

## Cognitive abilities of a central place forager interact with prey spatial aggregation in their effect on intake rate

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When foraging in a landscape, predators choose travelling directions according to their immediate knowledge of prey distribution within their perceptual fields and, when appropriate, to their past foraging experience. A substantial part of foraging theory is based on patch use in spatially implicit domains, and rarely has it considered foraging paths involving directional choices driven by memory and perception. Using a model mixing directed and random movements of a predator, we investigated how perception range and duration of spatial memory influence the long-term intake rate of a central place forager depending on prey spatial distribution. We found that intake rate increased and eventually saturated with increasing perception range regardless of prey spatial distribution. In contrast, the effect of spatial memory duration was mediated by the level of prey spatial aggregation. Assuming that an increase in memory or perception abilities has a cost, we found that it was not beneficial to possess simultaneously a wide perception range and a long-term spatial memory when prey distribution was aggregated. Moreover, when looking at the functional response of predators with different 'cognitive strategies', we found that those relying mainly on memory were limited by the prey global densities while those relying mainly on perception were limited by the level of prey aggregation. These results suggest that cognitive strategies might have evolved as a response to the prey spatial distribution and that prey spatial aggregation, not only prey global density, should be considered an important component of the functional response.

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Predators foraging on large spatial domains can optimize their foraging efficiency by maximizing the time they spend in prey-rich areas. In many foraging models (the so-called patch models, Stephens & Krebs 1986), the landscape is divided into patches that are well-defined geographical areas, generally corresponding to different habitat types with different levels of resource supply. However, in most natural situations, it is difficult to delineate the boundaries of such patches, either because there are no clear differences in prey local densities or because the sole indicator of the existence of a favourable patch for the predator is the detection of the prey itself (Krakauer & Rodriguez-Gironés 1995), especially if prey items are cryptic. To consider a wider range of prey distributions that include, but are not restricted to, the patch eye view of landscapes, a general representation of prey items as points in a continuous, two-dimensional space is needed. In this context of continuous spatial prey distributions, assessing the optimality of a predator's feeding strategy given a set of constraints (e.g. handling

time, detection range or satiation) involves considering two components: the matching between the foraging path geometry and the spatial resource distribution, and the allocation of time along the foraging path (Arditi & Dacorogna 1988). Most theoretical studies of foraging (e.g. Charnov 1976; Knoppien & Reddingius 1985; Krakauer & Rodriguez-Gironés 1995; Klaassen et al. 2006) have been concerned with time allocation only, which is mathematically equivalent to considering the case of a forager travelling along a one-dimensional habitat. Thus, studies on two- or three-dimensional environments have often neglected the influences of directional choices on foraging success (but see Benhamou 1992, 1994). Understanding foraging in two-dimensional habitats thus requires a more explicit spatial modelling of animal movement relating directional choices to behavioural states (Scharf et al. 2007).

Movement models based on random walks are frequently used to model foraging paths in two-dimensional habitats (Turchin 1998). Here 'random' does not mean that animals actually make their choice of direction at random, but merely that given the potentially large number of unknown factors involved, stochastic modelling is a parsimonious description of the sequence of directional choices during a foraging trip. Random walk models are diverse and have a long history of applications to describe

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individual movement (Pearson 1905; Patlak 1953). A frequently used model of individual movement is the correlated random walk (CRW) which accounts for the persistence in the direction of motion commonly observed in the field (Kareiva & Shigesada 1983). However, classical random walk models amount to a phenomenological description of animal paths whose goal is mostly the statistical estimation of the parameters (e.g. Kareiva & Shigesada 1983; Turchin 1998). Recent approaches using behavioural-dependent random walk models, in which behavioural states depend on environmental features (Morales et al. 2004), have allowed the gap between mechanistic studies of space use and phenomenological models of individual movement to be bridged and seem very promising to model individual movement in general (Börger et al. 2008; Patterson et al. 2008). Forerunner studies used these models to investigate the efficiency of searching strategies (Benhamou 1992, 1994; Zollner & Lima 1999) or to formulate a continuum of space use models ranging from random diffusion to the ideal free distribution (Farnsworth & Beecham 1999). Although there is no single mathematical framework to express behavioural-dependent random walk models (they are mostly algorithms derived from a baseline CRW model), their utility is now well established, and they represent a convenient framework to investigate how the information available to predators shapes foraging success in 'continuous' two-dimensional habitats with different resource distributions (Zollner & Lima 1999).

The available information to predators about prey spatial distribution (i.e. used during the searching phase of foraging behaviour) is the result of cognitive processes such as perception, learning and memory (Shettleworth 2001). The cognitive processes involved in foraging have been greatly simplified in earlier models. For instance, Charnov's marginal value theorem (1976) assumes predator knowledge of the resource spatial average, an assumption likely to be met only on a small foraging area compared to the predator's powers of perception. More recent models (e.g. van Alphen et al. 2003; Dall et al. 2005; Klaassen et al. 2006) have included a more mechanistic perspective of information processing during foraging behaviour, and cognitive abilities of animals related to the storage and retrieval of spatial information have been studied in a variety of contexts (Janson 1998; Healy et al. 2005). The cognitive abilities relevant in the search of prey items can be classified as (1) information acquisition, resulting from recent experience beyond the perceptual reach, and (2) retrieval of stored information about successful previous capture events (Thiele & Winter 2005). This classification particularly applies to vertebrate predators that often forage over large spatial domains wherein prey items are perceived within a finite perceptual range, and memorized profitable locations may be forgotten after some time. Perceptual range and spatial memory duration thus seem to be two key parameters determining the amount of spatial information a predator can gather about its prey distribution when foraging over a large spatial domain.

We investigated how perceptual range and spatial memory duration interact with prey spatial distribution in determining foraging success of a central place forager (CPF). This is a widely observed foraging behaviour in many species of vertebrate top predators (e.g. raptors, seabirds, sea mammals; Orians & Pearson 1979) and the one that inspired the formulation of the model presented here. In contrast to a more 'nomadic' forager, a CPF typically uses a restricted spatial domain and regularly returns to a central place (generally its nest) between consecutive foraging trips. Hence, a CPF is more likely to use information obtained in the past in a large, fixed spatial domain than a nomadic forager wandering in its ever-changing foraging domain.

