# How Search Images Limit Competition: The Role of Attention in Collective Foraging

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## Abstract

Many species forage collectively and this will shape how they search for prey. However, theories of visual attention and search image formation have not considered social foraging, and studies of collective foraging rarely consider cognitive constraints. Here, we connected these ideas and present an agent-based model of collective foraging on cryptic prey in agents that either can or cannot form search images. Agents focused on one prey type reduce its local density, biasing other agents to form search images for other prey types. This effect, attentional character displacement, may reduce competition, as foragers occupy separate regions of 'attention-space.' We found that the ability to modulate attention increases distance in attention-space and reduces competition, improving success rates. Agents that cannot modulate their attention benefit from foraging with those that can. We also found that some top-down control of search is critical to taking advantage of this effect. This cognitive-ecological approach to modeling collective foraging suggests that competition is a critical driver of the evolution of search images.

**Keywords**: search image, visual search, collective foraging, attentional allocation, sequential attentional priming

## Introduction

Humans and other animals live in a world awash with information, far too much to take in. Attention is a set of cognitive mechanisms for gating and prioritizing information for processing in working memory (Bernays & Wcislo, 1994). As attention is a limited resource (Dukas, 2004; Kahneman, 1973), animals performing attention-dependent tasks often miss other important information (as in, e.g., divided attention tasks; Dukas, 2001). For example, species that forage on cryptic prey often employ search images (Tinbergen, 1960), which bias a forager's attention towards the perceptual features of a sought prey type, improving their detection of that type and concurrently reducing their ability to detect other cryptic types (Dukas & Kamil, 2001; Reid & Shettleworth, 1992). Foragers using a search image display a biased diet, taking more of one prey type than its relative density in the environment (Tinbergen, 1960). Search images are most likely generated via a process of sequential attentional priming (Goto et al., 2014) and are a critical part of visual search in many species. A wide range of species have been shown to only be capable of utilizing a single search image at a time (Dukas & Kamil, 2001; Langley, 1996; Atema et al., 1980; Jackson & Li, 2004), and switching images to search for a new target type incurs a cognitive cost (Grubert et al., 2024; Reid & Shettleworth, 1992).

However, humans and many other species live and forage in groups. The effects of collective foraging on the characteristics of visual search have rarely been explored (Fernández-Juricic et al., 2004). When a group of animals is foraging, individuals may compete for prey items or preferred locations (e.g., Schneider, 1984). Search images and related attentional phenomena will tend to focus an individual's intake on a single prey type, potentially causing it to temporarily decrease the local density of that type. Nearby individuals will then experience a different abundance of prey types, biased away from the type preferentially taken by other members of their group. This increases the likelihood that these individuals will focus their attention on the prey type less taken. By increasing the relative proportions of their preferred prey that individuals take (Bond, 1983; Tinbergen, 1960), limited attention may therefore constrain competition between group members, effectively shunting each individual into a separate attentional niche, a process we refer to as "attentional character displacement." For example, imagine two birds foraging in a patch for two kinds of equally prevalent cryptic insects (similar to the situation studied by Tinbergen, 1960). If Bird1 happens to first encounter Insect1, it will form a search image for that prey type (as in, e.g., Jackson & Li, 2004). Bird1 will then primarily locate and consume prey of type Insect1, which will decrease its local population density, making Insect2 the more common prey item. Bird2 is then more likely to encounter Insect2, and focus its foraging on them, minimizing the competition between the birds. We predict that this effect should be beneficial for all members of the group, leading to improved collective foraging efficiency. This may also be one reason why attention appears to have evolved to disallow efficient dividing of attentional foci. Here, we simulate this process to explore how attention affects collective foraging. Though we focus on visual examples, selective attention likely operates similarly in other modalities (such as odour: Carlson et al., 2018; Atema et al., 1980) and across modalities (Mozolic et al., 2008). Our model is not specific to any one modality.

Search is a necessary component of foraging, even for targets that are in plain view. In a field of several identifiable prey types, an individual can detect a specific target either preattentively – relying on the popout effect (Westerberg & Schall, 2021) – or by allocating some portion of their attention to the target item. Sufficiently cryptic targets, which do not differ from the background enough to evoke the preattentive popout effect, are unlikely to be detected without using the available information to guide how attention is deployed (Wolfe, 2010). For example, bobwhite quail (*Colinus virginianus*) will adjust their rate of searching based on the crypticity of available prey (Gendron, 1986). It has even been suggested that crypticity evolves partly as a response to the sensory capabilities of predators and the dynamics of their attention use (Bond & Kamil, 2002).

Properties of visual stimuli, or specific abstractions from visual input, can be used to control the deployment of attention, using what is termed a guiding representation or feature detector (Wolfe & Horowitz, 2004). Common feature detectors include attributes such as color, size, and orientation, which can be processed in parallel across a field of potential targets. This preattentive processing guides attention allocation in both bottom-up and top-down ways, in tandem. Some aspects of highly salient stimuli may draw an individual's attention regardless of similarity to the target (bottom-up); at the same time, the individual will use learned features of their target to guide attention to specific items in the search set (top-down). For example, bright aposematic coloration draws potential predators' attention innately, but predators will learn to avoid these very salient stimuli and direct their attention elsewhere (e.g., Skow & Jakob, 2006). The salient properties of the target and the individual's past experience of successfully finding the target will thus allow for sequential attentional priming to influence visual search; the individual's search history can begin to affect what captures attention (Wolfe, 2010). For instance, if an individual has located a blue target, their attention in a subsequent search is more likely to be drawn towards blue targets – even if they are not explicitly searching for blue targets. In other words, visual search for cryptic targets requires focused attention, either cued by stimulus features or primed by the most recently detected target (Goto et al., 2014; Wolfe, 2010). Sequential attentional priming is the basis for how foragers form search images (Lamy & Kristjansson, 2013).

Our model is based on a simplified version of Guided Visual Search (Wolfe, 1994, 2021; Wolfe et al., 1989), one of the leading current theories of visual search (in humans). We also borrow heavily from earlier models of search image formation in animals (Bond, 1983; Dukas & Ellner, 1993; Gendron & Staddon, 1983). The resulting structure (Figure 1) incorporates what is known about both the psychology of visual search (in humans and non-humans) and the ecology of foraging on cryptic prey. As we are interested in the cognitive mechanisms that underlie searching and their evolution (specifically, their adaptive value), we additionally simulate some foragers that are unable to form search images, whose attention is always evenly divided across all stimuli. We mix the two kinds of foragers in different proportions, to explore the advantages conferred by directed attention and search images.

We hypothesized that the attentional character displacement effect would serve to reduce competition and improve success rates for all foragers, whether they are able to modulate their attention or not. This effect should be modulated by other effects related to group size, the number of prey types available, and the crypticity of the prey.

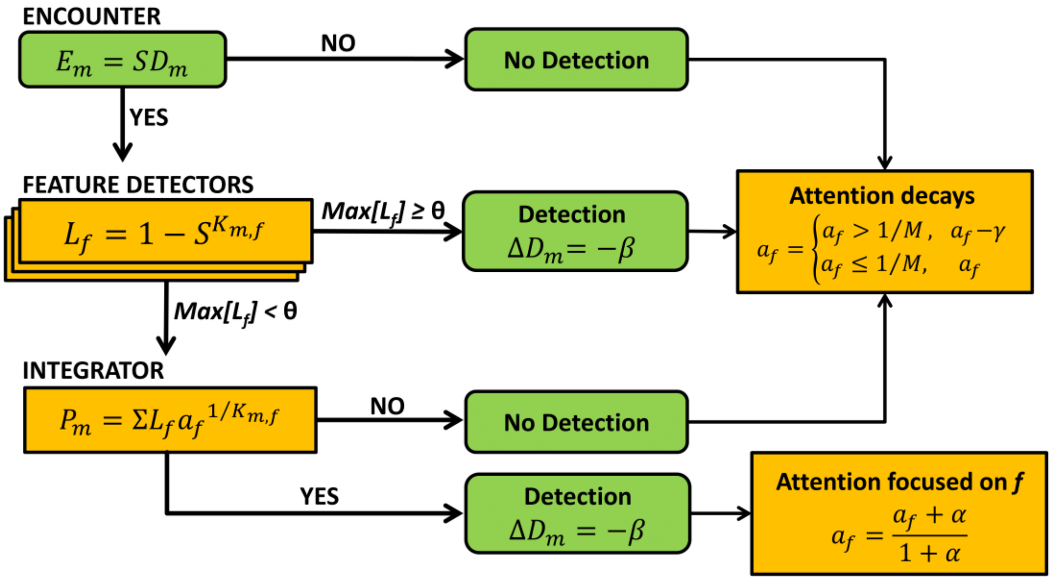

**Figure 1**. Flowchart for running the model. Green cells represent the outside world; yellow cells represent the perceptual system of the forager. The figure shows the process for a forager that can modulate their attention, a Q1 phenotype.

