

# The behavioral ecology of a cognitive constraint: limited attention

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Limited attention may constrain animal behavior in situations in which the rate of relevant information exceeds the threshold processing capacity of the brain. In the present study, we examine why attention is limited by quantifying how attention affects the ubiquitous problem of balancing foraging and antipredator activity. We analyze how a given attentional capacity affects feeding requirements, the optimal attentional focus during predator scanning, and the probability of detecting predators. Our model indicates that because of the complex interplay between the costs and benefits associated with a given attentional capacity, limited attention can be an optimal strategy, which allows effective and economical search for cryptic objects. *Key words:* attention, cognition, constraint, foraging, predation risk. [*Behav Ecol* 14:151–156 (2003)]

Limited attention implies that the brain can process information only at some finite rate. Limited attention may compromise performance in situations in which the rate of relevant information exceeds the threshold processing capacity of the brain. In such cases of information overload, animals can attend only to a portion of the information that may affect fitness (Broadbent, 1965; Dukas, 1998; Kastner and Ungerleider, 2000).

Recently, controlled laboratory studies with blue jays (*Cyanocitta cristata*) have indeed indicated negative effects of limited attention on performance. In one study, when jays focused on detecting cryptic targets at the center of the visual field, they were three times less likely to detect peripheral targets than when required to detect conspicuous targets at the center of the visual field. That is, even though the two experimental treatments (easy and difficult central detection) involved identical visual fields, identical conspicuousness of the peripheral targets, and identical frequencies of target appearance within the visual field, the difficult central detection treatment required more attention devoted to the center of the visual field, resulting in a much-reduced frequency of detecting the peripheral targets than during the easy central detection treatment (Dukas and Kamil, 2000). This experiment suggests that under natural settings, foragers engaged in a difficult food-searching task may be less likely to notice peripheral objects such as approaching predators, a conclusion in agreement with experimental data (Godin and Smith, 1988; Krause and Godin, 1996; Milinski, 1984; Milinski and Heller, 1978). In another blue jay experiment, when birds had to simultaneously search for two cryptic target types, their overall rate of target detection was 25% lower than when they had to search for only a single target type at any given time (Dukas and Kamil, 2001). That is, dividing limited attentional resources between two difficult tasks reduced performance compared with performance when focusing full attention on a single task.

Results of the blue jay experiments are consistent with research on the neurobiological mechanisms modulating

attention in humans and monkeys, which indicates that focusing attention on a given task is correlated with enhanced activity of the neurons processing that task and diminished activity of other neurons (Behrmann and Haimson, 1999; Kastner and Ungerleider, 2000; Moran and Desimone, 1985).

The experiments suggesting that limited attention constrains key behaviors such as predator avoidance and foraging raise the question of what determines attentional capacity and why it is limited. We evaluate this issue with a model of foraging under the risk of predation. Specifically, we consider two aspects of attention. First, for a given attentional capacity, what is the optimal focus of attention? Second, what is the optimal level of attentional capacity? Although we focus on attention, our analysis is relevant for a broad range of cognitive and physiological capacities that determine behavior, including learning rate, memory, digestive rate, and muscle power.

## The model

We imagine a foraging animal that, upon entering a patch, first pauses to search for possible predators. The probability that a predator is hidden in or near the patch is  $p_0$ . (See Table 1 for model parameters.) If the forager focuses its attention over a visual angle  $\theta$  for a fixed time  $t_s$  the detection probability equals

$$f(\theta) = \delta_0 e^{-\theta/a}, \quad (1)$$

where  $\delta_0$  and  $a$  are parameters relating the probability of detection to the animal's ability. First,  $\delta_0$  is a visual acuity parameter that represents the highest possible value of  $f(\theta)$  when full attention is devoted to the narrowest possible visual angle. For example, a higher  $\delta_0$  would mean a greater visual resolution, more-refined color vision, a higher sensitivity to minute movements, or more detailed information in memory about predators. Second,  $a$  denotes attentional capacity and indicates how the probability of detection changes when the animal attends to an angle wider than the minimal one. A low value of  $a$  implies a sharp decline in the probability of predator detection when attention is spread over a wide angle. In contrast, a high value of  $a$  implies that attention can be distributed over a wide angle with little reduction in detection probability.