Short-term spatial memory is already known to enhance foraging efficiency when prey items are spatially aggregated

(Benhamou 1994), because it allows predators to increase the sinuosity of their searching path and to slow down and concentrate the search effort in areas more likely to contain prey items. The latter phenomenon is called 'area-restricted' (or 'concentrated') search (Tinbergen et al. 1967) and it has often been observed in the field (see references in Benhamou 1992). Other studies (e.g. Zollner & Lima 1999) have shown that the perceptual range influences predators' search efficiency. However, to our knowledge, it is not yet known whether, and how, perceptual range and spatial memory duration interact to determine search efficiency for different kinds of prey spatial distribution. Intuitively, when prey spatial distribution is clumped, memorizing recent capture locations provides genuine information to the forager. In contrast, when prey items are randomly distributed, having a wide perception can be advantageous for a forager whereas possessing a long spatial memory would not because the locations of previous captures do not convey much information about local profitability. Therefore, having both a long memory and a wide perception need not necessarily be advantageous by default: the consequences of these two cognitive abilities are likely to be contingent on the type of spatial prey distribution.

In the following we start by assessing our intuitive predictions using a behavioural-dependent movement model of a predator feeding in a continuous space, and then explore the consequences of different cognitive strategies for the functional relationship between predator intake rate and prey density (i.e. the functional response, *sensu* Holling 1959). Finally, we discuss the generality of our findings for different types of realistic prey and predator interactions, and evaluate the consequences of relaxing the key assumptions of our model.

## THE MODEL

Our model describes the movement of a single predator feeding on static prey with different spatial distributions. Considering prey items as having a static distribution amounts to assuming that they are actually much less mobile than predators, not that they literally need to have fixed locations in space as sessile organisms. Our model is spatially explicit in that locations of both predator and prey are represented as points in a two-dimensional space that is assumed homogeneous in terms of prey capture (i.e. no refuges). We further assumed that prey individuals do not interact with each other, that they are identical in terms of how easy they are to capture and energetic content for the predator and, by considering a single predator, we do not consider intraspecific competition through either resource depletion or interference. The temporal sequence of locations visited by the predator is obtained from a behavioural-dependent random walk, whereas the locations with a prey individual result from an initial spatial point process (Stoyan & Penttinen 2000) followed by a progressive depletion during a simulation run. A simulation run is made of 100 000 time steps during which the predator makes a variable number of foraging trips starting from its central place and returning when a prey is captured. During the breeding season, a central place forager might be either provisioning its nest or feeding itself (provisioning versus self-feeding, McNamara & Houston 1997). The provisioning case we chose corresponds to feeding of the young, a situation where intake rate is strongly linked to individual fitness and therefore very likely to be maximized. We consider a 'single-loader' case, that is, a single prey is brought back to the nest at once (Lessells & Stephens 1983). Our fitness currency is the long-term intake rate estimated as the number of prey items harvested in a simulation run (including many foraging trips) divided by its duration. The model was written in the Pascal programming language, and all simulations were performed with the FreePascal compiler (<http://www.freepascal.org>).

We formulated two versions of the basic spatial foraging model to explore different aspects of how cognitive traits (perceptual range and spatial memory duration) interact with prey spatial distribution in determining foraging success. In the first version, the probability of prey capture after detection was constant and invariant with respect to cognitive parameters. This first, simpler version of the model was used as a baseline to investigate how cognitive abilities may trade off depending on the spatial distribution of resources and lead to differences in the long-term intake rate. In the second version, the capture probability was varied with the extent of perception and the length of memory to implement costs of increasing cognitive abilities.

*Predator Movement and Behaviour*

We considered that the forager's movement follows either a random search (navigation without use of perceived or memorized items), or a directed movement towards a perceived or memorized cue, be it a prey individual or a landmark. The former is modelled as a correlated random walk and the latter as a straight-line movement towards the cue. At each time step of a simulation run, the predator changes its location using either a random or a directed movement mode, depending on an internal behavioural state (see Table 1) that denotes the task it is currently engaged in. Each simulation run is made of 100 000 time steps.

*Movement model*

The foraging path is a sequence of changes of direction influenced by the behavioural states of the forager. It is a mixture of random and deterministic movements (see also Plank & James

2008). Let the predator's location at time  $t$  be  $X_t = (x_t, y_t)$ . For the sake of clarity, we define an arbitrary spatial unit  $u$  and an arbitrary temporal unit  $w$  to describe the movement of the predator. Assuming that the predator moves at a constant speed of  $1 u/w$ , the next location is obtained as:

$$X_{t+1} = (x_{t+1}, y_{t+1}) = (x_t, y_t) + (\cos\theta_{t+1}, \sin\theta_{t+1})$$

where the travelling direction  $\theta_{t+1} = \theta_{t+1}(I_{t+1})$  depends on the behavioural state variable  $I_{t+1}$  that can take values in  $\{N, A, M, R\}$  (see Table 1 for details). State  $N$  corresponds to an animal returning to the nest to deliver the prey item captured,  $A$  means the predator is attacking,  $M$  that the predator directs itself to a memorized location, and  $R$  that it is randomly searching according to a correlated random walk (concentration parameter  $\rho$  for consecutive changes of direction: 0.995). The foraging movements are adaptive in the sense that the predator reacts to changes around its current location to maximize its rate of energy acquisition according to transition rules between behavioural states.

The transition rules between the four behavioural states (see Appendix) are summarized as  $N > A > M > R$  where the inequality sign reflects a strict hierarchy of precedence. Thus, at each time step, the predator following a CPF strategy always favours returning to the nest with a prey captured over attacking (e.g. as a raptor would do when feeding its offspring), attacking a prey in sight over going to a memorized place (the predator is opportunistically searching for food), and going to a memorized place over randomly searching (it uses all information of prey locations available). Random search is therefore the default behavioural mode when the predator has no cues allowing it to perform other tasks. In contrast, bringing back the captured prey individual to the central place has precedence over all other tasks. A typical foraging trip according to these rules is presented in Fig. 1.

**Table 1**  
States of the behavioural variable  $I_t$  of the foraging model denoting the four mutually exclusive actions performed during a simulation run