## Methods

Our model represents how foragers' attentional resources are allocated as they engage with different prey types and how shifts in their attention affect relative prey densities. The model simulates a group of $N$ agents foraging in a patch containing $M$ different prey types. The model is not explicitly spatial; instead, we simulate the rate of prey encounters. We assume foragers are searching for prey in a patch that does not deplete (only the *relative* densities of prey types change) and which they never leave. Time is simulated in discrete steps. The simulation steps in the model are diagrammed in Figure 1.

At any time point $t$, each prey type $m$ is present in the environment at a certain relative density $D_m(t)$ ($\Sigma D_m(t) = 1$). Initially, all prey types are present in equal proportions (all $D_m(0) = 1/M$). At each time step, the relative density of each consumed prey type decreases by an amount $\beta$, so that the new prey densities are given by

$$D_m(t+1) = \frac{D_m(t)(1-\beta n_m(t))}{1-\sum_{j=1}^{M} \beta n_j(t) D_j(t)}, \qquad \text{(Equation 1)}$$

where $n_m$ is the number of foragers that consumed prey type $m$ at time $t$.

Prey items are detectable because of their degree of difference from the background (or conspicuousness), $K$, on any of several feature dimensions (such as color, shape, odor…). Prey type $m$ differs from the background on feature dimension $f$ by $K_{m,f}$, so that each prey type is characterized by a vector of conspicuousness, $K_m$. For simplicity, we set each prey item to only differ from the background on one feature dimension, unique to its prey type. For example, if there were two prey types, their conspicuousness vectors might be: $K_1 = \{0.5, 0\}$, $K_2 = \{0, 0.8\}$. All prey items of a certain type are identical.

We simulate foragers that have perceptual systems modelled after Guided Search (Gendron & Staddon, 1983; Wolfe et al., 2011). Each forager has a set of feature detectors (FD), which can detect prey based on their difference from the background on a specific feature dimension (e.g., a forager might have feature detectors for color, shape and movement). Because each prey type differs from the background on only one feature dimension, each feature detector will only be activated by one prey type, and we give each agent as many FD as there are prey types (we employ this simplification for tractability; it has no effect on the model's generality). Foragers distribute their attention across their FD based on their history of prey encounters. FD can also be activated pre-attentively by prey items that are sufficiently different from the background.

Foragers search for prey at a specific search rate, S. Previous work has shown that search rate has a marked effect on foraging success, as foragers that search more quickly will cover more ground but risk overlooking inconspicuous prey (Dukas & Ellner, 1993; Gendron, 1986; Gendron & Staddon, 1984). The probability that a forager encounters a prey item of type $m$ at timestep $t$ is,

$$E_m(t) = SD_m(t) \qquad \text{(Equation 2)}$$

(see Gendron & Staddon, 1983). If prey is encountered, a forager must then perceive the item. The feature detector (FD) for a dimension $f$ is activated by prey type $m$ to a degree

$$L_f = 1 - S^{K_{m,f}} \qquad \text{(Equation 3)}$$

(Clark, 2003). The slower a forager is searching (lower S) and the more conspicuous the encountered prey item is (higher $K_{m,f}$), the more strongly the FD is activated.

If the FD is sufficiently strongly activated, the forager detects the prey item preattentively, using just that dimension (e.g., a brightly colored prey item will pop out even if it is cryptic on other dimensions). We denote the required threshold activation $\theta$ (all FDs have the same threshold; Blough, 1992). This defines crypsis in the current model: a cryptic prey type is one for which $\max[L_f] < \theta$; all other types are conspicuous. When an FD is activated sufficiently, the prey item is immediately detected. We assume, for simplicity, that all prey are equally nutritious, delicious, and easy to capture and consume once detected. We also assume that foragers are familiar with all prey types, so learning and initial acceptance of prey play no role in the model.

If no FD is sufficiently activated for the encountered prey to be non-selectively detected, the outputs of all FDs are sent to the attention-driven integrator (Treisman & Gelade, 1980). The input to the integrator from each FD is weighted by the proportion of attention devoted to that dimension (simulating top-down control of search; this makes the current model a Dimension-Weighting Account of attentional priming, *sensu* Lamy & Kristjansson, 2013). Attention, in the current model, is a set of tunable weightings over the FDs, $A(t) = [a_1(t), a_2(t), \ldots, a_F(t)]$. We set

$\Sigma A(t) = 1$, such that the entire attention of the agent is engaged at all times (we ignore any attention that must be reserved for vigilance, which is itself a function of predation risk and group size). All agents have the same total attentional resources. The integrator is activated such that the probability of detection of an encountered prey item of type *m* is given by

$$P_m(t) = \sum_f L_f a_f(t)^{\frac{1}{K_{m,f}}} \qquad \text{(Equation 4)}$$

(Dukas & Ellner, 1993). One could argue that the integrator should be able to detect any prey item as long as it differs from its background to any degree. However, the integrator is slow. Our model is a fixed speed of search model, which means the integrator has only until the forager moves on (shifts its gaze, for instance) from the encountered prey to detect it. When prey are less conspicuous, the forager might not search slowly enough to detect a prey item attentively.

Finally, attention is (re)allocated as a function of detections and non-detections of prey. Initially, inputs from all FDs are weighted equally, $a_f(0) = 1/M$. When a forager detects a prey item of type *m* using its integrator, its attention to all prey types changes:

$$a_f(t+1) = \begin{cases} m = f, & a_f(t) + \alpha/1 + \alpha \\ m \neq f, & a_f(t)/1 + \alpha \end{cases} \qquad \text{(Equation 5)}$$

In other words, attention to the detected prey type increases by a factor $\alpha$, and attention to all other prey types decreases, such that the forager's total attention is still engaged ($\sum a_m(t) = 1$). For a timestep in which a forager does not detect any prey, or if the forager detects prey preattentively, attention to all prey types decays towards the mean by a factor $\gamma$:

$$a_f(t+1) = \frac{C_f}{\sum_{j=1}^{M} C_j}, \quad C_f = \begin{cases} a_f(t) > 1/M, & a_f(t) - \gamma \\ a_f(t) \leq 1/M, & a_f(t) \end{cases}. \qquad \text{(Equation 6)}$$

In other words, when prey are detected, attention asymptotically approaches 1 for the detected types (if they are cryptic) and 0 for all other types (Bond, 1983; Goto et al., 2014). Search images gradually decay towards the mean if prey are not consistently detected or are detected preattentively (without engaging the integrator).

To examine the value of search images in collective foraging, we simulate foragers that can modulate their attention as defined above (*Q1* phenotype) and foragers that cannot (*Q0*), whose attention distribution over prey types is fixed ($a_f(t) = 1/M$ at all times for all *f*). Across simulations, we vary the proportion of foragers in a group who can modulate their attention, *PopQ*.

To limit the variable space to be explored, we fixed some variables. Each forager's foraging efficiency and search rate were set to $\beta = 0.006$ and S = 0.5, respectively. Each simulation was run for 500 time steps. $K_1$, the conspicuousness of the first prey type, was set to {0.5, 0} (i.e., this prey type differs from the environment only on the first feature dimension, by a fixed amount). We first simulate situations where there are only two prey types ($M = 2$), for which we also set the rate of attention focusing, $\alpha$, to 0.7 and the rate of attention decay, $\gamma$, to

0.025. We examine the effects of varying N (the size of the group), $K_2$ (the conspicuousness of the second prey type), and *PopQ* (the proportion of the group that can modulate their attention). We then explore the effects of increasing the number of prey types (M = 4 or 6), for N = 5 only. In these simulations, we also systematically vary $\alpha$, $\gamma$, $K_2$ and *PopQ*.

In all simulations, our primary output measures of interest are success rate and the amount of competition-reduction. Success rate was defined as the proportion of timesteps in which a forager captured (any) prey. Competition-reduction refers to the mean distance in attention-space between foragers. Two foragers attending to two different prey types are far apart in attention-space, and thus compete with each other less, than foragers that are attending to the same prey type (meaning they are close in attention-space). To quantify the competition-reduction foraging groups attained we devised a measure of the distances between foragers in attention space, Z. The mean attention-distance of a forager *i* from all other foragers is given by,

$$Z_i = \frac{1}{T(N-1)} \sum_{t=1}^{T} \sum_{j \neq i}^{N} \sqrt{\sum_{f=1}^{M} (a_{i,f}(t) - a_{j,f}(t))^2} \qquad \text{(Equation 7)}$$

where *T* is the duration of the simulation. Z expresses the M-dimensional Euclidean distance between agents in attention-space, averaged over all agents and over the duration of the simulation. This measure has several advantages: it is linear, has a well-defined range (see Supplementary Materials), and is defined for any value of *M* and $N > 1$. $Z_i$ is a measure of the degree of competition between a forager and its group-mates. If $Z_i = 0$, the forager experiences a lot of competition, as their attentional focus is the same as that of every other group member; if $Z_i$ approaches its maximal value, the forager experiences as little competition as possible.