Figure 1A shows the detection probability,  $f(\theta)$ , as a function of attentional focus,  $\theta$ . The rate at which  $f(\theta)$  decreases with  $\theta$  depends on the attentional capacity parameter,  $a$ , as already

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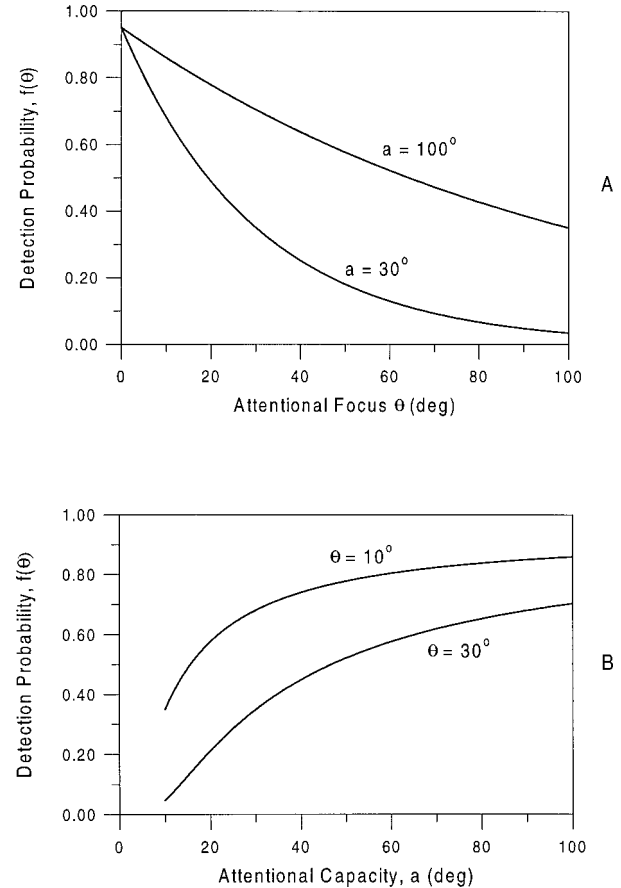
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**Table 1**  
**Symbols and parameters**

Symbol	Meaning	Units	Basic Values
$\theta$	Attentional focus	degree	—
$\theta_{\max}$	Maximum $\theta$	degree	180 degrees
$f(\theta)$	Detection probability	—	Equation 1
$t_s$	Scan time per attentional focus	seconds	60 s
$\delta_0$	Visual acuity parameter	—	0.95
$a$	Attentional capacity	degree	30 degrees
$n$	Number of sectors used (decision variable)	—	—
$n_{\max}$	Maximum number of sectors	—	30
$T_s$	Total search time for $0 \leq \theta \leq \theta_{\max}$	seconds	$T_s = nt_s$
$t$	Time period during day (duration $t_s$ )	—	—
$T$	Total number of time periods	—	600
$d$	e.g., day in winter	—	—
$D$	Total number of days	—	100
$x = X(t, d)$	Forager's internal energy reserves	grams	—
$x_{\max}$	Maximum energy reserves	grams	2000 g
$c(a, \delta_0)$	Metabolic cost	grams/day	Equation 2
$q_1$	Cost coefficient	grams/day/degree	0.033
$q_2$	Cost coefficient	grams/day	1100
$k$	Nonlinear cost coefficient	/degree	.05/degree
$q_n$	Overnight cost factor	—	0.3
$c_n$	Overnight metabolic cost	grams	Equation 3
$p_k$	Predator's kill probability	—	Equation 4
$p_{k0}$	Kill probability coefficient	—	0.1
$p_{k1}$	Kill probability coefficient	/grams	0.0001
$p_0$	Probability that predator is present	—	0.1
$I$	Rate of food intake when foraging	grams/day	6000 g/day
$N$	Number of periods spent foraging, after search	—	10
$F(x, t, d)$	Fitness, i.e., probability of survival	—	Equation 5
$V_r$	Future fitness if rest	—	Equation 9
$V_f$	Future fitness if scan and forage	—	Equation 10
$D(x, t, d)$	Optimal number of search sectors $n$	—	—