Behavioural state $I_t$	Movement rules
$N$ ='Return to nest' The predator has a directed movement to the nest where it has a prey item to deliver	$\theta_{t+1}(N) = \tan^{-1}(y_N - y_t, x_N - x_t)$ where $X_N = (x_N, y_N)$ are the coordinates of the nest and $X_t = (x_t, y_t)$ the current position of the predator
$A$ ='Attack prey at sight' The predator has perceived at least one prey individual within its perceptual field and directs itself towards the closest prey from its current position	$\theta_{t+1}(A) = \tan^{-1}(y_A - y_t, x_A - x_t)$ where $X_A = (x_A, y_A)$ are the coordinates of the prey being attacked, with $d(X_t, X'_i)$ where $d$ is distance and $X'_i$ are the coordinates of all prey items within a distance $\delta$ from the predator
$M$ ='Go to a memorized place' The predator goes to the closest memorized profitable location that is still in its memory	$\theta_{t+1}(M) = \tan^{-1}(y_M - y_t, x_M - x_t)$ where $X_M = (x_M, y_M)$ are the memorized coordinates of the closest profitable place to the nest. A profitable place is defined as the location of a previously caught prey individual. When a captured prey is brought to the nest, its capture location becomes stored in memory and a time-in-memory variable $T_t$ is incremented. At each time step we update that variable according to $T_{t+1} = T_t + 1$ . If $T_{t+1} > \tau$ , then the capture location is forgotten and the behavioural state becomes $I_{t+1}=R$ instead of $M$
$R$ ='Random search' In the absence of any cue, the predator performs a correlated random walk to search for prey items in the landscape	The next direction is $\theta_{t+1}(R) = \theta_t + \alpha_{t+1}$ where $\alpha_{t+1}$ is a random variable drawn from a symmetric wrapped normal distribution of standard error $\sigma=0.1$ (concentration parameter of the turns $\rho=0.995$ ). This is a classical correlated random walk (Bovet & Benhamou 1988)

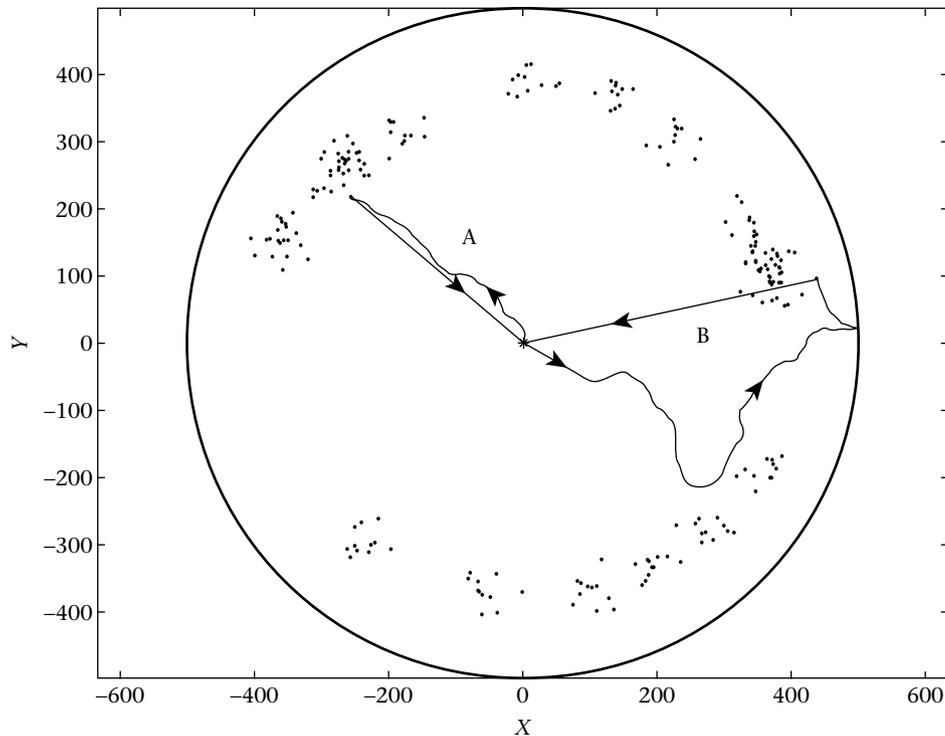
The states correspond to different rules for computing the changes in direction of the forager. The function  $\tan^{-1}(y, x)$  returns to any vector  $(x, y)$  its direction with respect to the  $X$  axis.

*Cognitive variables*

We focus on two key cognitive aspects involved in spatial foraging, one related to the spatial memory and the other to the perception of prey in space. The cognitive variables we consider represent limits to the amount of spatial information that a predator can gather and process during its foraging activities. The memory duration,  $\tau$ , is defined as the length of time (in temporal units  $w$ ) that a location where a prey was captured remains in the predator's memory. Since the predator always comes back to the nest after each prey capture, and memory would be useful only when its duration is greater than that of the return trip, a memory duration  $\tau$  of zero means the forager leaves the nest without information about the last location where a prey was captured, while  $\tau > 0$  means it has at least one capture location in mind (see Table 1 and Appendix for details). The perceptual range (or, equivalently, detection radius) is denoted as  $\delta$  and it corresponds to the maximum distance (in spatial units  $u$ ) at which a prey item is perceived. The perceptual range is assumed to be isotropic, that is, the forager can detect prey items within a distance of  $\delta$  of its current position in every direction. The memory duration is only concerned with places where the forager was able to capture a prey and that potentially represent profitable places for the predator.

*Prey Spatial Distribution*

The prey spatial distribution was modelled as a spatial point process (Stoyan & Penttinen 2000) whose initial abundance  $N$  was set at the start of each simulation. Because we assumed that the forager's movements were fast compared to prey demographic processes, we did not consider prey renewal, and therefore prey items are monotonically depleted over time during a simulation.



**Figure 1.** Illustration of two typical foraging trips starting and ending at the nest (star) extracted from a 100 000-steps simulation run. The arrows indicate the route taken. In foraging trip (A), the forager has no information about prey locations (dots) at the start and performs a CRW until it finds a prey, captures it, and brings it back to the nest. In foraging trip (B), the forager starts in a straight line towards a memorized profitable location, but soon forgets it because its memory duration  $\tau$  is short and it switches to random search mode (CRW). It then bounces at the boundary and eventually catches a prey that it brings back to the nest. Cognitive parameters used in these simulations are memory duration  $\tau = 110$  time steps and detection radius  $\delta = 5$  pixels, with an 'Aggregated' (10 overlapping clusters of 20 individuals) prey spatial distribution.

The situation we have considered is analogous to that of a predator foraging during the breeding season in a given area and leaving it at the end of the season when prey are scarce. We considered both Poisson and Poisson cluster point processes to account, respectively, for complete spatial randomness and aggregation of the prey spatial distribution. A Poisson cluster process is a spatial point process wherein centres of point clusters are uniformly distributed in space and points belonging to each cluster are drawn from a probability distribution defined at each centre. We chose a bivariate Gaussian distribution with standard deviation  $s$ ; the resulting point process is called a Thomas process (Stoyan & Penttinen 2000).