We ran 50 simulations for each set of parameter values. Group size was varied (N = 2, 5, or 10, at *M* = 2 only), as was the crypticity of the second prey type, $K_2 = \{0, x\}$, where $x = (0.5, 0.6, 0.7, 0.8, 0.9, 1)$. We also varied *PopQ* from 0 to 1 (0, 0.5, and 1 for N = 2; 0, 0.2, 0.4, 0.6, 0.8, and 1 for N = 5; etc.) and *M* = 2, 4, or 6 (at N = 5 only).

The model was implemented in Python, and output from the Python script was analyzed in *Mathematica* (v.12.0, *Wolfram Technologies*). Data were analyzed using one-, two- and three-way ANOVAs on N, $K_2$, and *PopQ*. Bonferroni corrections were applied to all post-hoc tests. A significance level of 0.01 was used for all tests. Since *PopQ* is (theoretically) a continuous variable, we also examined its effects using linear regressions, conducted separately for each group size (we report regression coefficients, *b*, for all regression analyses).

## Transparency and Openness Statement

*Data availability*: Code for running the model and analyzing the results, along with raw model outputs, are provided in our OSF repository (Ighalo & Miller, 2025).

*Analysis code availability*: all the code used to analyze results is available in the OSF repository (Ighalo & Miller, 2025).

*Materials availability*: other than the code used to run the model and analyse the results, there are no associated materials for this study.

*Reporting Standards*: We report all measures in the study; no data were excluded and numbers of simulation runs (50 per condition) were selected based on the anticipated power of statistical analyses.

## Results

### *Two prey types*

We first examined a simple condition, with two prey types ($M = 2$); we varied the number of foragers (N), the proportion of those that can modulate their attention (*PopQ*), and the relative conspicuousness of the two prey types (by changing $K_2$).

Larger groups had lower success rates (SR; Figure 2A). As there were no direct interactions between foragers in the model, this effect can only be modulated via relative prey densities, suggesting that the decrease in SR with group size was due to increasing competition over prey. This interpretation is further supported by the finding that increasing *PopQ*, the proportion of foragers who are able to modulate their attention, increased success rates at all group sizes (Figure 2A; 2-way ANOVA: Effect of *N*, F(2,980) = 2283, $p < 0.001$; effect of *PopQ*, F(10,980) = 424.1, $p < 0.001$; *N*PopQ* interaction, F(7,980) = 91.93, $p < 0.001$. Post-hoc tests showed all *N*s differed from each other, *PopQ* = 0 differed from 0.1, 0.2, and 0.4, and *PopQ* = 0.1 differed from 0.3). We assume that this effect results from a decrease in direct competition as foragers avoid each other in attention-space; we explicitly test this hypothesis below.

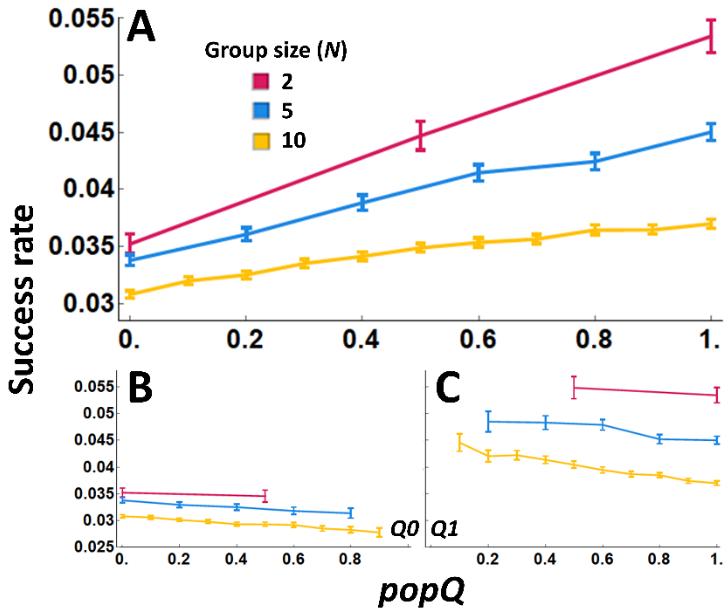

**Figure 2**. The effects of *PopQ* (the proportion of the group that can modulate their attention; x-axes) on success rate (y-axes) across group sizes (colors) for all foragers (**A**), Q0 foragers only (**B**) or Q1 foragers only (**C**). Data are averaged over all values of $K_2$. Error bars show ± SEM (across simulation runs).

The effect of *PopQ* on SR depended on group size, such that greater proportions of the group being able to modulate their attention had a smaller effect in larger groups (linear regressions: *N*=2, F(1,148) = 804, $p < 0.00$, $b = 0.02$; *N*=5, F(1,298) = 1345, $p < 0.001$, $b = 0.01$; *N*=10, F(1,548) = 1845, $p < 0.001$, $b = 0.006$). This is presumably because, with only two prey types, it is harder for foragers in larger groups to move away from each other in attention-space (see below).

Overall, Q1 foragers (who can modulate their attention) had higher success rates than Q0 foragers at all levels of prey conspicuousness (Figure S1), all *PopQ* values (Figure 2B,C), and all group sizes (Figure 2B,C; 3-way ANOVA: effect of $N$, F(2,1686) = 1012, $p < 0.001$; effect of *PopQ*, F(10,1686) = 132.7, $p < 0.001$; effect of phenotype, F(1,1686) = 6148, $p < 0.001$). However, in groups larger than 2, both phenotypes did better when Q1 foragers were rare (Figure 2B,C; Table S1). The overall SR nonetheless increased with *PopQ* due to the greater SR of the increasingly common Q1 phenotype. Increasing the conspicuousness of one prey type, unsurprisingly, increased SR (Figure S1) as well as increasing the proportion of prey taken that were of that type (Figure S2; Table S2).

Increasing *PopQ* decreased competition over prey by increasing attentional displacement for Q0 foragers (Figure 3A) but increased competition for Q1 foragers (Figure 3B). In other words, as the proportion of the group that could modulate attention grew, those Q1 foragers moved to the edges of attention-space (focusing on one or the other prey type, creating search images), increasing their distance from Q0 foragers. However, increasing the number of Q1 foragers increased the concentration of attention at the edges of attention-space, increasing the competition for Q1 foragers. As noted above, this led to a decrease in success rate for the Q1 phenotype as *PopQ* increased, especially in larger groups (Figure 2C). These effects were stronger in smaller groups (Figure 3; Table S3), as larger groups occupy attention-space more densely, consequently suffering higher levels of competition at all values of *PopQ* (Figures 2, 3). These effects were also stronger when one prey type was more conspicuous (Figure S3), as more of the agents tended to focus on that type.

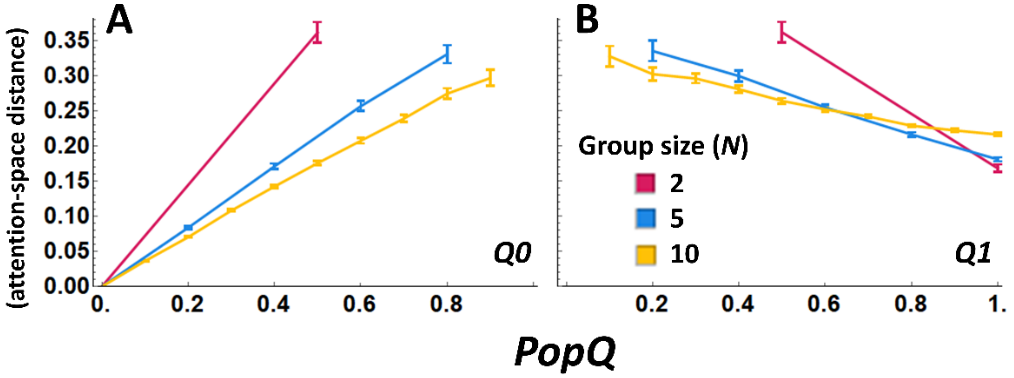

**Figure 3**. Distance between foragers in attention-space (Z; y-axes) across group sizes (N) as a function of *PopQ* for Q0 (**A**) and Q1 (**B**) foragers. Data are averaged over all values of $K_2$. Error bars show ± SEM.