described. Figure 1B shows how the detection probability,  $f(\theta)$ , changes as a function of attentional capacity,  $a$ , for a fixed attentional focus,  $\theta$ . Note that an increase in attentional capacity produces a decelerating increase in  $f(\theta)$ , for any given attentional focus,  $\theta$ , with limiting value  $\delta_0$  as  $a \rightarrow +\infty$ . Conceivably, an increase of neuronal capacity could also increase  $\delta_0$ . This increase, however, would also involve a decelerating relationship, because  $\delta_0$  is necessarily limited to 1.



**Figure 1**

Detection probability  $f(\theta)$ : as a function of attentional focus,  $\theta$ , for two values of attentional capacity,  $a$  (A); as a function of attentional capacity,  $a$ , for two values of attentional focus,  $\theta$  (B).

We consider a given patch, included within the forager's visual field. In searching the entire patch (total angle  $\theta_{\max}$ ), the forager attends sequentially to contiguous sectors  $S_j$  of angle  $\theta = \theta_{\max}/n$ , for some integer  $n$ . The time,  $t_s$ , to complete one local search, with attentional focus,  $\theta$ , is assumed fixed, independent of  $\theta$ . Thus,  $t_s$  can be thought of as the minimal time required for image formation and inspection. Assume that the chance of more than one predator being in the patch is negligible. Then, given that a predator exists in the patch, the probability of detecting it in total search time  $T_s = nt_s$  is equal to

$$\sum_j \Pr(\text{detect existing predator in } S_j) \Pr(\text{predator is in } S_j).$$

The first probability in this sum is equal to  $f(\theta)$ . Also,  $\Pr(\text{existing predator is in } S_j) = 1/n$ . Consequently the probability of detecting the predator in time,  $T_s$ , equals  $f(\theta) = f(\theta_{\max}/n)$ . The tradeoff involved in choosing the size  $\theta = \theta_{\max}/n$  of separate search sectors is that small  $\theta$  (large  $n$ ) provides a high detection probability, but requires a long-time  $T_s = nt_s$  to search the patch. Thus, careful searching (using a narrow focus of attention) reduces the risk of predation, but decreases the amount of time available for foraging or other activities.

#### Relating attentional capacity to fitness

To calculate the optimal attentional focus and optimal attentional capacity, we need to evaluate the effects of

attention on fitness. We use a standard dynamic-state variable model (Clark and Mangel, 2000), in which fitness is defined as the probability of survival over a given time span, for example, winter. The dynamic model employs two time variables,  $t$  ( $1 \leq t \leq T$ ) denoting time periods during a typical day, and  $d$  ( $1 \leq d \leq D$ ) denoting days. Each time period  $t$  has duration  $t_s$ , the search time per sector. The state variable  $x = X(t, d)$  denotes the forager's internal energy reserves (grams of fat, lipids) at the beginning of period  $t$  on day  $d$ . We assume that  $0 \leq x \leq x_{\max}$  (where  $x_{\max}$  denotes maximum possible reserves). The forager dies of starvation if  $x$  reaches zero.

Total metabolic cost (grams per day) is

$$c(a, \delta_0) = \frac{q_1 a e^{ka}}{1 - \delta_0} + q_2, \quad (2)$$

where  $q_1$ ,  $q_2$ , and  $k$  are cost coefficients, specified so that cognitive costs (the first term in Equation 2) amount to approximately 15% of total metabolic costs. The parameter  $k$  is the nonlinear cost coefficient. It reflects the fact that an increase in brain volume is associated with a decelerating increase in computational power (Allman, 1999; Deacon, 1990; Zhang and Sejnowski, 2000). That is, a linear increase in cognitive capacity would require an accelerating increase in brain volume and its associated costs. In the basic version of the model,  $a$  and  $\delta_0$  are taken as given constants, but later, we consider the question of optimal attentional capacity.