#### Spatial Domain

We considered a circular habitat of radius  $500 u$  centred on the predator's nest and with reflective boundaries (i.e. the predator turns back when it encounters the boundary). While other boundaries (e.g. periodic, Benhamou 1992) have been used in simulation studies, we think that reflective boundaries are the most logical in our case given that the central place forager considered here would be feeding on a restricted and circular spatial domain. Preliminary simulations showed that the predator always tended to deplete the locations closer to its nest even though prey were distributed over the entire spatial domain. When the predator uses only a small fraction of its spatial domain, the distance from prey (or prey clusters) to the nest becomes the major driver of intake rate, making it impossible to assess the effect of cognitive abilities on intake rate at different prey spatial distributions. To disentangle the effect of the distance between prey and the nest from that of cognitive abilities, we constrained the predator to travel for a while away from the nest before capturing its prey so we could assess the

role of orientation to favourable places. We thus restricted the prey spatial distribution to a ring comprised within radii  $[350, 400] u$ . This is analogous to considering that the predator had quickly depleted the surroundings of its nest at the start of its breeding season.

The first version of the model then assumes that the probability of capturing a prey once it was detected is constant and equal to 0.5 (see Table 2) and thus is invariant to changes in the predator's cognitive abilities. Nevertheless, it is unlikely that great cognitive abilities (i.e. very long memory and far-sighted perception) can be attained without eventually being detrimental to some component of the long-term intake rate (see Discussion). In the next section we describe the second version of the model including a decrease in capture probability with increasing cognitive abilities.

#### Decreasing Capture Probability

We modelled decreases in capture probability with increasing  $\tau$  and  $\delta$  as a means of assessing the cost in terms of loss of food intake for certain values of these cognitive parameters. This is only one of the many ways in which costs might be introduced and, depending on the

**Table 2**  
List of variables and parameters used in the foraging model

Symbol	Meaning and units
$E$	Intake rate (number of prey harvested/simulation time)
$\tau$	Memory duration (in temporal units $w$ )
$\delta$	Detection range (in spatial units $u$ )
$N$	Total (initial) number of prey individuals
$s$	Prey spatial dispersion: standard error of the Gaussian distribution around the cluster centre (in spatial units $u$ )
$P_c$	Capture probability once a prey is reached

kind of predator and environment being considered, this choice of foraging costs would be more or less suitable (see Discussion). We used an exponentially decreasing function for the capture probability to denote that the costs of memory and perception are accelerating as  $P_c = 0.75 \exp(-3\delta/\delta_m - 3\tau/\tau_m)$  where  $\delta_m$  and  $\tau_m$  are the maximum values allowed for the detection range and memory duration, respectively. We set  $\delta_m = 25u$  and  $\tau_m = 1250w$  (in the cost-free case the intake rate is saturated for these values so they represent convenient ‘limit values’). The function used for the capture probability was chosen so that the probability of finding a prey in the absence of cognitive abilities is 0.75. When both  $\delta$  and  $\tau$  reach half of their possible values, the probability is less than 0.05, which means that high values of both parameters lead to low capture probability. The convex shape of the function implies that an additional unit of  $\delta$  or  $\tau$  is more costly in terms of capture probability as  $\delta$  or  $\tau$  increases, which seems biologically plausible since the greater the cognitive abilities, the harder it is to improve them without detrimental effects to other abilities involved in prey capture.

## MODEL ANALYSIS

### Intake Rate as a Continuous Function of Cognitive Abilities

We first calculated the intake rate  $E$  assuming a capture probability that is constant and equal to 0.5 (although changing  $P_c$  between 0.1 and 0.9 did not qualitatively change the results). Then, to investigate the effect of cognitive costs, we modified the first model by decreasing capture probability with increasing  $\tau$  and  $\delta$  while keeping all other parameters constant.

We varied the cognitive parameters  $\tau$  and  $\delta$  to form 2500 combinations in the ranges of [10, 1250] for  $\tau$  and [1, 25] for  $\delta$  for the three prey spatial distributions. While other, more subtle methods of exploring parameter space and assessing the optimality of cognitive parameters could have been used (e.g. genetic algorithms, Mitchell & Taylor 1999), we thought a simpler method of exploring how long-term feeding rate changes in the parameter space was sufficient at this stage of the research. For a given initial global abundance  $N$ , we considered three spatial distributions of prey (Fig. 2): complete spatial randomness (Poisson), overlapping clusters (Aggregated), nonoverlapping clusters (Patchy). These distributions represent a gradient of increasingly clumped prey distributions. The Aggregated distribution corresponds to  $s = 30u$  while the Patchy one corresponds to  $s = 5u$ .

The global prey abundance  $N$  was set to 200 prey items for the three spatial distributions, and it was divided into 20 clusters of 10 items for the Aggregated and Patchy distributions (we also considered a global abundance of  $1000 = 50 \times 20$  prey individuals to verify whether results were affected by the choice of the initial prey abundance). For each pair  $(\tau, \delta)$  and for each type of prey

spatial distribution, we calculated the intake rate  $E$  averaged over 50 simulations each 100 000 time steps long.

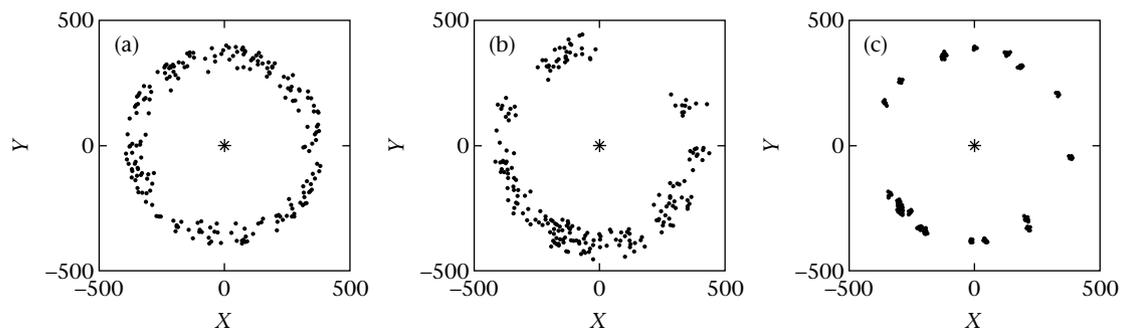
### Intake Rate as a Continuous Function of Prey Spatial Distribution

We next considered predators that have four contrasting ‘cognitive strategies’ represented by different combinations of the cognitive parameters (Table 2). These strategies were Limited ( $\tau = 10, \delta = 1$ : both poor memory and poor perception abilities), Memorizer ( $\tau = 500, \delta = 1$ : good memory but poor perceptual abilities), Perceiver ( $\tau = 10, \delta = 10$ : opposite to the Memorizer) and Unlimited ( $\tau = 500, \delta = 10$ : unconstrained by either cognitive feature). The value  $\tau = 500$  was chosen because it was a period long enough to allow the predator to go from the nest to a memorized cluster’s location where it had captured a prey before. In contrast,  $\tau = 10$  depicts a situation in which the predator leaves the nest oriented in the direction of a previous capture location during only 10 steps, hence ‘remembering’ only the overall direction of its previous attack. We set  $\delta$  to 1 and 10 to represent either a perception at the spatial scale of the pursuit ( $\delta = 1$ ) or a perception at the scale of the prey cluster ( $\delta = 10$ ). We excluded high values of  $\delta$  that preclude perception over the entire spatial domain (which is theoretically possible but not typical of the situation considered here). For each cognitive strategy, we evaluated the effect of varying the total number of prey  $N$  and the level of local aggregation on the average intake rate  $E$ . We used the standard deviation  $s$  of the bivariate Gaussian deviate positioned at each of 20 cluster centres as the aggregation parameter because of its intuitive interpretation and its independence of the number of prey in each cluster provided there are enough prey per cluster. Indeed, a Poisson cluster process with only two or three points in each cluster is not distinguishable from a Poisson process. We used 2500 combinations of  $N$  (in [220, 1200]) and  $s$  (in [1, 50]), beginning with enough points to observe a clustered distribution with 20 clusters. For each combination of  $N$  and  $s$  and for each cognitive strategy, we calculated the intake rate  $E$  averaged over 50 simulation runs each 100 000 time steps long. As we investigated the response of four different cognitive strategies to the continuous variation in prey global density and spatial aggregation, we assumed no cognitive costs (i.e. capture probability was constant and invariant to changes in  $\tau$  and  $\delta$ ). Because cognitive parameters were held constant for each cognitive strategy, their inclusion would not change the results.

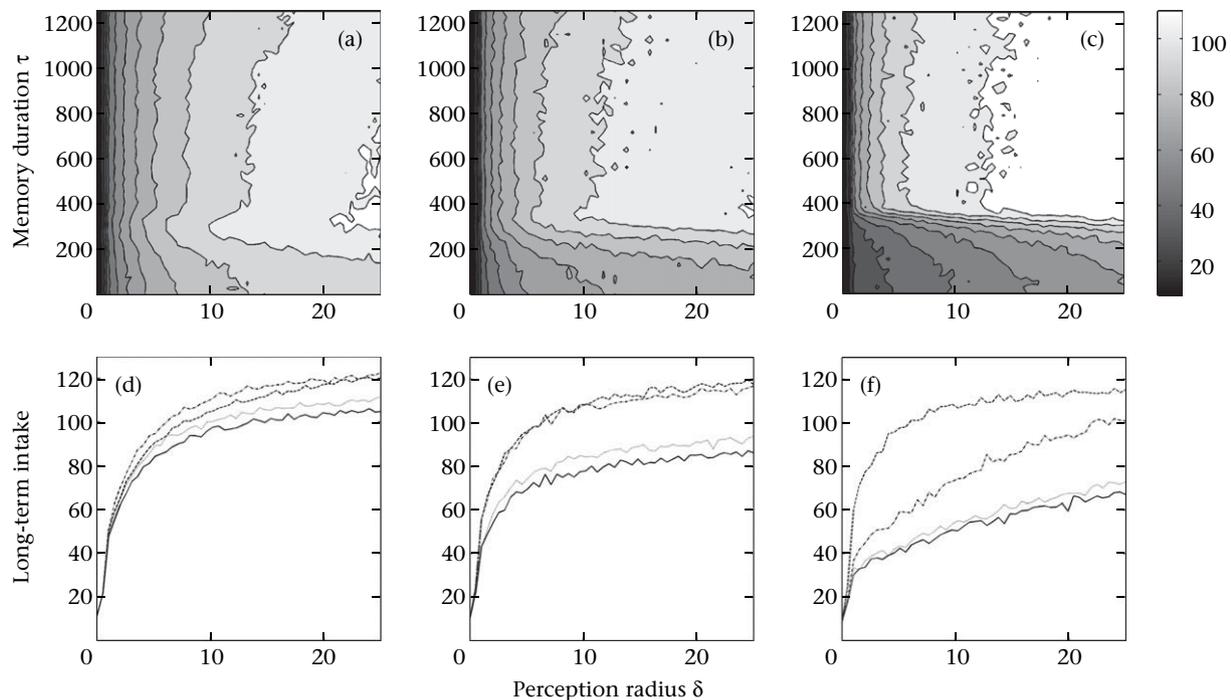
## RESULTS

### Intake Rate as a Continuous Function of Cognitive Abilities

When prey spatial distribution was completely random (Fig. 3a) the intake rate  $E$  increased with the perception radius  $\delta$  but barely



**Figure 2.** The three kinds of prey spatial distributions used: (a) Poisson, (b) Aggregated and (c) Patchy. The predator’s nest is located at the centre of the circle (star), and all locations with prey are distributed within a ring away from the centre (see The Model).



**Figure 3.** Long-term intake (number of prey items captured in a simulation run) as a function of the perception radius (distance of detection  $\delta$ ) and the memory duration (time to forget a prey capture location  $\tau$ ), for three kind of spatial distributions (a) Poisson, (b) Aggregated, (c) Patchy. No cognitive costs are assumed here. Plots (d), (e) and (f) represent 'slices' of the above contour plots (a, b, d, respectively) for various values of the memory duration  $\tau$  (continuous line  $\tau = 0$ , dotted  $\tau = 153$ , dash-dotted  $\tau = 306$ , dashed  $\tau = 612$ );  $\tau > 0$  means the predator leaves the nest with at least one previous capture location in memory.

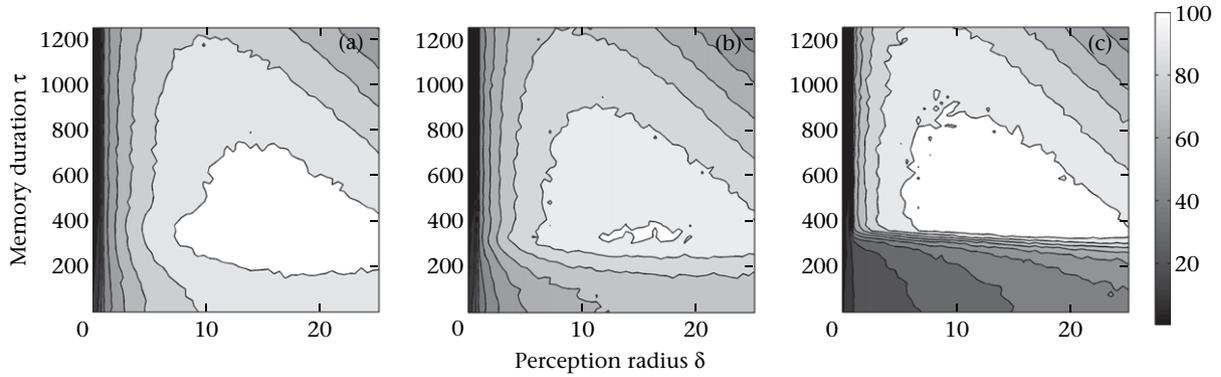
with memory duration  $\tau$ . The increase of  $E$  with respect to  $\delta$  eventually saturated for large values of the perception radius (Fig. 3d). Only a small region of parameter space ( $\tau$  in [350,400]) showed an increase of  $E$  with the memory duration when prey spatial distribution was 'random'. Strictly speaking, the prey spatial pattern was not completely random since prey items only had a uniform probability of occurring at each site within the ring away from the nest, thus leaving a large gap between the ring containing prey items and generating a 'virtual aggregation' (sensu Wiegand & Moloney 2004) within the ring (Fig. 2a). Therefore, the small increase in the intake rate mentioned above is likely to be caused by the relative advantage that a predator that had memorized any captured prey location would have compared to an uninformed predator undergoing a CRW upon departing the nest. While such a memorized location would not always provide genuine information about local prey density, it would allow the forager to go in a straight line to an area (the ring in Fig. 2) more likely to contain prey, hence enhancing the intake rate. This relative advantage is, however, small (Fig. 3a) so that  $E$  might be considered almost constant with respect to  $\tau$  in the Poisson case. In contrast, when prey spatial distribution was Aggregated or Patchy,  $E$  increased and eventually saturated with respect to both the perception radius  $\delta$  and the memory duration  $\tau$ . Note that small values of  $\tau$  can increase the intake rate; this is because even  $\tau = 1$  provides at least one step in the direction of a prey cluster (provided the distribution is clumped and the cluster not depleted) which improves the overall orientation of the forager. The saturation of  $E$  with respect to memory duration occurred around  $\tau = 400$  which corresponds to the memory duration needed to go from the nest to the ring of the spatial domain containing prey items. Comparing the intake rates for the Patchy (Fig. 3c) and Aggregated (Fig. 3b) distributions showed that the increase of  $E$  with  $\tau$  was steeper when the prey pattern was more clumped. The shape of the relationship between  $E$  and the perception radius  $\delta$  was in contrast unchanged for any

spatial prey distribution, although small values of  $\tau$  tended to delay the saturation of  $E$  with respect to  $\delta$  in Aggregated and Patchy prey distributions (Fig. 3e, f).

Overall, we found that intake rate was a saturating function of both cognitive parameters for clumped prey distributions (Fig. 3). It is worth recalling that the latter result was obtained assuming a cost-free nature (for capture probability) of increasing any of the two cognitive parameters. However, when capture probability was modelled as a decreasing function of either cognitive parameter, the intake rate generally declined (as we expected) for large values of detection radius and memory length (Fig. 4). We found that the intake rate was maximized and roughly constant for a wide set of combinations of  $\tau$  or  $\delta$ :  $350 < \tau < 450$  and  $7 < \delta < 20$  (Fig. 4). However, the maximum of  $E$  with respect to  $\tau$  was clearer when prey spatial distribution was Aggregated (Fig. 4b) or Patchy (Fig. 4c) than in the Poisson case (Fig. 4a) because the relative increase of  $E$  with respect to  $\tau$  was bigger. Indeed, the differences  $E_{\max} - E(\tau = 0)$  are approximately 7, 15 and 50 prey items per simulation run for the Poisson, Aggregated and Patchy prey spatial distributions (Fig. 4). For the Poisson distribution (Fig. 4a), the rather small increase of the intake rate  $E$  with  $\tau$  (when  $350 < \tau < 400$ ) for different values of  $\delta$  is due to the choice of distributing prey items in a ring around the nest (see above and Fig. 2). Had prey not been distributed in a ring,  $E$  would have decreased monotonically with  $\tau$ , and shown a maximum at negligible memory duration. We recall that prey were distributed in a ring surrounding the nest (Fig. 2) to disentangle the variation in the intake rate caused by changes in the cognitive parameters from the stochastic variation in the closeness of prey items to the nest (see above).

#### Intake Rate as a Continuous Function of Prey Spatial Distribution

We assessed the sensitivity of different cognitive strategies to variation in prey aggregation  $s$  and global abundance  $N$ . Depending



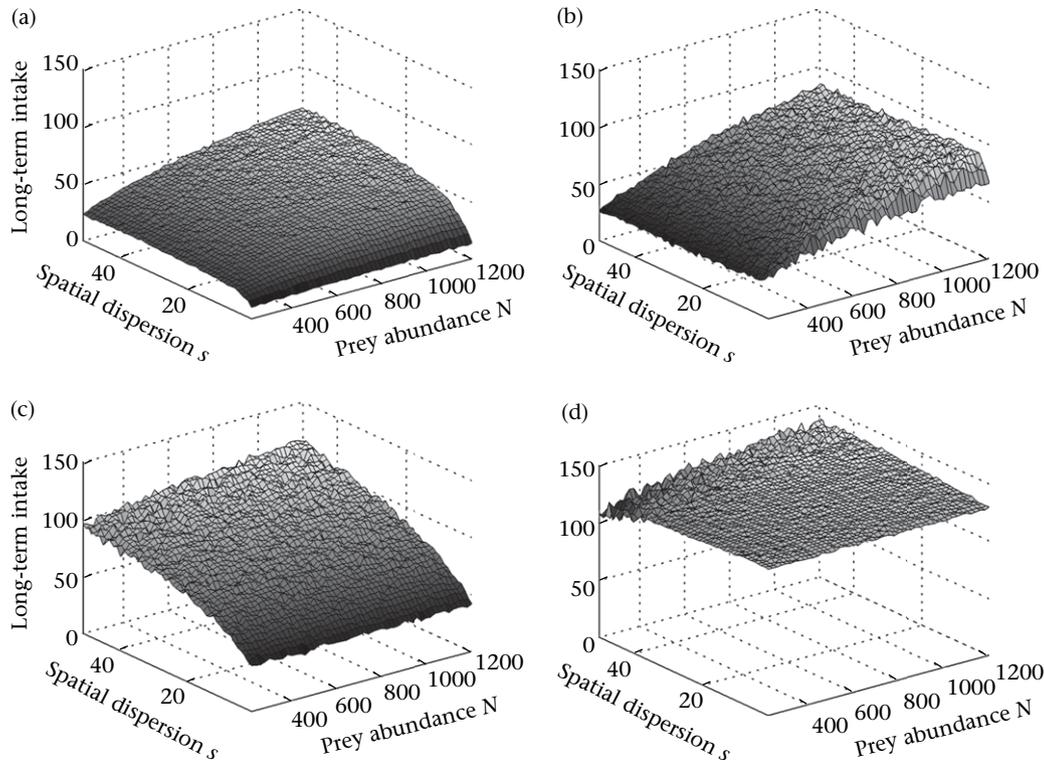
**Figure 4.** Long-term intake as a function of memory duration and perception radius, for three kind of spatial distributions: (a) Poisson, (b) Aggregated, (c) Patchy. Same contour plot as presented in Fig. 3 except for the existence of a decreasing capture probability (see The Model) reflecting the existence of costs to increased cognitive abilities.

on the type of information available to a predator as a result of its cognitive strategy, its average intake rate was limited either by the global density and/or the level of prey aggregation. Predators were Unlimited (good perception and memory), Memorizers (small perception and large memory), Perceivers (small memory and large perception) and Limited (small memory and reduced perception). Intake rate was an increasing but decelerating function of total prey abundance  $N$  (Fig. 5) in the Limited (Fig. 5a) and Memorizer (Fig. 5b) cases: we actually recovered the classical functional response shape (Holling 1959). The novelty is the addition of another axis to the classical functional response, depicting the effect of spatial aggregation on intake rate. The aggregation axis shows that when the predator had a very short memory, the level of dispersion  $s$  of prey spatial distribution (the opposite of aggregation) limited the intake rate (Fig. 5a, c). Increasing prey spatial aggregation reduced the intake rate of predators with wide

perception but short-term memory (Perceivers). In contrast, foragers with good memory but poor perception (Memorizers) were able to forage in any kind of spatial distribution and their intake rate was limited only by prey global density (Fig. 5b). Unlimited predators with good memory and perception had a constant intake rate for all values of prey abundance and spatial aggregation (Fig. 5d).

**DISCUSSION**

In the absence of cognitive costs, one of our general results is that, regardless of prey spatial distribution, intake rate increases and eventually decelerates with increasing detection radius. Only when the prey spatial distribution is aggregated would the intake rate increase significantly (and again eventually saturate) with the duration of spatial memory (see Benhamou 1994 for a similar



**Figure 5.** Long-term intake as a function of prey abundance ( $N$ ) and prey dispersion ( $s$ ) for four kinds of cognitive strategies: (a) Limited, (b) Memorizer, (c) Perceiver, (d) Unlimited. No cognitive costs are assumed here. See text for details of strategies.

result). Saturation means that after some threshold level, all other things being equal, longer memory or wider perception offers limited advantage. However, the saturation of the intake rate is obtained assuming that improving cognitive abilities can only provide benefits in terms of increasing the long-term intake rate. Under these circumstances, since the intake rate decelerates with large values of either cognitive parameter but might still be increasing slightly (except for a randomly distributed prey pattern: the intake rate is almost constant with respect to memory duration), natural selection would be expected to lead to ever-increasing cognitive abilities. This, however, is far from realistic since all species have a maximum possible perceptual radius and a maximum possible duration of spatial memory under the limits fixed by both environmental and phylogenetic constraints. Large values of cognitive abilities are thus unlikely to be unconstrained. In addition, an optimum set of values for each type of prey spatial distribution could result from a trade-off between the costs and benefits of cognitive abilities. It is worth mentioning, however, that the quantification and even the existence of such costs is still a matter of debate (Dukas 1999).

These costs could be physiological (e.g. additional tissues requiring energy) or ecological (e.g. decreased rate of prey discovery or prey capture, or even wrong information, see below; see Dukas 1999 for a discussion on the subject). We chose to model cognitive costs by directly incorporating the effect of spatial memory duration and perceptual range on the capture probability. A reason why capture probability might decline with cognitive parameters is information overload (Krakauer 1995): the rate of information processing by the brain is finite (Dukas 2002) and thus having to process more and more information may hinder the capacity of foragers to focus on the real-time environment and to be reactive to the sudden appearance of prey in their perceptual ranges. We recognize, however, that, depending on the predator species at hand, other costs might be more relevant (e.g. travel costs) and thus we advocate seeing the decreasing capture probability more as phenomenological rather than mechanistic modeling of cognitive costs.

We therefore predict that only species exploiting aggregated, nonephemeral food resources should have evolved a long spatial memory, because when resources are randomly distributed in space, the optimum duration of memory should be almost zero, as there would be no benefits (but costs) of having a longer spatial memory for foraging. In our model, the optimum memory duration for a randomly distributed prey is not zero, because spatial memory is useful to find more rapidly the region away from the predator's nest where prey items are located (prey ring in Fig. 2). This increase in intake rate from longer memory duration is, however, rather small when prey have a Poisson distribution (Fig. 3a) and thus spatial memory of capture events is expected to be rather ephemeral whenever prey spatial distribution is completely random. When the prey distribution is aggregated, both extending spatial memory duration and extending perceptual range are possible strategies, but extending perceptual range might be more difficult depending on the habitat structure. Many physical constraints (e.g. land cover and physical obstacles) might, in fact, maintain the detection radius to a short-distance range. When there are strong limitations to perception, aggregated prey distribution should enhance spatial memory.

Predicting the relationship between intake rate and cognitive abilities becomes substantially more complex when resources have spatiotemporal dynamics (but see Mueller & Fagan 2008). Having seasonal resource dynamics is qualitatively different from the case of an unpredictable, stochastic variation in resource abundance, and the two cases need to be considered separately.

Seasonal deterministic variation, however, is more likely to be observed at large temporal scales, and, since our model is tuned to small temporal scales, considering unpredictable resource dynamics seems a more relevant concern. Assuming that predator movement takes place in a span ranging from seconds to minutes, the foraging process considered here would represent weeks to months. At such short timescales, although demographic renewal may be considered negligible as a first approximation, prey spatial distribution may change through either diffusive or directed movement. In our model we assumed that prey items were static, which corresponds to natural situations where the amplitude of prey movements are negligible compared to that of the predators (e.g. raptor–vole system). However, some prey species have movement abilities not so different from those of their predator (e.g. wolf–elk system, Fortin et al. 2005). In the case when prey are very mobile, the advantages of memory should fade (compared to our finding of increased intake rate in static aggregated prey distributions), because of either the blurring of prey spatial patterns or the appearance of unpredictability in the location of prey clumps. Such unpredictability would be an example of cognitive costs, because memory would convey irrelevant information (Hirvonen et al. 1999) about the spatial prey pattern. The idea that prey might move in reaction to predator searching strategies is not new: Tinbergen et al. (1967) first suggested that prey items are sometimes spaced out as a protection against predators using area-restricted searching (i.e. widening their effective detection radius beyond their perceptual range by locally enhancing their path sinuosity after prey detection, using their short-term memory). To counter the effects of predators with a long spatial memory, prey individuals would similarly be expected to move away from prey clusters (at large spatial scales) so as to reduce their degree of spatial aggregation and consequently their predictability for the predator (Mitchell & Lima 2002). To study these situations where both predator and prey can adjust their strategies to each other, a game-theoretical framework will probably be needed (Lima 2002).

A second main result of our model, although perhaps less intuitive (see Results: intake rate as a continuous function of prey spatial distribution), concerns the relationship between spatial distribution and abundance of prey, and the intake rate. Most predator–prey models of population dynamics and foraging behaviour consider the functional response to relate predator intake rate only as a function of prey densities (Solomon 1949; Holling 1959; reviewed in Jeschke et al. 2002). The functional response embodies a number of behavioural processes related to the consumption of prey by a predator (search, attack, capture, digestion, interference with other predators, etc.). In experimental and field studies, the functional response is typically measured as the relationship between predator intake rate and prey density at a given spatial scale. By considering only the effects of prey density, most empirical measurements of the functional response neglect its spatial distribution by implicitly assuming free mixing (i.e. prey individuals have the same probability of being captured by the predator over space) at the spatial scale considered. The free-mixing assumption holds true when prey items are randomly distributed in space or when the spatial area considered is relatively small, so that all prey items can be easily perceived and reached by the predator. However, wild prey populations have nonrandom distributions (Nachman 2006), such as the Aggregated and Patchy distributions considered in this paper, which should call into question the interpretation of functional responses solely based on average prey density at a given (and often arbitrary) spatial scale. Our results have shown that the intake rate is affected

by the spatial clumping of the prey when a predator forages from a central place in a large spatial domain (compared to its movement and perceptual ranges). Predators that have a large perceptual range and long memory are able to capture the same number of prey items for all prey abundances and spatial distributions. They are only limited by the time it takes to commute between hunting sites and the nest and their functional response is a constant, independent of both prey abundance and spatial distribution (albeit in a different context, a constant functional response has already been observed in predatory mites, e.g. Sabelis et al. 2005). By contrast, the intake rate of 'Memorizers' depends only on prey global density (the level of spatial aggregation does not change the intake rate) and it can be depicted as a classical Holling type II functional response. Good perceivers with a poor memory, however, were more limited by the spatial aggregation of prey than by their global density since the total number of prey items had almost no effect on the intake rate. The extent of prey spatial aggregation as well as prey density should therefore be taken into account in population dynamics, when this is possible, in accordance with the predator's cognition. However, foragers using the 'Perceiver' strategy may not be so common in nature because perceptual range is often constrained by habitat structure and by physical limits to perception, while acquiring spatial memory would seem relatively easy, at least for vertebrates. Therefore, while the Holling type II functional response seems to represent well the intake rate of the potentially numerous 'Memorizer' CPF, the functional response of predators relying on large-scale perception should also include prey spatial distribution since the level of spatial aggregation is a key factor limiting their intake rate. The effect of spatial aggregation for 'Perceivers' might be tested in the laboratory or in semiexperimental environments by perturbing the spatial memory of the predator, for example by keeping the level of spatial aggregation constant but moving the clusters' centres each time the predator eats a prey, so as to decrease the effect of spatial memory on intake rate (e.g. as done in Thiele & Winter 2005). Frugivores would seem good candidates for this type of empirical testing (monkeys: Janson 1998; bats: Thiele & Winter 2005) since they tend to use discrete resources that are relatively easy to manipulate.

Although we have considered four contrasting cognitive strategies, individual foragers using these strategies behaved identically throughout the foraging bout. When the spatiotemporal prey dynamics leads to unpredictable prey locations from the predator's viewpoint, more complex adaptive behaviour might appear. For instance, as the spatial distribution of their food resources becomes more variable, sheep, *Ovis aries*, switch from using spatial memory to sampling behaviour (Hewitson et al. 2005). Therefore, an adaptive rule, such as 'only use spatial memory when resources are persistent over time' may evolve. Moreover, several vertebrate foragers are social and hence individuals can potentially interfere with each other, either directly (e.g. fight) or indirectly (e.g. resource depletion), owing to aggregative responses when resources are clumped. A long spatial memory may thus be beneficial for an isolated predator in aggregated prey distributions but it may promote interference, so that a constrained foraging rule such as 'go to the closest favourable place unoccupied by conspecifics' might be used. It is also likely that several phenotypes with different foraging strategies may coexist in a population, the most common example being 'producer–scrounger' games (Giraldeau & Caraco 2000). When the prey distribution is stable over time, 'producers' may use spatial memory to locate prey aggregations and thus produce public information with their spatial utilization distribution. In turn, 'scroungers' may use that public information to locate prey patches without having to memorize their locations. These issues of adaptive cognitive strategies, interference and

behavioural variability within the population are promising open avenues for further research on the spatial aspects of foraging behaviour.

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## APPENDIX: TRANSITION RULES FOR PREDATOR MOVEMENT

In this Appendix, we present the rules used to model the switches between the four behavioural states  $\{N, A, M, R\}$ .

$A \rightarrow N$  or  $A \rightarrow R$

The  $N$  state ('Return to nest') is triggered at time  $t + 1$  by the capture of a prey item at time  $t$  when the predator is close enough to the focal prey ( $d(X_t, X_v) < u$  where  $u$  is the arbitrary spatial unit and  $X_v$  the position of the focal prey pursued). The capture happens with probability  $P_c$  given that the prey is encountered. We set  $P_c$  to 0.5, but the main results remain unchanged for other constant values (we also tried 0.1 and 0.9). When  $d(X_t, X_v) < u$  and prey capture is unsuccessful, the predator begins a random search movement  $R$  (correlated random walk). An unsuccessful capture thus happens with probability  $1 - P_c$ .

$M \rightarrow A$  or  $M \rightarrow R$

The animal switches from 'memory'  $M$  to 'attack'  $A$  state when at least one prey item comes within its perception radius  $\delta$  and direct itself to the closest item. When a formerly memorized place towards which the predator directs itself goes out of its memory, the predator resumes random search  $R$ . The same thing happens after the predator has crossed the whole circular domain and eventually reaches the boundary (without finding any prey to attack during this time).

$N \rightarrow M$  or  $N \rightarrow R$

When the predator has come back to the nest ( $d(X_t, X_N) < u$  where  $X_N$  is the nest location), it might switch to either  $M$  or  $R$  mode depending on whether there are still profitable places stored in its memory ( $M$  mode) or it has no cue to direct itself ( $R$  mode).

$R \rightarrow A$

The animal switches from 'random search' to 'attack' mode when at least one prey comes within its perception radius (more formally if there exists a prey with location  $X'_i$  verifying  $d(X_t, X'_i) < \delta$ ).