We next explored to what extent foragers capitalize on their ability to move apart in attention-space, relative to the optimal strategy. Theoretically, there is a position in attention-space for each forager that would maximize the overall reduction in competition (occupying these positions does not guarantee that each forager's SR will be maximized, as increased attentional bias also affects success rates). We first calculated this maximal mean distance in attention-space ($Z^*$) for each group (see SI Text). $Z^*$ was then compared to the actual values of $Z$

achieved by our simulated groups. *Z* varied with *PopQ* and $K_2$ (Figure 4. 2-way ANOVA [excluding data for which *PopQ* = 0]: effect of *PopQ*, F(4,1470)=329, $p < 0.001$; effect of $K_2$, F(5,1470)=1237, $p < 0.001$; *PopQ**$K_2$ interaction, F(20,1470)=100, $p < 0.001$; post-hoc tests showed that all comparisons were significant except $K_2 = 0.8$ *vs.* 0.9 or 1, and $K_2 = 0.9$ *vs.* 1). Q1 foragers achieved greater Z than Q0 foragers when they were less common, but this trend reversed when the Q1 phenotype became the majority (Figure 4; Table S4). Most importantly, we found that our groups failed to approach the maximal competition-reduction possible (Figure 4), rarely even achieving half the possible benefit, and that this shortfall increased with increasing *PopQ* (Table S5). This likely resulted from a lack of coordination between foragers in our model, causing them at times to all focus their attention on the same prey.

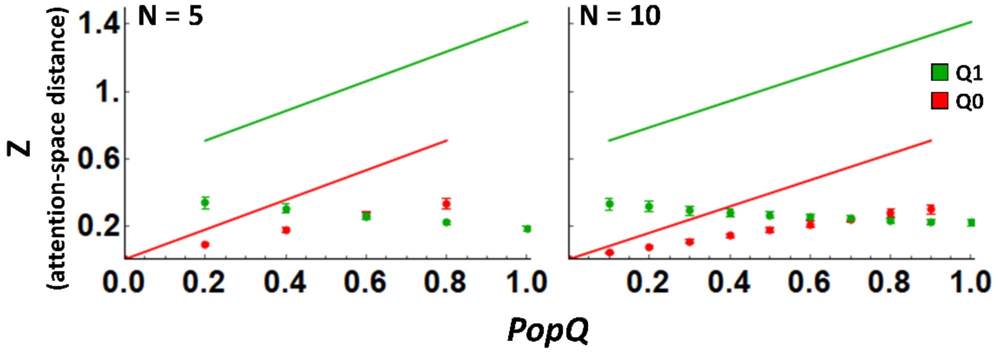

**Figure 4**. Distance in attention-space (Z) as a function of *PopQ* and phenotype. N = 5 (left panel) or 10 (right panel). Lines show $Z^*$ for Q1 (green) or Q0 (red) foragers, points show the mean values achieved by simulated groups. Error bars show ± SEM.

In summary, we found that larger foraging groups compete over prey more, leading to lower success rates. Individuals that can modulate their attention allocation (denoted Q1) do better than those that cannot by moving to different regions of attention space, which acts to decrease competition for all agents. However, due to the lack of complex top-down control or coordination between agents in our model, our groups failed to take full advantage of the competition-reduction benefits of such attentional character displacement. One reason for this is that, with only two prey types, there are limited options for large groups to spread out in attention space. We therefore next explored the effects of increasing the number of prey types.

### *More than two prey types*

For simplicity, we fixed group size at N = 5 for these simulations. We set the number of prey types to $M = 2$, 4 or 6, the last of these allowing us to explore a situation where there are more prey types than foragers, which should allow for no competition (if each forager specializes in a different prey-type). We also restricted the range of conspicuousness values (K) we explored, as the possible values increase dramatically with *M*. We allowed each prey type to differ from the background (on their own unique feature dimension) by either 0.5 or 0.8; so, for $M = 4$, for example, we simulated K = {.5,.5,.5,.5} (all prey differ from the background by 0.5), {.5,.5,.5,.8}, {.5,.5,.8,.8}, {.5,.8,.8,.8} and {.8,.8,.8,.8}. We report results averaged over all values of K, for simplicity. All other details of the simulation were unchanged.

Contrary to our predictions, we found that increasing *M reduced* SR in both phenotypes (Q1 and Q0), independent of *PopQ* (Figure 5A,B; 3-way ANOVA: effect of *M*, F(2,5986) = 1088, $p < 0.001$; effect of *PopQ*, F(5, 5986) = 2.74, $p = 0.02$; effect of phenotype, F(1,5986) = 314.5, $p < 0.001$; *M**phenotype interaction, F(2,5986) = 111.5, P < 0.001; *PopQ**phenotype interaction, F(3,5986) = 0.52, $p = 0.67$ [the *M*PopQ* interaction could not be estimated as it had 0 *df*]). Equally surprising, agents were on average closer to each other in attention space when the number of prey types increased (Figure 5C,D; 3-way ANOVA: effect of *M*, F(2,5986) = 635.7, $p < 0.001$; effect of phenotype, F(1,5986) = 1055.9, $p < 0.001$; effect of *PopQ*, F(5,5986) = 206.3, $p < 0.001$; *M**phenotype interaction, F(2,5986) = 36.57, P < 0.00001; *PopQ**phenotype interaction, F(3,5986) = 282.3, $p < 0.001$).

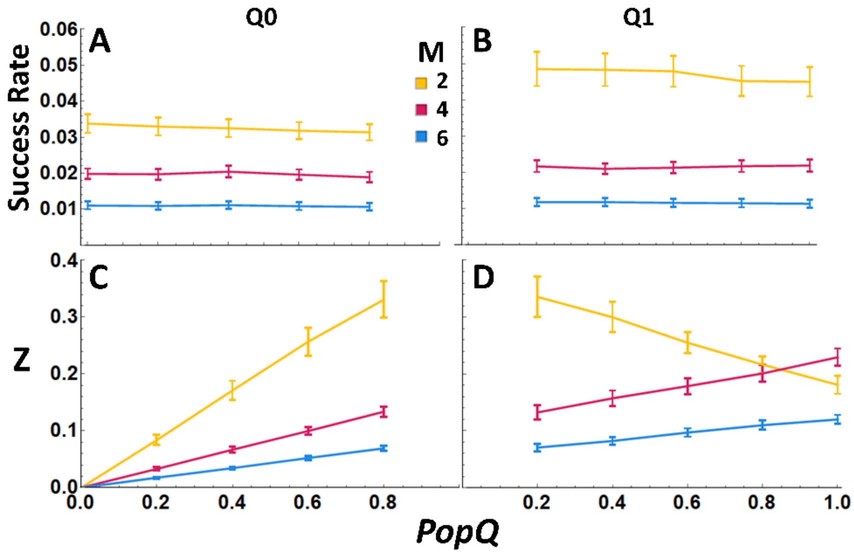

**Figure 5**. Success rate (A, B) and distance in attention-space (C, D) for Q0 (left) and Q1 (right) agents when there are 2 (yellow), 4 (pink) or 6 (blue) prey types. Error bars show ± SEM (across simulation runs).

This effect was caused by the lack of top-down control of attention in our model. As the number of prey types increases, agents are more likely to encounter a wider range of prey, preventing them from forming a robust search image for any one type. Indeed, we found that the mean attention paid to each prey type decreased with increasing *M* (Figure S4), and the range within which attention to one prey type varied (over the course of a simulation) also decreased with increasing *M*, but was not affected by group size (Figure S5). In other words, in the absence of top-down control to limit exploration of novel prey, increasing the number of possible prey types dilutes the attention directed toward each type.

In confirmation of this explanation, we found that increasing the rate at which search images form - the rate of attention focusing ($\alpha$) - and concurrently decreasing the rate at which they decay ($\gamma$), thereby increasing the chances that attention can be focused onto a single prey type, increases the success rate of Q1 agents but not Q0 agents (Figure 6A,B; Table 1), and also increases the distances both phenotypes maintain from each other in attention space (Figure 6C,D; Table 1).

| Effect | Q1 agents | | Q0 agents | |
|---|---|---|---|---|
| | SR | *Z* | SR | *Z* |
| *PopQ* | F(4,2235) = 1.03<br>*p* = 0.39 | F(4,2235) = 14.9<br>***p* < 0.001** | F(4,2235) = 1.18<br>*p* = 0.32 | F(4,2235) = 2206.4<br>***p* < 0.001** |
| {α,γ} | F(2,2235) = 460.3<br>***p* < 0.001** | F(2,2235) = 4665.3<br>***p* < 0.001** | F(2,2235) = 0.39<br>*p* = 0.68 | F(2,2235) = 4505.3<br>***p* < 0.001** |
| Interact | F(8,2235) = 0.97<br>*p* = 0.46 | F(8,2235) = 2.60<br>***p* = 0.008** | | F(8,2235) = 983.9<br>***p* < 0.001** |

**Table 1**. ANOVA results for simulations with increased search image formation rate (α) and decreased search image decay rate (γ). The table shows the results of 2-way ANOVAs on the effects of *PopQ* and {α,γ} (and their interaction) on both Success Rate (SR) and distance in attention-space (*Z*) for Q1 and Q0 agents separately. Significant results are bolded. See main text for details.

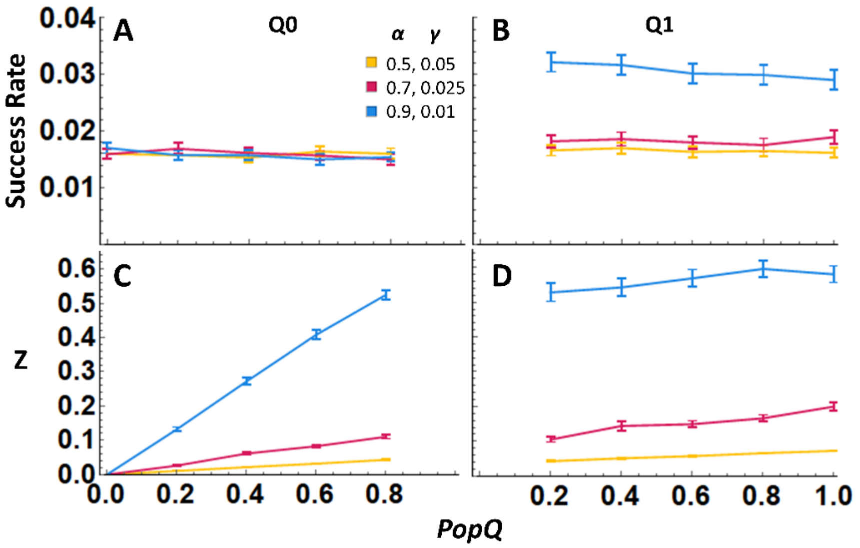

**Figure 6.** Effects of changing attention modulation rate on success rate (A,B) and mean distance in attention space (C,D) for Q0 (A,C) and Q1 (B,D) agents. N = 5; *M* = 4.

## Discussion

We simulated a group of foragers searching for cryptic prey. Under these conditions, foragers compete with each other for prey items, especially if some prey types are more conspicuous. We enabled some of our foragers to modulate their attention, forming search images based on their past prey captures. Foragers that formed a search image for a specific prey type captured more of that type, thereby reducing its relative density. This increased the chances that others in the group would encounter, and subsequently focus their attention on, other prey types, reducing the amount of direct competition between foragers. We call this effect, whereby foragers are shunted into different regions of attention-space, attentional character displacement. We show that our model reproduces this effect, even though we did not explicitly build it into the simulations.

We note that this effect should not be limited to cases of collective foraging. Our model contains no direct interactions between foragers - they only affect each other by altering the local densities of the various prey types. Thus, any situation in which foragers succeed each other at the same resource patch faster than the prey there can completely replenish should allow for attentional character displacement to occur, and the effect will provide competition-reduction benefits to the foragers under any such conditions.

Agents in our simulations were unable to achieve the maximal competition-reduction possible, or even come close to it. Several effects interacted to cause this. First, our model includes little top-down control of attention (except in the sense that search images, once formed by bottom-up priming processes, persist to guide future searches). Having limited attentional capacity, agents will do best when they form, maintain and exploit a single search image, rather than working to form one and switching upon detection of a different prey type. This is likely achieved in real animals via top-down guidance of attention to specific targets (Wolfe, 2021), which our model does not include. This lack of search image persistence likely increased the rate at which foragers changed or lost their search images, limiting the effectiveness of the attentional character displacement. Future work could increase the complexity of agents' top-down control of search (as in, e.g., Wolfe, 2021), which would likely improve performance.

Second, when there are few prey types, there are only a few attentional niches to occupy, and large groups of foragers will tend to overfill attention-space, returning them to a highly competitive regime. Conversely, when there are many prey types, foragers rarely encounter the same type several times in a row - which is required in our model for forming a robust search image. The agents therefore rarely focus their attention on any prey type, negating the benefits of search images. Increasing the rate at which attention is focused (as a function of the number of prey encounters) alleviated this problem, as in models where a single prey detection is enough to completely shift the attentional focus (Bond, 1983; however, this mechanism is contradicted by later empirical data, Reid & Shettleworth, 1992). This mechanism suggests an interesting prediction: animals should benefit from the ability to modulate their rate of attention focusing as a function of environmental conditions (number of cryptic prey types, degree of conspecific competition). For example, there may be environmental conditions under which it is maladaptive to create search images, despite prey being cryptic (such as when there are many types of low-abundance prey). As far as we are aware, no empirical data exist on this question.

To focus on the cognitive underpinnings of search, we made several simplifying assumptions in our model, which may need to be relaxed in future work to better simulate real conditions. First, we assumed that all prey types are initially equally prevalent. Though the relative densities of different prey species likely vary a lot over time and across patches, for a wide variety of reasons (including their own ability to find food), there are some common evolutionary dynamics that can act to stabilize a range of phenotypes within a species (such as color morphs). For example, so-called Rock-Paper-Scissors dynamics may stabilize the relative densities of several morphs at similar levels (e.g., San-Jose et al., 2014). Sufficiently different morphs may require predators to form separate search images (and this effect may itself stabilize polymorphisms; Bond, 2007). Despite this, it would be informative in future work to simulate situations in which one prey type is initially more common than others. This has previously been shown theoretically to have an effect on predation rates and on the future evolution of prey crypticity (Bond & Kamil, 2002).

Second, all our agents had identical attentional resources, and they engaged their full attention in foraging at all times. There are obviously other things that foragers need to pay attention to, and some of these are known to vary with group size (such as the need for vigilance; Beauchamp, 2019). It is also known that there are individual differences in attention capacity. For example, the total number of items that can be held in working memory (an aspect of attention) varies considerably across individuals in humans (Conway et al., 2008) and mice (Kolata et al., 2005). In our model, though we did not vary this parameter, we assume that greater total attention capacity would result in greater foraging success, partly because we do not simulate any of the physiological costs of cognition (e.g., Dukas, 1999). Future work might also explore how total attention capacity interacts with the (in)ability to modulate attention.

Our results suggest that some of the selective pressures that may have driven the evolution of attention relate to group foraging. We simulated agents that either could (Q1) or could not (Q0) modulate and focus their attention. Q1 foragers almost always did better than Q0 foragers, though this advantage disappeared when there were many prey types (Figure 5A,B) or when all prey were very hard to find (e.g., Figure S1). This is partially a result of the non-linear benefits to detecting cryptic prey when attention is focused on them (Equation 4; see Dukas & Ellner, 1993). Additionally, in mixed groups, Q0 agents also benefit passively from the attentional focusing of Q1 agents; as the former move to the edges of attention-space, focusing on specific prey types, the former are left with reduced competition for other prey types. The cost of switching targets, the time required to shift attentional focus to a new prey type, may dampen the advantages of being a Q1 agent, but the competition-reduction benefits render this cost relatively minimal. Taken together, these results suggest that one reason attention cannot be effectively divided may be to retain this competition-reduction effect (which would disappear if agents could form multiple attentional foci at the same time). Of course, there are many other reasons for the structure of attention being as it is (Krauzlis et al., 2023).

As noted above, our model involves no direct interactions between foragers, who can only affect each other via their effects on relative prey densities. However, many species that forage in groups may employ various forms of coordination and cooperation which might further enhance the effectiveness of dividing attention-space between individuals. For example, Butler's gartersnakes (*Thamnophis butleri*) prefer to aggregate with conspecifics that have been consuming a different diet, which should further reduce competition (Lyman-Henley & Burghardt, 1994). In many species that forage socially, individuals function as either producers (who locate resources independently) or scroungers (who follow producers and may copy their choices; Caraco & Giraldeau, 1991). Producers and scroungers face different challenges and have different opportunities (e.g., Ranta et al., 1998), and this may further enhance and interact with the effects of attentional character displacement (for example, producers might benefit more from forming and then discarding search images faster, switching targets to stay ahead of scroungers). Additionally, there may be other direct competitive effects that operate in social foragers but are not captured in our model, such as kleptoparasitism and interference. For example, some bird species have been observed to prioritize searching for prey items of the type that their conspecifics have already found (even when novel prey types are more easily accessible). Birds also compete by leading conspecifics away from food, and even stealing food from others (Bugnyar & Kotrschal, 2004; García et al., 2014). Mechanisms such as these might make the effects of limited attention even more beneficial.

Our results can also be placed into the context of generalist and specialist dietary behaviour. Generalist feeders are favored over specialists in cases where there is high temporal variation in food availability (Behmer & Joern, 2008). In theory, an individual with a relatively flexible food intake will better respond to rapid environmental variation than individuals with a more rigid food intake. We could consider our Q0 foragers, whose attention is always divided between all possible prey types, analogous to generalists, and our Q1 foragers as specializing on the prey their attention is focused on. We do indeed find that the advantage Q1 foragers have over Q0 foragers disappears in situations where there are lots of different prey types (Figure 5A,B) or when all prey are especially hard to find (they all have low conspicuousness; Figure S1). In both of these cases, when reducing the overall success rate – making food harder to find – those who can divide their attention evenly between prey types do better than (or as well as) those who bias themselves towards one prey type.

Our study is significant as it brings together theories of sequential priming in visual search (primarily focused on humans), search images (mostly studied in non-human animals), and collective behavior, fields that address similar questions but, unfortunately, rarely interact. Our model might serve as a framework within which to integrate these differing perspectives on social foraging.

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# Supplementary Material

## SI Text: finding the optimal distance in attention-space, Z*

In order to quantify how much competition reduction foragers gain from attentional character displacement, we created a measure, Z, that captures the distance in attention space between a forager and all other members of the group (see main text for details). Z expresses the Euclidean distance in $M$-dimensional space between group members. Here, we derive the maximal possible value of Z, which we denote Z*. This value can be used to determine how effective groups are at taking advantage of the benefits of attention modulation. Z* depends on the group size, N, the number of prey types, $M$, and on the proportion of the group that can modulate their attention, *PopQ*.

We begin with the simpler case, where *PopQ* = 1 and all foragers can move in attention space. We note one additional key restriction: in our model, each forager's attention is fully engaged at all times, so that the sum of its attention to all prey types must equal 1. Under these constraints, the ideal position for any forager is at one edge of attention space, where its attention is fully engaged in one prey type. There are $M$ such edges in the space.

In cases where $M \geq N$, each forager can focus on a different prey type and the distance between all pairs of foragers, as well as the mean distance, will be

$$Z^* = \sqrt{2} \qquad \text{(Equation S1)}$$

If $M < N$, some agents will co-occupy the same edges of attention-space (i.e., be focused on the same prey type). Of the $M$ possible edges, $N \bmod M$ edges will house $\lceil N/M \rceil$ (the ceiling of $N/M$, the closest integer rounding the fraction up). The remaining $M - (N \bmod M)$ edges will house $\lfloor N/M \rfloor$ (the floor of $N/M$, rounding the fraction down). In each case, foragers have a distance of $\sqrt{2}$ from those occupying other edges and a distance of 0 from those occupying the same edge as themselves. As a result, foragers in the more densely occupied edges will experience a mean distance from all others of $((N - \lceil N/M \rceil)\sqrt{2})/(N-1)$ and foragers at the other edges will experience a mean distance of $((N - \lfloor N/M \rfloor)\sqrt{2})/(N-1)$. In sum, then, the mean maximal distance attainable by the agents is:

$$Z^* = (((N \bmod M)\lceil N/M \rceil(N - \lceil N/M \rceil)\sqrt{2}) / (N - 1) + (M - (N \bmod M))\lfloor N/M \rfloor(N - \lfloor N/M \rfloor)\sqrt{2}) / (N - 1)) / N \qquad \text{(Equation S2)}$$

Equation S2 will simplify to Equation S1 in cases where $M \geq N$.

The more difficult case is when *PopQ* < 1 and only some of the foragers can move in attention space. For legibility, we here denote *PopQ* as simply q. In this case, only qN foragers are free to move in attention space. Their optimal positioning is still at the edges of the space. The distances between them will be as above. In addition, however, they will each have a smaller distance from those foragers that cannot move, whose attention remains at $1/M$ on each dimension of attention space. Distances between members of the two phenotypes will be

$\sqrt{(M-1)/M}$, and there will be (1 – q)N of these. There will therefore be three possible distances:

$$A = ((qN - \lceil qN/M \rceil)\sqrt{2} + (1-q)N\sqrt{(M-1)/M}) / (N-1) \quad \text{(at a more populated edge)}$$
$$B = ((qN - \lfloor qN/M \rfloor)\sqrt{2} + (1-q)N\sqrt{(M-1)/M}) / (N-1) \quad \text{(at a less populated edge)}$$
$$C = qN\sqrt{(M-1)/M} \quad \text{(in the center)}$$

Combining these with the numbers in each condition gives:

$$Z^* = ((qN \bmod M)\lceil qN/M \rceil A + (M - (qN \bmod M))\lfloor qN/M \rfloor B + (1-q)C) / N \quad \text{(Equation S3)}$$

Figure S6 shows the values of Z* for a range of values of N, *M*, and *PopQ*.

**Table S1**. Results of linear regressions on the data in Figure 2B and 2C, for success rate. A separate regression was run on the data for each group size (N) and each phenotype (Q0 or Q1) across all values of *PopQ*. The table gives the F-ratio (with degrees of freedom), P-value, and regression coefficient (*b*) for each line.

| N | Q0 foragers | | | Q1 foragers | | |
|---|---|---|---|---|---|---|
| | F | P | *b* | F | P | *b* |
| 2 | F(1,98) = 0.99 | 0.32 | -0.001 | F(1,98) = 2.75 | 0.10 | -0.003 |
| 5 | F(1,248) = 38.5 | < 0.00001 | -0.003 | F(1,248) = 92.3 | < 0.00001 | -0.005 |
| 10 | F(1,498) = 151 | < 0.00001 | -0.003 | F(1,498) = 389 | < 0.00001 | -0.008 |

**Table S2**. Proportion of prey taken that are of type 2 as a function of *PopQ* and $K_2$. A separate 2-way ANOVA was run for each group size (N). Each column shows one effect ($K_2$, *PopQ*, and their interaction) and each cell gives the F-ratio, P-value, and effect size ($\eta^2$) for that effect. Significant post-hoc (PH) comparisons (for which $p < 0.01$) are noted below each cell. The top table gives results for Q1 foragers, and the bottom table for Q0 foragers.

**Q1 foragers**:

| N | $K_2$ | *PopQ* | $K_2$ * *PopQ* |
|---|---|---|---|
| 2 | F(5,887) = 233, P < 0.001, $\eta^2 = 0.52$ | F(1,887) = 0.09, P = 0.76, $\eta^2 = 0.00004$ | F(5,887) = 2.67, P = 0.02, $\eta^2 = 0.006$ |
| | PH: all different except 1 vs. 0.8 and 0.9 | PH: no difference | |
| 5 | F(5,4469) = 19.79, P < 0.001, $\eta^2 = 0.43$ | F(4,4469) = 0.30, P = 0.88, $\eta^2 = 0.0001$ | F(20,4469) = 0.37, P = 1.00, $\eta^2 = 0.0007$ |
| | PH: all different except 0.9 vs. 0.8 and 1 | PH: no differences | |
| 10 | F(5,16435) = 2393, P < 0.001, $\eta^2 = 0.335$ | F(9,16435) = 5.01, P < 0.001, $\eta^2 = 0.001$ | F(45,16435) = 0.78, P = 0.86, $\eta^2 = 0.001$ |
| | PH: all different except 0.9 vs. 1 | PH: 0.9 and 1 different from 0.3 and 0.4 | |

**Q0 foragers**:

| N | $K_2$ | *PopQ* | $K_2$ * *PopQ* |
|---|---|---|---|
| 2 | F(5,888) = 184.3, P < 0.001, $\eta^2 = 0.48$ | F(1,888) = 0.007, P = 0.93, $\eta^2 = 0.000004$ | F(5,888) = 0.60, P = 0.70, $\eta^2 = 0.002$ |
| | PH: all different except 0.9 vs. 0.8 and 1 | PH: no difference | |
| 5 | F(5,4468) = 612, P < 0.001, $\eta^2 = 0.35$ | F(4,4468) = 1.06, P = 0.38, $\eta^2 = 0.0005$ | F(20,4468) = 0.58, P = 0.93, $\eta^2 = 0.001$ |
| | PH: all different except 0.9 vs. 0.8 and 1 | PH: no differences | |
| 10 | F(5,16427) = 1406, P < 0.001, $\eta^2 = 0.25$ | F(9,16427) = 5.77, P < 0.001, $\eta^2 = 0.002$ | F(45,16427) = 1.29, P = 0.09, $\eta^2 = 0.002$ |
| | PH: all different except 0.9 vs. 1 | PH: 0 different from 0.4, 0.6 and 0.9 | |

**Table S3**. Results of linear regressions on the data in Figure 3, for distance in attention-space (Z). A separate regression was run on the data for each group size (N) and each phenotype (Q0 or Q1) across all values of *PopQ*. The table gives the F-ratio (with degrees of freedom), P-value, and regression coefficient (*b*) for each line.

| N | Q0 foragers | | | Q1 foragers | | |
|---|---|---|---|---|---|---|
| | F | P | *b* | F | P | *b* |
| 2 | F(1,98) = 4749 | < 0.00001 | 0.72 | F(1,98) = 621 | < 0.00001 | -0.39 |
| 5 | F(1,248) = 15521 | < 0.00001 | 0.42 | F(1,248) = 1035 | < 0.00001 | -0.20 |
| 10 | F(1,498) = 31553 | < 0.00001 | 0.33 | F(1,498) = 1132 | < 0.00001 | -0.12 |

**Table S4.** Results of Paired-sample T-tests comparing the distance in attention-space (Z) achieved by Q0 foragers and Q1 foragers, at each level of *PopQ* (excluding 0 and 1). The table gives the t-test statistic (all *df* were 299) and P-value for each test. Separate tables are given for N = 5 and N = 10 (this analysis was not run on N = 2 as there can be no difference in Z when there is only one forager of each phenotype).

**N = 5**

| *PopQ* | Q1 mean Z | Q0 mean Z | t(299) | P |
|---|---|---|---|---|
| 0.2 | 0.34 ± 0.25 | 0.08 ± 0.06 | 23.15 | < 0.001 |
| 0.4 | 0.30 ± 0.18 | 0.17 ± 0.12 | 34.17 | < 0.001 |
| 0.6 | 0.25 ± 0.12 | 0.26 ± 0.18 | -0.43 | 0.67 |
| 0.8 | 0.22 ± 0.10 | 0.33 ± 0.23 | -10.63 | < 0.001 |

**N = 10**

| *PopQ* | Q1 mean Z | Q0 mean Z | t(299) | P |
|---|---|---|---|---|
| 0.1 | 0.33 ± 0.25 | 0.04 ± 0.03 | 22.77 | < 0.001 |
| 0.2 | 0.30 ± 0.20 | 0.07 ± 0.05 | 26.33 | < 0.001 |
| 0.3 | 0.30 ± 0.17 | 0.11 ± 0.07 | 31.62 | < 0.001 |
| 0.4 | 0.28 ± 0.15 | 0.14 ± 0.09 | 38.40 | < 0.001 |
| 0.5 | 0.26 ± 0.13 | 0.18 ± 0.12 | 33.34 | < 0.001 |
| 0.6 | 0.25 ± 0.12 | 0.21 ± 0.14 | 12.50 | < 0.001 |
| 0.7 | 0.24 ± 0.11 | 0.24 ± 0.16 | 0.78 | 0.63 |
| 0.8 | 0.23 ± 0.09 | 0.27 ± 0.19 | -5.90 | < 0.001 |
| 0.9 | 0.22 ± 0.09 | 0.30 ± 0.20 | -7.92 | < 0.001 |

**Table S5.** Results of one-sample T-tests comparing the distance in attention-space (Z) achieved by our simulated groups to the maximal possible. Each *PopQ* level was compared to its own maximum (excluding 0; second column of the table). The table gives the T-test statistic (all *df* were 299) and p-value for each test. Separate tables are given for N = 5 and N = 10 (this analysis was not run on N = 2).

**N = 5**

| *PopQ* | Max Z | All Mean Z | t(299) | P |
|---|---|---|---|---|
| 0.2 | 0.283 | 0.13 ± 0.10 | -25.76 | < 0.001 |
| 0.4 | 0.566 | 0.22 ± 0.14 | -42.27 | < 0.001 |
| 0.6 | 0.707 | 0.26 ± 0.14 | -56.10 | < 0.001 |
| 0.8 | 0.849 | 0.24 ± 0.11 | -96.31 | < 0.001 |
| 1 | 0.849 | 0.18 ± 0.10 | -118.83 | < 0.001 |

**N=10**

| *PopQ* | Max Z | All Mean Z | t(299) | P |
|---|---|---|---|---|
| 0.1 | 0.141 | 0.07 ± 0.05 | -26.27 | < 0.001 |
| 0.2 | 0.283 | 0.12 ± 0.08 | -35.64 | < 0.001 |
| 0.3 | 0.393 | 0.16 ± 0.10 | -38.44 | < 0.001 |
| 0.4 | 0.503 | 0.20 ± 0.12 | -45.77 | < 0.001 |
| 0.5 | 0.581 | 0.22 ± 0.12 | -50.33 | < 0.001 |
| 0.6 | 0.660 | 0.23 ± 0.12 | -60.45 | < 0.001 |
| 0.7 | 0.707 | 0.24 ± 0.12 | -69.60 | < 0.001 |
| 0.8 | 0.754 | 0.24 ± 0.10 | -86.65 | < 0.001 |
| 0.9 | 0.770 | 0.23 ± 0.10 | -98.51 | < 0.001 |
| 1 | 0.786 | 0.22 ± 0.09 | -107.61 | < 0.001 |

**Figure S1**. Success rate (prey taken per time step) for Q0 (left panels) and Q1 (right panels) foragers in the model, as a function of *PopQ* (x-axes) and the conspicuousness of prey type 2, $K_2$ (colours). Each row shows the data for a different group size, N.

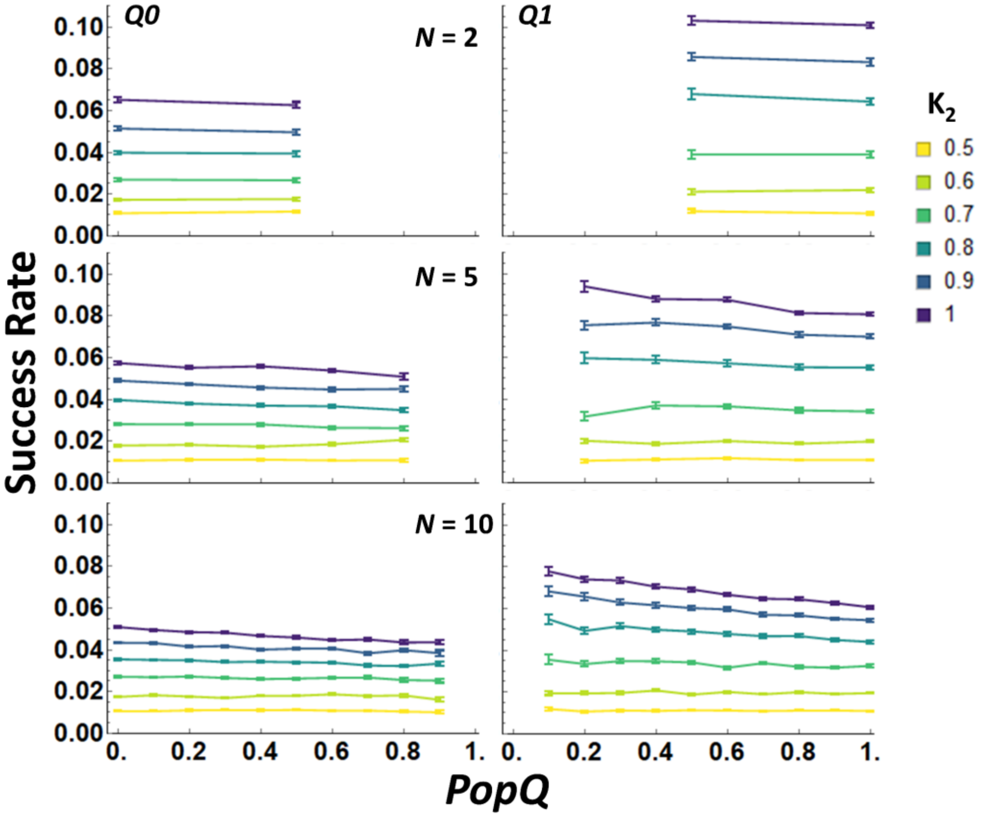

**Figure S2**. Proportion of prey taken that are of type 2, for Q0 (left panels) and Q1 (right panels) foragers in the model, as a function of *PopQ* (x-axes) and the conspicuousness of prey type 2, $K_2$ (colours). Each row shows the data for a different group size, N.

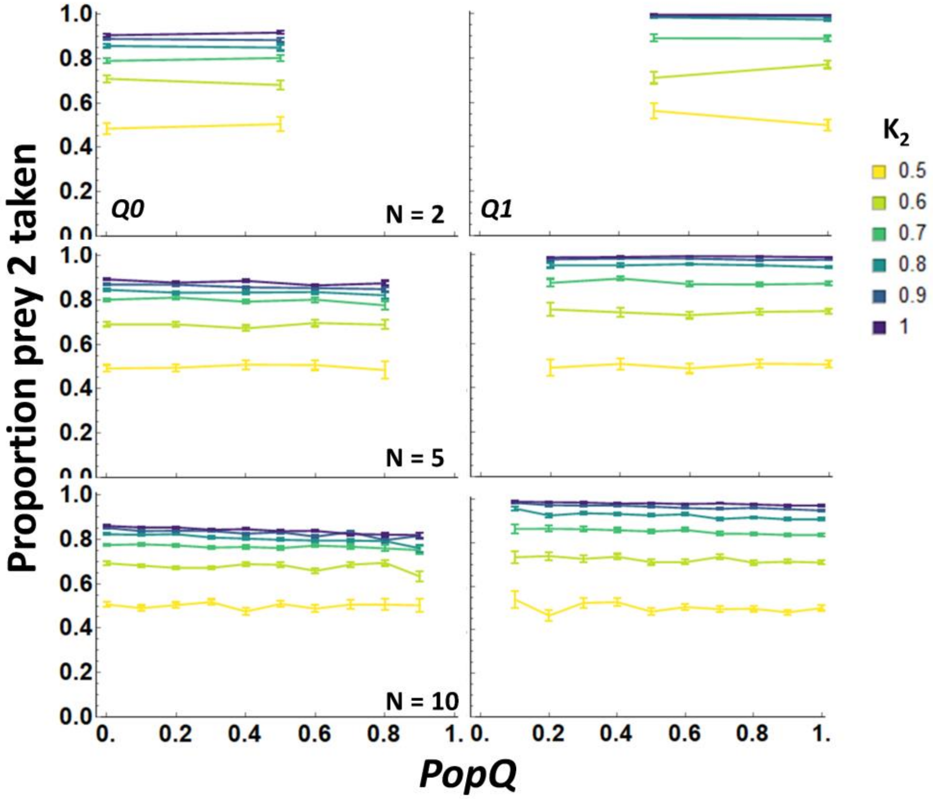

**Figure S3**. Mean distance in attention-space (Z), for Q0 (left panels) and Q1 (right panels) foragers in the model, as a function of *PopQ* (x-axes) and the conspicuousness of prey type 2, $K_2$ (colours). Each row shows the data for a different group size, N.

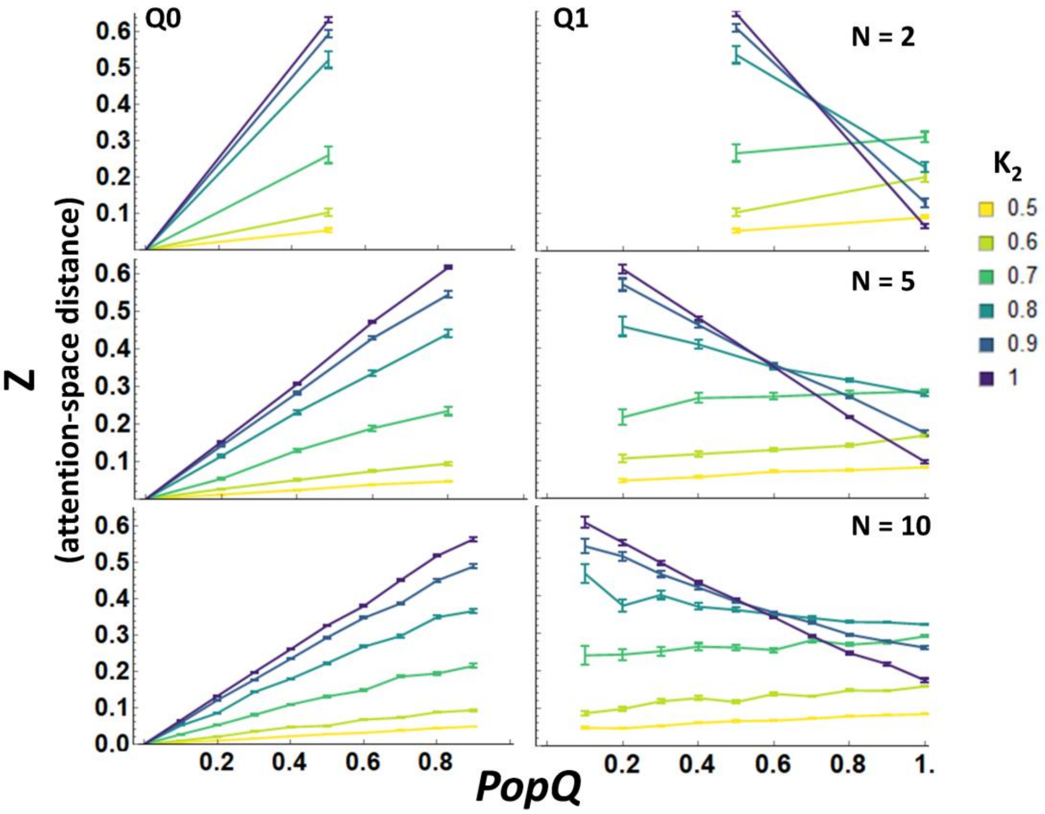

**Figure S4**. The mean attention level paid to each prey type as a function of *PopQ* (x-axes) and the number of prey types (*M*; different subplots). Data are averaged over all conspicuousness values ($K_2$). Note the different y-axis ranges in the separate subplots. Colors indicate prey types. Error bars show ± SEM. As the number of prey types increases, attention to each type is diluted.

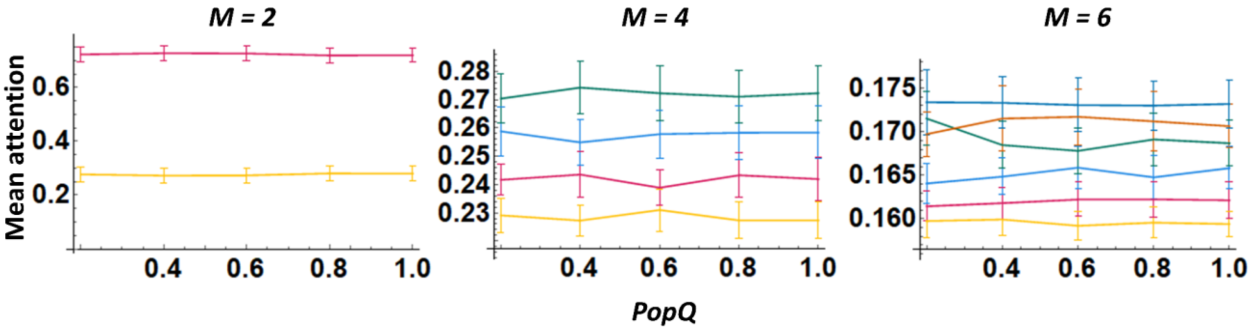

**Figure S5**. The mean range over which attention varies (within a simulation) as a function of *PopQ* (x-axes) and group size (N; top panel) or number of prey types (*M*; bottom panel). Changing N has no effect on attention range, but increasing *M* reduces agents' ability to focus on a single prey type, reducing the range over which their attention varies. Error bars show ± SEM.

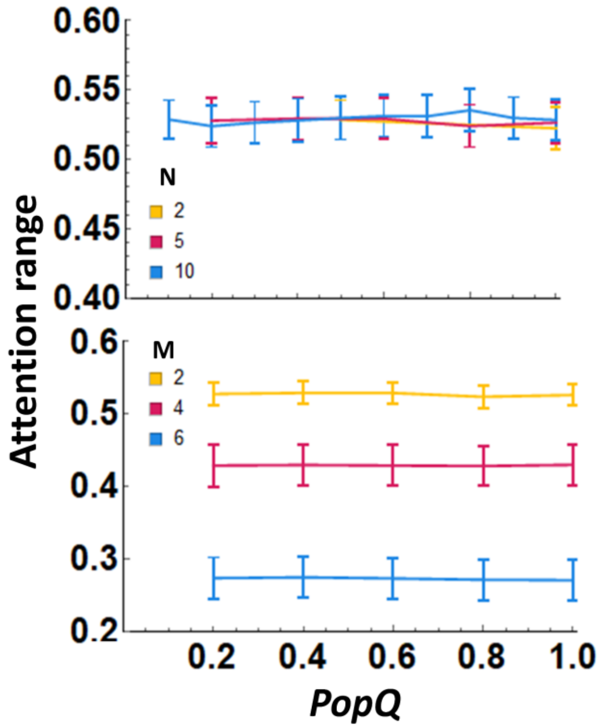

**Figure S6**. Values of the maximal possible mean distance in attention space (Z*) as a function of group size (N; x-axes), the number of prey types (*M*; lines), and the proportion of the group that can modulate their attention (*PopQ*; top panel, *PopQ* = 1, bottom panel, *PopQ* = 0.5).