Total daylight hours have duration  $T_{\text{day}} = T_s/3600$ ; the rest,  $24 - T_{\text{day}}$  being night-time. Reserves are reduced overnight by the amount

$$c_n = q_n c(a, \delta_0) \frac{24 - T_{\text{day}}}{24}, \quad (3)$$

where the factor  $q_n$  relates night-time (resting) metabolic costs to day-time costs. The forager must retire with  $x > c_n$  in order to avoid starvation.

If not currently searching or foraging, the forager decides whether to rest in the next period,  $t$ , or to enter a new patch and start scanning for predators. If it opts to scan, it decides also on the search strategy it will use (i.e., on the angle of attentional focus  $\theta = \theta_{\max}/n$ ). It continues scanning until it either detects a hidden predator or completes scanning the area. In the latter case, it then forages for  $N$  periods. We assume that the forager can not be successfully attacked while scanning (peripheral vision detects movement and allows the forager to escape), but it will be attacked if it forages when an undetected predator is present. The predator's probability of success,  $p_k$ , depends on the forager's energy reserve mass:

$$p_k = p_{k0} + p_{k1} x, \quad (4)$$

where  $p_{k0}$  and  $p_{k1}$  are predation-risk coefficients. Food intake rate while foraging is denoted by  $I$  (grams per period).

The optimization objective is the probability of survival to period 1 on day  $D + 1$  (e.g., the start of the breeding season). We introduce the fitness function (Clark and Mangel, 2000):

$$F(x, t, d) = \max \Pr(\text{forager survives from } t, d \text{ to } I, D + 1, \text{ given that } X[t, d] = x). \quad (5)$$

This definition only applies if the forager is not currently scanning or foraging. When the forager is scanning or foraging, we do not need to define  $F$  because no decision is made in this case, by assumption. The dynamic programming equations for  $F(x, t, d)$  are:

$$F(x, T, D) = \begin{cases} 1 & \text{if } x > c_n \\ 0 & \text{otherwise} \end{cases}, \quad (6)$$

$$F(x, T, d) = \begin{cases} F(x - c_n, 1, d + 1) & \text{if } x > c_n \\ -63.80 & \text{otherwise} \end{cases} \quad (7)$$

$$F(x, t, d) = \max\{V_r, V_f\}, \quad (8)$$

where  $V_r$  and  $V_f$  are the future fitness values if the forager rests or commences foraging, respectively. These fitness values are given by:

$$V_r = F(x - \Delta c, t + 1, d). \quad (9)$$

where  $\Delta c$  denotes metabolic cost per period. Also:

$$V_f = \max_{\theta} \left\{ \begin{aligned} & p_0 \left( \sum_{j=1}^n \frac{f(\theta)}{n} F(x - j\Delta c, t + j, d) \right) \\ & + (1 - f(\theta))(1 - p_k) F(x - n\Delta c, t + n, d) \\ & + (1 - p_0) F(x - n\Delta c + NI, t + n + N, d) \end{aligned} \right\}. \quad (10)$$

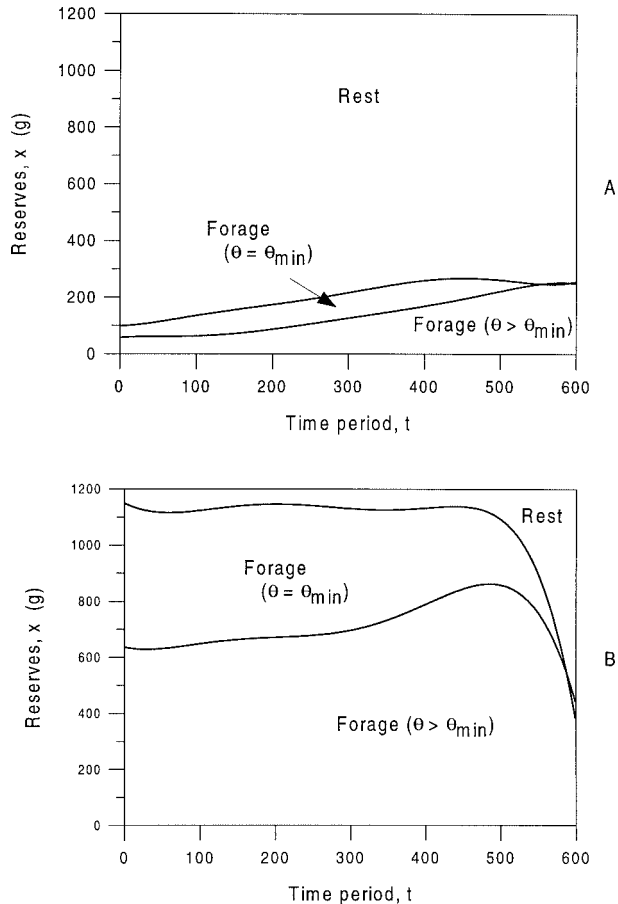
Equations 9 and 10 require explanation. In Equation 9, the resting forager experiences metabolic cost  $\Delta c$ ; the time index,  $t$ , advances to the next period,  $t + 1$ . In Equation 10, the forager initiates a foraging bout. With probability  $p_0$ , a predator is concealed in the patch. For given sector angle  $\theta = \theta_{\max}/n$  the probability that the predator is in  $S_j$  is  $1/n$ , and the probability of detecting it there is  $f(\theta)$ . If it is detected in the  $j$ th sector  $S_j$ , the forager flees, having expended cost  $j\Delta c$  and used up  $j$  time intervals. The predator goes undetected with probability  $[1 - f(\theta)]$ , but the forager escapes the attack with probability  $1 - p_k$ , having expended  $n\Delta c$  and used up  $n$  time intervals during the search. Finally, with probability  $(1 - p_0)$  there is no predator, and the forager obtains food,  $NI$ , using up  $n + N$  periods in scanning and foraging. In Equation 10, the range of  $n$  is  $1 \leq n \leq n_{\max}$  except that  $n$  is also  $\leq T - t$ , the number of periods remaining in the day.

The dynamic programming Equations 6–10 are solved numerically in the usual way, yielding the values  $F(x, t, d)$  and also the optimal state- and time-dependent search decisions  $n = D(x, t, d)$ . (State levels,  $x$ , are discretized in the calculation, and linear interpolation is used for intermediate values of  $x$ . These and other technical details are described by Clark and Mangel [2000].)

## RESULTS

### The optimal focus of attention

Figure 2A indicates the optimal angle of attentional focus as a function of time of day,  $t$ , and current level of reserves,  $x$ , assuming a moderate level of attentional capacity,  $a = 30$  degrees. First, with low reserves, the forager should scan a patch somewhat superficially by using a wide attentional focus (Figure 2A, lower region) and then feed, in order to quickly build up its reserves. These low reserve levels would not normally be encountered by an optimal forager, unless it had experienced a run of encounters with predators that prevented it from foraging. Second, with moderate reserves, the forager should scan carefully, narrowing its focus of attention to the minimal angle  $\theta = \theta_{\max}/n_{\max}$  (Figure 2A, middle region). Finally, with large reserves, the forager should rest (Figure 2A, upper region). With a much larger attentional capacity,  $a = 70$  degrees rather than 30 degrees, increased food requirements cause a large increase in the overall proportion of time spent foraging and an increase in the time spent searching for predators by using a broad attentional focus (Figure 2B).

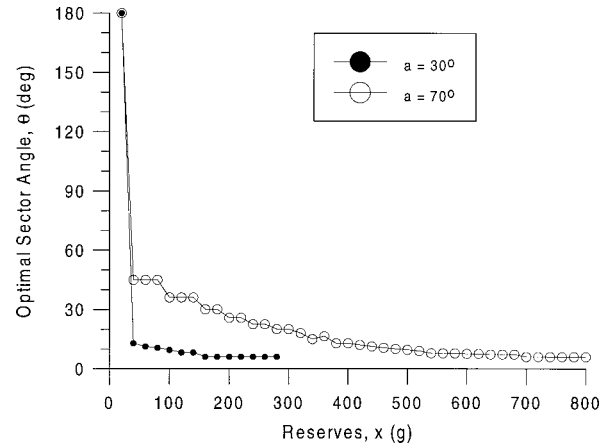


**Figure 2**  
Optimal search strategy as a function of time of day,  $t$ , and current reserve level,  $x$ . Attentional capacity parameter  $a = 30$  degrees (A);  $a = 70$  degrees (B). (Curves are smoothed to remove effects of discretization. The unsmoothed curves do not cross.) For reserves  $x$  below the lower curve, the forager searches quickly with a wide attentional focus so as to rapidly replenish reserves. When reserves  $x$  lie between the two curves, the forager initiates searching using the most narrow attentional focus ( $\theta = 6$  degrees) before foraging. Finally, if current reserves  $x$  are above the upper curve, the forager rests, allowing its reserves to decline. Basic parameter values are given in Table 1.

Detailed cross sections of Figure 2 at midday are shown in Figure 3. With  $a = 30$  degrees, the optimal behavior often involves highly focused attention ( $\theta = 6$  to 13 degrees). Only a forager with low reserves would search with broader attentional focus, and only until it had been able to obtain some food. In contrast, a larger attentional capacity ( $a = 70$  degrees) results in a broader attentional focus even for medium levels of reserves.

#### Optimal attentional capacity

Figure 4 shows fitness values (for  $d = 1$ ,  $t = 1$ ,  $x = 100$  g) as a function of attentional capacity  $a$  (with  $\delta_0 = 0.95$  held constant), for two degrees of nonlinearity ( $k$ ) in metabolic cost (Equation 2). For small  $k = 0.05$ , corresponding to mild nonlinearity, the fitness curve is relatively flat, having a maximum at  $a = 40$  degrees. This is the optimal capacity, for the case  $k = 0.05$ . For larger  $k = 0.10$  (stronger nonlinearity in cost,  $c[\delta_0, a]$ ), the fitness curve is maximum at  $a = 24$  degrees, and declines sharply at larger values of  $a$ , reaching  $F = 0$  at  $a = 60$  degrees.



**Figure 3**  
Optimal attentional focus,  $\theta$ , as a function of current reserves  $x$  and attentional capacity  $a$  at midday ( $t = 400$ ). At the extreme, when reserves are nearly depleted, the forager performs a single rapid search with the widest attentional focus ( $\theta = 180$  degrees) and then forages. (An optimal forager would almost never get into this situation.) Otherwise, the forager searches with a narrow focus of attention. Lower curve ( $a = 30$  degrees): Here the optimal scan angle,  $\theta$ , is between 6 and 13 degrees, except at the lowest level of reserves considered ( $x = 20$  g). Upper curve ( $a = 70$  degrees): The optimal attentional focus is between 6 and 45 degrees.

## DISCUSSION

### Optimal attentional parameters

A narrow focus of attention ( $\theta = \theta_{\min}$ ) reduces the risk of predation (Figure 1A) but uses time that could otherwise be devoted to foraging or resting. It is optimal to use narrow attentional focus as long as reserves are sufficiently high (Figures 2 and 3). A larger attentional capacity would allow a broader attentional focus, reducing the time spent scanning for predators relative to foraging activity. Increased attentional capacity, however, is also assumed to increase metabolic costs, which must be balanced by increased daily food intake, in turn necessitating increased foraging duration, and hence further exposure to predation risk. The optimal attentional capacity is the capacity level  $a$  that maximizes fitness subject to these conflicting factors. Thus, although high attentional capacity increases the probability of detecting predators, it may not match the predation cost associated with the extra feeding duration necessary to maintain a larger volume of brain tissue. The extra feeding may replace a portion of either resting or vigilance time, with the latter possibly requiring adopting a broader attentional focus (compare low regions in Figure 2A,B).

The model predicts a relatively narrow focus of attention under a wide range of reserve levels and values of attentional capacities (Figure 3). This prediction seems to agree with the design of various sensory systems, in which a small portion of the sensory field extracts high-quality information from the environment while the rest of the sensory field has much decreased acuity. That design may require sequential allocation of the high-sensitivity area throughout the whole sensory field in order to analyze complex objects and detect cryptic items. This is similar to the sequential allocation of focused attention to one sector angle at a time in our model. The most familiar example for such cognitive design is in the eye of many species. For example, in humans, only the fovea, which covers about 0.01% of the retinal area and 1.7 degrees of the visual field, receives and transmits very high quality of visual information. Overall, the information from the fovea and its

immediate surroundings covering the central 10 degrees (2%) of the visual field is processed by more than 50% of the primary visual cortex (also called V1 and striate cortex) and probably even larger proportions of higher visual areas such as V4 and MT (Azzopardi and Cowey, 1993; Van Essen and Anderson, 1995; Wandell, 1995). That is, the eye and especially the brain depict a strong bias in the amount of neuronal investment per unit of sensory area. A similar bias is also found in the auditory and somatosensory systems (Catania and Kaas, 1997; Kandel et al., 1995: 329; Knudsen et al., 1987; Koppl et al., 1993; Schuller and Pollak, 1979).

Although our discussion indicates that there is some optimal allocation of limited resources within sensory systems, it does not reveal the location of the information bottleneck. For example, is visual acuity limited owing to a constraint on fovea size or a limit on the volume of the visual cortex? At least in primates, neither the eyes nor the optic nerve is the limiting factor because the amount of visual information attended to at any given time is approximately 0.02% of the information received by the eyes and 1% of the information transmitted by the optic nerve (Van Essen and Anderson, 1995; Van Essen et al., 1991, 1992). It is striking that the primate brain can process only such a tiny fraction of the available visual information at any given time, even though approximately 60% of the entire primate neocortex is devoted to vision (Barton, 1998; Van Essen et al., 1992).

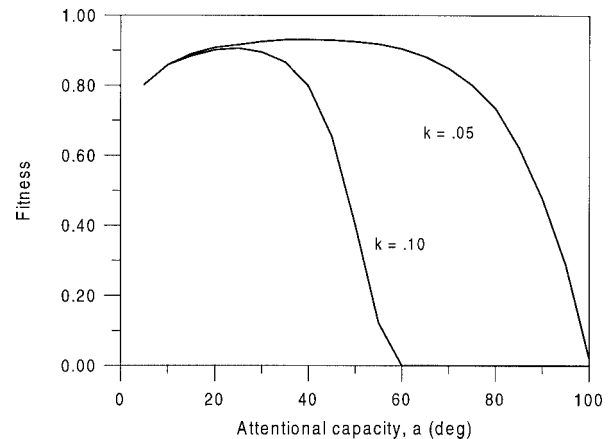
### Relationship to other models

Our model is similar to existing behavioral models in predicting that the balance between foraging and antipredator activity would depend on the forager's state of energy reserves, with more time devoted to foraging and less time spent on vigilance when reserves are dangerously low (see Clark and Mangel, 2000; Lima, 1998; McNamara and Houston, 1990). Explicitly, in our model, when reserve levels are below a threshold value, the forager widens the area scanned per unit time and thus decreases the total time devoted to vigilance (Figure 2, low region). Our model, however, goes a step further than previous predator vigilance models by explicitly evaluating optimal attentional parameters.

In the hypothetical case of unlimited attention, the forager can scan the whole visual field at the same time with the maximally feasible probability of detection. Limited attention, however, implies that an increase in the visual angle attended to at any given time results in decreased detection probability (Figure 1A). Our analysis of the optimal focus of attention is similar to an earlier examination of optimal search rate (Gendron and Staddon, 1983), with search rate redefined as the area attended to per unit time (see Dukas, 1998). Either approach predicts a narrow attentional focus, resulting in low search rate while searching for cryptic objects.

### Other currencies, constraints, and behavioral strategies

In our model, we assumed that energy is the limiting factor and ignored other resources. However, research on physiological tradeoffs is inconclusive about the role of energy expenditure in determining observed physiological capacities and life history traits (Diamond, 1996; Reznick et al., 2000; Rose and Bradley, 1998). It is possible that the correlation between the net rate of energy gain and fitness may vary depending on the species, biological system, and time. An algorithm that includes rates of energy gain and mortality (see Clark, 1993; Clark and Mangel, 2000; Gilliam, 1990) may provide fair general approximation to fitness, but that algorithm may require modification once specific details on limiting factors are revealed.



**Figure 4**

Fitness  $F(x_1, 1)$  ( $x_1 = 100$  g) as a function of the attentional capacity,  $a$ , for two degrees of nonlinearity in metabolic cost. For  $k = 0.5$  (weakly nonlinear cost), the fitness function is relatively flat, with a peak at  $a = 40$  degrees. For  $k = 10$  (stronger nonlinearity), fitness peaks at  $a = 24$  degrees and drops sharply for larger values of  $a$ .

Exactly as we are uncertain about the most relevant currency to employ in the formal model, we have not addressed all feasible constraints that may affect limited cognitive abilities in general and attentional capacity in particular. For instance, the length of embryonic development may limit size and complexity of brain parts. Although the benefit from increased volume of brain components may select for increased developmental time, other factors such as season length or selection on early reproduction may counter such selection pressure.

Finally, for mathematical convenience, we assumed that the forager always scans the whole visual angle for predators. An alternative strategy in cases of limited vigilance time is to focus attention only on parts of the visual field; these parts may be chosen either randomly or based on experience with the directions from which predators are most likely to approach. The latter strategy is merely a modification of the model by Dukas and Ellner (1993), in which foragers optimally allocate limited attention to a selected set of food types based on their quality and conspicuousness. Applied to predator vigilance, this model implies devoting more attention to dangerous angles, ignoring or devoting a wide focus of attention to safe angles.

### Evaluating the model

A basic assumption of the model concerns the relative cost of brain tissue. Although some information indicating the high cost of brain exists (see Hawkins, 1985), we need critical empirical information, which may be gathered by genetic or experience-dependent manipulation of the size of brain parts (Dukas, 1999). One tractable model system for measuring physiological costs of brain tissue is *Drosophila*, in which manipulation of brain volume has already been performed (Barth and Heisenberg, 1997; Heisenberg, 1997; Heisenberg et al., 1995). Another assumption is about a nonlinear increase in cost with increased capacity. This assumption is based on data that indicate that an increase in brain volume is associated with a higher ratio of neuronal connections to neuronal cells and, consequently, a decelerating increase in computational power with volume (Allman, 1999; Deacon, 1990; Thorpe and Thorpe, 2001; Zhang and Sejnowski, 2000). This assumption may be tested with comparative data. For

example, existing comparative information on the volume of brain parts processing vision in birds and mammals (Barton, 1998; Brooke et al., 1999; Joffe and Dunbar, 1997) may be augmented with data on visual ability in such species.

On the behavioral side, much is known about antipredator vigilance (Lima, 1998; Lima and Dill, 1990); yet, explicit data on the focus of attention is scarce. Most birds possess limited ability to move the eyes independently of the head, so head direction can be taken as an approximation for the direction of attention. The scan angle, or the focus of attention, may be inferred either from an analysis of subsequent head fixations, or from the rate of head movement while scanning. