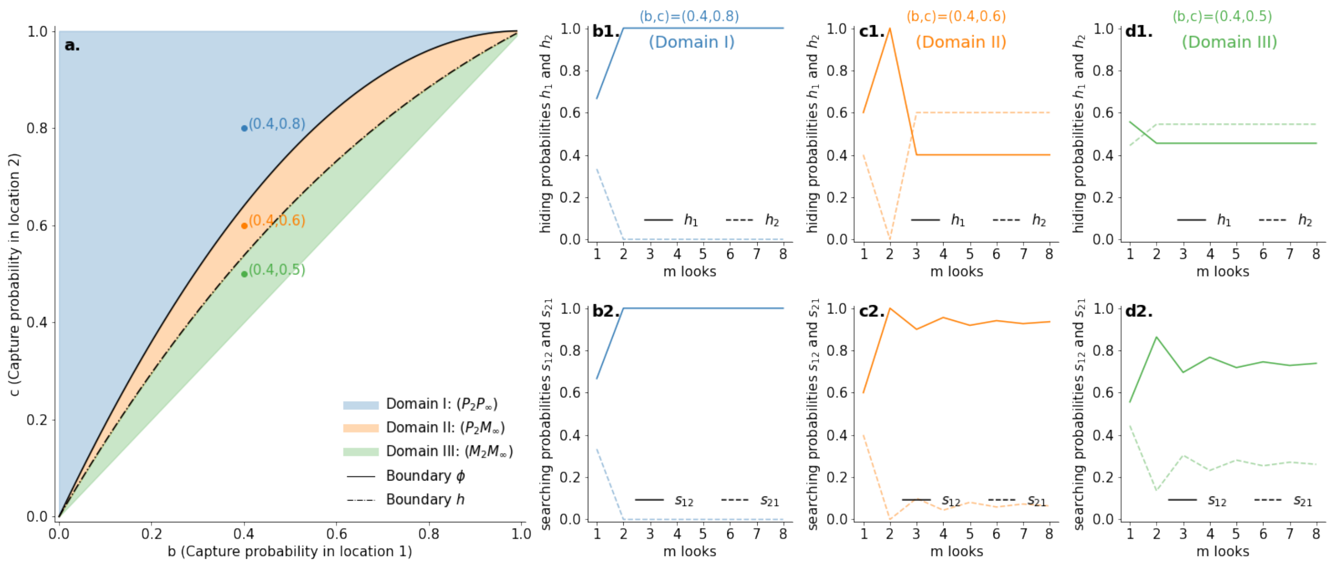

Figure 2: For n=2 locations, with capture probabilities b and $c > b$, the (b,c) space can be divided into three domains which define the nature of the hider and searcher strategies. (a) The (b,c) space can be divided into three domains. In Domain I (e.g. blue dot), the players have pure strategies in all games $\Gamma_m, m > 1$.. In Domain III (e.g. green dot), the players have mixed strategies in all games $\Gamma_m, m > 1$. In Domain II (e.g. orange dot), players have pure strategies if $m = 2$ and mixed strategies otherwise. (b-c-d) Optimal hiding (b1,c1,d1) and searching (b2,c2,d2) probabilities for the three representative couples of probabilities (p_1,p_2) presented in Figure a ((b) blue dot, (c) orange dot, (d) green dot). h_1 and s_{12} are represented by plain lines, while h_2 and s_{21} are represented by dashed lines.

5.1.2 A general solution to the two-locations game

Let's find the equations of the three distinct domains. For the case $m = 2$ the saddle point condition (3) becomes

$$v_1 = \frac{bc}{b+c} \leq f(b, c, 0).$$

If we solve the above inequality for c in terms of b, we get

$$c \geq b(1 - b + \sqrt{b^2 - 2b + 5})/2 \equiv \phi(b)$$

This defines the function g which is drawn as a thick line in Figure 2a. If (b, c) lies above ϕ, then Γ_2 has a pure strategy solution, otherwise Γ_2 has a mixed strategy solution.

For the case $m = 3$, the saddle point condition (3) becomes

$$v_2 \leq f(b, c, 1).$$

If we replace v_2 by $b + (1 - b)\frac{bc}{b+c}$ and solve the inequality for c in terms of b, we get

$$c > 2b - b^2 \equiv h(b)$$

This defines the function h which is drawn as a dashed line in Figure 2a. If (b, c) lies above $\phi = h$, then $\Gamma_{m>2}$ has a completely mixed strategy solution, and a pure solution otherwise.

To sum up, the curves ϕ and h delimitate three domains. A pair (b,c) in the domain I (blue) lies above both ϕ and h, thus Γ_2 and $\Gamma_{m\geq 3}$ have a pure strategy solution. We called this domain "$P_2 P_\infty$". A pair (b,c) in the domain III (green) lies under both h and g, thus Γ_2 and $\Gamma_{m\geq 3}$ have a mixed strategy solution. We called this domain "$M_2 M_\infty$". A pair (b,c) in the domain II (orange) lies above h thus Γ_2 has a Pure solution ("P_2..."). However, the pair (b,c) lies under Φ, thus $\Gamma_{m\geq 3}$ have a mixed strategy solution ("...M_∞"). We called this domain "$P_2 M_\infty$"

Moreover, based on the usual results for the bi-matrix games, we can obtain a general expression for the values as well as for the optimal hiding and searching strategies, based on the capture probabilities b and c and the parameter m only. Our main result is the following.

Theorem 2 *Consider the game Γ_m with two locations with capture probabilities $0 < b \leq c \leq 1$ and m searches. The nature of the solution depends only on the capture probabilities b and c. Let E= $\frac{(1-b)(1-c)}{2-b-c}$. Let $r_1 = \frac{E-\sqrt{E(E+4)}}{2}$ and $r_2 = \frac{E+\sqrt{E(E+4)}}{2}$. For $m = 1$ there is a unique completely mixed strategy solution with value $v_1 = \lambda = bc/(b+c)$*

(I) If $c > 2b - b^2$ then there is a pure strategy solution (there is a saddle point: hiding and searching in location 1). The Hider should always goes to location 1, and the Searcher should always start by searching location 1 ($h^* = 1$ and $s^* = [1, 2]$). Moreover, the value is given by

$$v_m = 1 + (1-b)^{m-1}\left(\frac{bc}{b+c} - 1\right), \forall m \geq 1.$$

- *(III) Let's present Domain III before Domain II for simplicity. If $c < b\left(1 - b + \sqrt{b^2 - 2b + 5}\right)/2$ then Γ_m has a completely mixed solution. The Hider should hide in location 1 with probability $h_1 = \frac{1-c}{2-b-c}$ and in location 2 with probability $h_2 = \frac{1-b}{2-b-c} < h_1$. The Searcher should search location 1 first with probability $s_{12} = \frac{c-b+(1-c)v_{m-1}-(1-b)v_{m-2}}{(v_{m-1}-v_{m-2})(2-b-c)}$ and should search location 2 first with probability $s_{21} = 1 - s_{12} < s_{12}$. The searching probabilities converge and we have*

$$lim_{m\to\infty} s_{12}(m) = \frac{r_2(1-c) + (b-1)}{(r_2 - 1)(2 - b - c)}$$

Moreover, the value is given by

$$v_m = 1 + \frac{1 - r_2 - v_1}{r_2 - r_1} r_1^m + \frac{r_1 + v_1 - 1}{r_2 - r_1} r_2^m, \forall m \geq 0$$

- *(II) If* $b\left(1 - b + \sqrt{b^2 - 2b + 5}\right)/2 < c < 2b - b^2$, *then the solution of* Γ_2 *is pure, while the solution of* $\Gamma_{m \geq 3}$ *is completely mixed. For m=2, the Hider should always goes to location 1, and the searcher should start by searching location 1 (*$h^* = 1$ *and* $s^* = [1, 2]$*). For m=3, the Hider should hide in location 1 with probability* $h_1 = \frac{1-c}{2-b-c}$ *and in location 2 with probability* $h_2 = \frac{1-b}{2-b-c} < h_1$*. The Searcher should search location 1 first with probability* $s_{12} = \frac{r_2(1-c)+(b-1)}{(r_2-1)(2-b-c)}$ *and should search location 2 first with probability* $s_{21} = 1 - s_{12} < s_{12}$*.*

To sum up, the space (b, c) is divided into 3 domains which dictate the behavior of the players (2a). Moreover, for the hider, there are rapid changes in locations (the optimal hiding strategies become not independent of m) as we approach the deadline $m = 0$. As shown in the Fig. (2c1), the optimal hiding strategy for the game Γ_2 consists in hiding in location 1 with probability $h_1 = 1$, but this conclusion does not hold for the game Γ_1 or Γ_3. In contrast, the optimal hiding strategies do not change when m increases if m is 'sufficiently' high (e.g. $m > 4$ in the Fig. (2c1). The rapid changes in locations are particularly visible for a pair (b,c) located in the Domain II (orange). This suggests that the behavior of the game is more "monotonous", when one hiding location is clearly better than the other ($b << c$) or when the hiding locations are very similar ($b <\approx c$).

5.2 The case with n=3 locations

To further understand the game Γ_m, we have solved the case of n=3 locations. Briefly, the main result is the following theorem.

Theorem 3 *Consider the game Γ_m with n=3 locations with capture probabilities denoted by p_1, p_2 and p_3, with $0 < p_1 < p_2 < p_3 < 1$.*

The (p_1, p_2, p_3) space can be divided into up to 15 distinct domains dictating the strategies players should adopt for all the games $\Gamma_m, m > 0$. Some domains are absent when p_1 is above a threshold.

The exact caracterisation for the boundaries of Fig. 3a, and the conditions for their existence are detailed in Supplementary Materials. Concerning the players strategies, we have plotted in Figs. 3b,c,d these strategies for three representative domains. The strategies for the 15 different domains can be found in Supplementary Materials. The Hider should either avoid locations 2 and 3 and hide in location 1 ($h_1 = 1$, $h_2 = 0$, $h_3 = 0$, see e.g. Fig. 3b1 for m=8), avoid only 3 and hide in either 1 or 2 ($h_1 < h_2 \neq 0$, $h_3 = 0$) , see e.g. Fig. 3b2 for m=8) , or hide in either location 1, 2 or 3. In this latter case, the prey should hide more in the worst location than in the best location ($h_1 < h_2 < h_3 \neq 0$, , see e.g. Fig. 3b3 for m=8). For large m, the Searcher would use the permutation 123 with the highest probability ($\forall s, s \leq s_{123}$, Figs. 3b2,c2,d2), meaning that the Searcher would concentrate its efforts on the locations with the lowest capture probabilities (e.g. location 1).

As for the case $n = 2$ locations, we can observe rapid changes in locations towards the deadline $m = 0$. This is particularly striking for a triplet (p_1,p_2,p_3) located in Domain 12: the hiding probabilities become independent of m when m is greater than 7. In contrast, for a triplet located in Domain 1 ("location 1 is greater than the two oth[illegible], or in Domain 14 ("locations 1 and 2 are similar", the hiding probabilities become independent of m more rapidly.

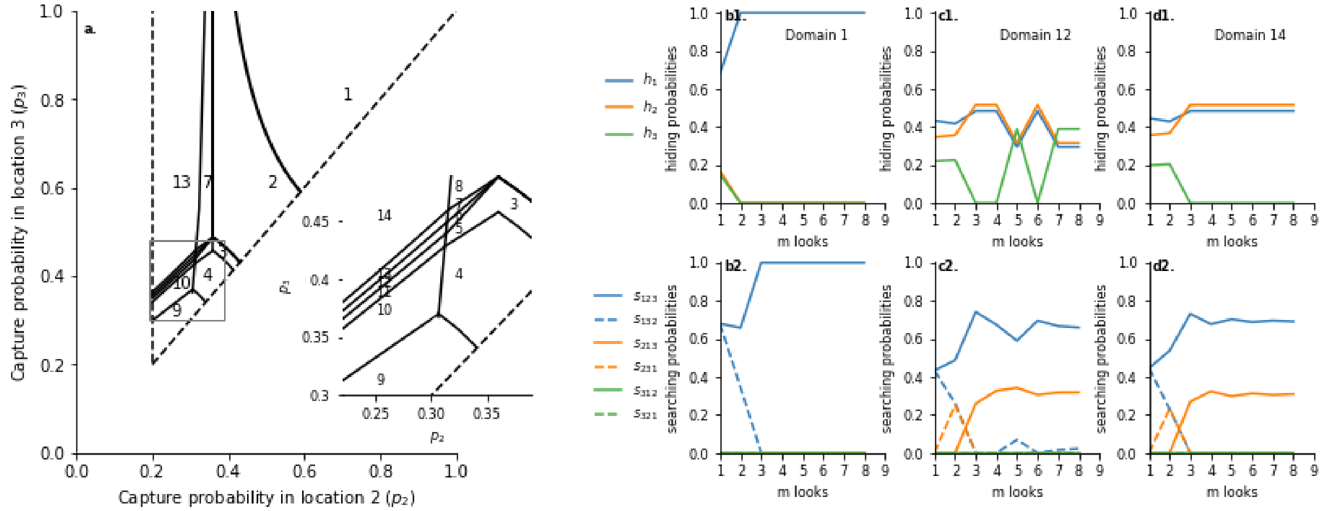

Figure 3: The (p_1,p_2,p_3) space can be divided into up to 15 distinct domains. (a) For p_1=0.2, the space (p_2,p_3) is delimited into 14 (out of 15) different domains (magnified view of the grey box is plotted in the bottom left). The vertical line $p_2 = p_1$ indicates that $p_1 < p_2$. (b-c-d) Hiding and searching strategies for 3 (out of 15) representative domains. (b) The optimal Hider strategy h^* (b1-c1-d1) and an optimal Searcher strategy s^* (b2-c2-d2) for a triplet (p_1, p_2, p_3) located in Domain 1. (b), Domain 12 (c) or Domain 14 (d).

5.3 A Game with only one good hiding location

In order to caracterize how the presence of a further hiding location affects the Γ_m game, we consider the particular case of the Γ_m game with 1 good hiding location G, with probability of capture of $g < 1$ and N=n-1 bad locations B with probability of capture of p_{BAD}. Note that there are n locations in total.

By symmetry arguments, we can limit our analysis to only these two following hiding strategies: G (hiding at the good location 1) and B (hiding at a random bad location). The Searcher has at most n searching strategies, which consists in searching the good location in the i-th position

$(1 \leq i \leq n)$ and searching a bad location otherwise.

5.3.1 The case in which the Hider can't escape from bad locations ($p_{BAD} = 1$).

Let's choose $p_{BAD} = 1$ (if the Hider is found, there is certain capture). For $m \geq n$, by dominance arguments, we can conclude that the game has always a saddle point (G, GB^{m-1}) : searching location G first, and hiding in location 1. For $m < n = N + 1$, by dominance arguments, we can reduce further the number of the Searcher strategies to only two: B^m which inspects m bad locations randomly and GB^{m-1} which inspects the good location (first) and $m - 1$ random bad locations. If the good location is inspected on the t'th search and the Hider is there, the Searcher payoff is 1 if the pursuit is successful and is v_{m-t} if it is not. Since v_m is increasing in m, searching the good location in period $t = 1$ dominates. For $m \leq N$, the game is reduced to a 2×2 payoff matrix as follows, where v_m denotes the value of the game Γ_m

Searcher/Hider	G	B
GB^{m-1}	$g + (1-g)\, v_{m-1}$	$\frac{m-1}{N}$
B^m	0	$\frac{m}{N}$

(4)

Thus,

Lemma 4 *The game $\Gamma(m)$, $m \leq n$ has the saddle point (G, GB^{m-1}) if and only if*

$$g + (1-g)\, v_{m-1} \leq \frac{m-1}{N} \tag{5}$$

The values are given by

$$v_m = \begin{cases} g + (1-g)\, v_{m-1} & \text{if } g + (1-g) \leq \frac{m-1}{N}. \\ \frac{-(m/N)(g+(1-g)v_{m-1})}{(-1/N)-(g+(1-g)v_{m-1})} & \text{otherwise} \end{cases} \tag{6}$$

For $m \geq n$, the game $\Gamma(m)$ has the saddle point (G, GB^{m-1}).

The following theorem shows that we can determine the nature of the solution (Pure or Mixed) of Γ_m based only on m,g and n. Moreover, for m sufficiently large, the Hider should always hide in the good location, and the Searcher should always play GB^{m-1}

Theorem 5 *For fixed $n \geq 1$ and $0 < g < 1$, let's define a threshold for m as follows $m_{th} = 1 + N - 1/g = n - 1/g$.*

- *For $m \geq m_{th}$, if $\Gamma(m)$ has the pure saddle point (G, GB^{m-1}) then so does $\Gamma(m+1)$. The Hider should always hide in the good location, and the Searcher should always play GB^{m-1}. The value is given by $v_m = g + (1-g)v_{m-1}$*

- *For $m < m_{th}$, if $\Gamma(m)$ has a mixed solution, then so does $\Gamma(m+1)$. The Hider should hide in the good location with probability $h_G = \frac{1}{1+N(g+(1-g)v_{m-1})}$ and in a bad location with probability $h_B = 1 - h_G$. The Searcher should play GB^{m-1} with probability $s^{GB^{m-1}} > s^{B^m}$. The value is given by $v_m = \frac{m(g+(1-g)v_{m-1})}{N(g+(1-g)v_{m-1})+1}$*

We have $\nabla m_{th}(N, g) = (1, \frac{1}{g^2})$. As $g < 1$ by definition, the quality of the best location has a stronger impact on the boundary between the pure and mixed solutions regimes than the number of locations.

5.3.2 The case when the Hider can escape from bad locations ($p_{BAD} < 1$)

We now generalize the previous result by letting p_{BAD}, the probability of capture in the bad locations, be different from 1 ($p_{BAD} \leq 1$). The Hider has still two strategies. However, for the Searcher, the dominance arguments do not always hold. The Searcher has n strategies, each consists in searching the good location G in the i-th position, with $1 \le i \le n$. We define $M = min(m, n)$. The $N \times 2$ payoff matrix is given by

$$\begin{array}{lll} \text{Searcher / Hider} & G & B \\ GB^{M-1} & g + (1-g)v_{M-1} & \frac{Mp_{BAD}}{N} + \frac{(1-p_{BAD})}{N} \sum_{1 \le j \le M, j \ne 1} v_{m-j} \\ BGB^{M-2} & g + (1-g)v_{M-2} & \frac{Mp_{BAD}}{N} + \frac{(1-p_{BAD})}{N} \sum_{1 \le j \le M, j \ne 2} v_{m-j} \\ \dots & \dots & \dots \\ B^{M-1}G & g + (1-g)v_{M-n} & \frac{Mp_{BAD}}{N} + \frac{(1-p_{BAD})}{N} \sum_{1 \le j \le M, j \ne n} v_{m-j} \end{array} \tag{7}$$

Lemma 6 *The game Γ_m has a pure saddle point with hiding at location G, and searching at location G first if*

$$g + (1-g)v_{m-1} \le \frac{(M-1)p_{BAD}}{n-1} + \frac{1-p_{BAD}}{n-1} \sum_{j=2}^{n} v_{m-j}. \tag{8}$$

Thus, the value v_m is given by $v_m = \begin{cases} g + (1-g)v_{M-1} \text{ if Eq.(8)} \\ \frac{(M-1)p(1-g)+g(1-p)+(1-g)(1-p)\sum_{j=1}^{M} v_{m-j}}{2-p-n+g(n-1)} \text{ otherwise} \end{cases}$

Theorem 7 $\forall n \in \mathbb{N}$, *for any $m \ge n$,*

if Eq. 6 holds, then $h_G(m) = 1$ and $h_B(m)$=0

otherwise, $h_G(m) = \frac{1-b}{n-(n-1)g-b}$ and $h_B(m) = \frac{1-g}{n-(n-1)g-b}$.

The Theorem 7 above indicates that the hiding probabilities are known for a given $m \ge n$, and are not a function of the previous values. It should be noted that "$\Gamma(m)$ has a pure solution" $\Longrightarrow$

"$\Gamma(m+1)$ has a mixed solution" only for "large" m, v.i.z. m should satisfy (see Supplementary Materials)

$$g \leq \frac{v_{m-1} - v_{m-n}}{n - 1 - \sum_{j=2}^{n} v_{m-j}} \tag{9}$$

Simulations indicates qualitatively that, as before, for a given m, the values of the Γ_m Game increases with an increasing number of locations, while they decrease with a decreasing g (the lowest the capture probability in the best location, the lowest the value).

5.4 The general case n $\geq$ 4

Here, we propose some conjectures for higher values of n, based on the computation of the recursion (equation 2) with custom-made Python scripts (see Supplementary Materials) and on our understanding of the cases n=2, n=3 and the case with only one good location. First, for large $m >> n$, the optimal hiding strategies do not change with an increasing number of looks m. In other words, for large m, the formula for h_i is not a function of m.

Second, when a hiding location is clearly "good enough" in comparison to the others, the hider has a pure strategy which consists in hiding exclusively in the best location. In this case, the value v_m is given by $p_1 + (1 - p_1)v_{m-1} \forall m > 1$. Thus, the quality of the best location (probability p_1) drives the variance of the overall capture probability, as it was pointed out by a PCA (Figure S5). When the capture probabilities p_i are "relatively close to each other", the prey should use a mixed strategy. For $m >> n$, this strategy consists surprisingly in hiding more in location n, which has the highest probability of prey capture, than in the best locations. For instance, in the domain II of the game with $n = 2$ locations, $h_2 > h_1$ for $m \geq 3$, Fig. 2c1. Similarly, in the domain 12 of the game with $n = 3$ locations, $h_3 > h_2 > h_1$ for $m \geq 7$. , Fig. 2c1 There are also other regimes in which the prey has a strategy set composed of pure and mixed strategies (avoid j locations and hide in the remaining n-j locations), (see for instance Figure S4, or Fig. 2d1 where $h_3 = 0$ while $h_2 > h_1$).

Third, for large m an optimal Searcher strategy consists in concentrating its efforts on the locations with the lowest capture probabilities. The strategy $[1, 2, ..., n]$, which consists in searching locations in increasing order, would be prioritized. If $0 < s_j < 1$ (permutation j should be used with a probability which is neither 0 nor 1), s_j depends on m but converges for increasing m.

6 Discussion

6.1 The Γ_m game, a framework which generalises previous search-and-pursuit games

Our model improves the degree of realism of search and pursuit of previous games. In the original game G_k^{2014}, the budget (per round looks) k implicitly drops to 0 when the prey evades capture. In the game G_k^{2015}, k resets to its original value whenever the prey is found, with a probability β. Here, we use a finite total budget m of resources in all rounds, being time, eggs, "munitions" or internal state. Our model led to qualitative and quantitative results which can be summed up as follows: (1) The predator foraging success decreases with spatial complexity (number of hiding places and quality of the best location). (2) We can observe rapid changes in locations just before the protagonists reach the deadline. This is particularly observable for e.g. the Domain 12 in

Fig. 3, where the location with the highest hiding probability changes as m becomes lower than 8. This behavior near the deadline is reminiscent of the dynamic optimisation models reviewed in [HKE80]. Conversely, when m is above an undetermined threshold, the optimal hiding strategies become independent of the number of looks m. In other words, there is a uniformly optimal strategy for Γ_m when "m is sufficiently large". This means that the prey can minimise the probability of capture and carry out the optimal strategy without even knowing the budget of the predator (also called deadline in Lin and colleagues [LS16]) is unknown. (3) For large m, depending on a complex interplay between the capture probabilities p_i, the prey should either hide more in the worst locations and less in the best locations, or on the contrary avoid totally the worst locations. When the location 1 is "clearly better" than the others, the optimal strategy would consist in keeping hiding in the same place (location 1) over and over, as long as m is greater than 1 (4) For large m, the predator should concentrate his efforts on the locations in which the prey capture probabilities are the lowest. For instance, in the game with $n = 2$ locations, the probability of inspecting location 1 first (s_{12}) is higher than the probability of inspecting location 1 last (s_{21}) whatever the domain I, II or III. 2b2-c2-d2. This is highly counter-intuitive at first glance. We discuss these results in turn.

6.2 Leveraging some of the model's assumptions

Some assumptions of the model are the following (1) The prey does not change her location when the predator is searching until it is found (the rash prey hypothesis). (2) all locations are equally easy to search and there aren't any travel costs between locations. (i.e. searching cost one look in every locations) (3) The parameter m can only decrease over "time" (time moves forwards). (4) The number of escape moves of the prey is bounded by m, *i.e.* there is no fatigue in the prey indicating that the drive to survive is stronger than losing energy. (5) The individual capture probabilities p_i in each location i do not evolve over time. (6) The Γ_m game is a zero-sum two players game (7) The predator is aware of the total number of locations. (8) The prey knows the budget m of the predator and bases her decisions accordingly. Both players know the number and qualities (p_i) of locations but not the strategy chosen by the other at each round. (9) The prey can decide where it will hide after a pursuit and all locations are equally affordable. We discuss here a few of these assumptions of our model.

The hiding locations and their connectivity patterns in our model are supposed equivalent, and a more accurate representation would consist in representing hiding locations as the nodes of a weighted graph. The nodes would be networked together thanks to weighted edges [AG06], as a first step towards either the consideration of 3D continuous geometrical environments or that some location requires more investment to search. The Γ_m corresponds to the search game of a mobile hider in a fully connected graph but with a finite budget. The search problem of a mobile hider was solved by [Gal80] and the value is $\frac{(1+\epsilon)\mu}{\rho}$ where μ is the Lebesgue measure and ρ the maximal discovery rate. With a few modifications of the equation, we can take into account spatial features (connectivity and heterogeneity of locations) and considered whether higher graph connectivity increases the value of the game.

Incomplete information game with predators having *a priori* ideas concerning the number of locations and capture probabilities could be Bayesian updated [Alp+19]. A promising perspective would be the application of our framework to the robotic problems of search-and-pursuit in polygonal environments with visibility polygons when characterizing the environment as a collection of discrete locations is more tricky [Li+18]. The model proposes indeed new optimal searching strategies which could be easily implemented for the development of autonomous navigating agents.

6.3 Counterintuitive prey strategies

The previous search-and-pursuit games and our Γ_m game share a global result: the parameter space (p=$\{p_i\}$) can be divided into domains, in which the prey should either always go to location 1, or hide differently. In the original model G_k^{2014}, the prey knows that if it successfully escapes, it would win, or lose otherwise (that is why the number of looks k was lower than n). For $k < k_{threshold}$, the prey plays a equally-attractive strategy (making $h_i p_i$ constant $\forall i$). Moreover, an increasing number of looks k also encourages the prey to always hide in the best locations [GC14]. Indeed, as the number of looks increases, it is more likely to be found. Thus, for $k > k_{threshold}$, it should hide in location 1 (with the lowest capture probability). In the Γ_m game, evading once the predator is not sufficient to win the game because the predator can retry an attack if it has enough resources. Even for a large m, always hiding in the location 1 may not be the best strategy. The conclusions of the original model of 2014 and our model seem therefore to mismatch, but we solved this discrepancy by pointing out that the G_k^{2014} was a particular case of our Γ_m game. The most surprising result concerning the hiding strategies was that, for $m >> n$, the prey should sometimes hide more in the worst locations than in the best locations, which is quite counter-intuitive. We provide an explanation next.

First, we remind that the predator wants to capture the prey before a deadline, not necessarily as soon as possible. As in all zero-sum games, the objectives of both protagonists are opposing. We imagine a predator thinking with a minimax point of view. It might be tempted to inspect the locations with the highest capture probabilities first, and to inspect the locations in decreasing order of the capture probabilities. However, if the prey is hidden in location 1 (with the lowest capture probability), the predator loses twice. Not only does it wasted n searches, but it also ends up in the location with the lowest capture probability, and another round is very likely to start. Instead, inspecting the locations in increasing order of capture probabilities seems beneficial. If the prey is in location n, the predator loses again n searches, but the latter is very likely to capture the prey in location n, and thus win the game. If the prey is in location 1, the predator is unlikely to catch the prey, but at least it will not lose many looks, and it may be better for the predator to encounter the prey as many times as possible. Conversely, the only chance for the prey to survive is by driving the budget m down quite quickly to reach the absorbing state m=0. A prey acting in a minimax point of view would try to waste the predator's budget m, even if it implies to hide in the locations with the highest capture probabilities (location n), as it is important to make big decreases in m. Once m gets closer to the deadline, such risks may no longer be needed, and the prey would hide in the locations with the lowest capture probabilities. Somewhat similar considerations of opposite dual motivations are at the heart of [Cla20] about searching with deadlines. However, in our work, the predator must keep an eye on its budget, and it doesn't need to find the prey as soon as possible.

Of course, in natural environments, the observed hiding patterns may differ given that the prey has also other objectives, such as maximising foraging (the best hiding locations may be very costly) or the presence of intraspecific competition (ideal free distribution patterns)[CB15].

6.4 Structurally complex environments

The discrete locations in our model can be interpreted in a wide range of ways: hiding places, space coordinates, discretized angles of escapes, snapshots of visibility, and prey habitats at a larger scale. We have shown that the overall capture probability decreases with an increasing number of locations for a given number of looks m, which is consistent with a large body of ecological work. Although often underlooked, it is well-known that habitat structural complexity is a major determinant of predator-prey interactions ([CC82], [Hil75]), notably since MacArthur works on biogeography [MP66], where the structure of the environments is one of the ingredient of "all interesting biogeographic patterns". The prey density or predator's avoidance success is thus positively correlated with the habitat structure, by limiting the number of predator-prey encounters. These phenomena have been described for different biological scales and organisms from bacteriophages and bacteria [Lou+20], immune cells migrating in 3D matrices [Sad+20], to damselfly and perches hunting in structurally complex Myriophyllum algae [WB04]. We now qualify this finding by claiming that the prey's success is even more related to the quality of the *best* location than the *number* or heterogeneity of locations. When location 1 is "good enough", the prey's strategy consists in always hiding in that location. Although being predictable, her losses would be worse if it would have hidden in an other location. It is such a low capture probability that it worth hiding in there all the time. Defining a location "good enough" depends on the quality of the other locations. The fact that the quality of a location depends on extrinsic factors (the quality of the other locations) is reminiscent of the marginal value theorem in foraging ecology, in which the same rationale was made for food patches. The presence of a very good refuge thus matters more than a large number of refuges of average quality.

7 Acknowledgements and funding

We acknowledge Jake Clarkson for fruitful discussions. This work was supported by the École Doctorale SSBCV Centre val de Loire and an ENS Lyon Ph.D. fellowship to P.C. in Tours under the supervision of J.C.

8 Data accessibility

The data that support the findings of this study is available on a Github online repository (See Supplementary Materials)

9 Authors' contributions

J.C., S.G. and S.A. conceived the idea of the paper. J.C. and S.A. supervised the work. S.G. and S.A. formalised the game. S.A. provided most of the search game literature. J.C. and P.C. provided most of the biological literature. P.C. ran the simulations, analysed the game, and wrote the first version of the manuscript. Various drafts were amended by S.A. and J.C. The final version was approved by all authors.

10 Competing interests

We declare we have no competing interests.

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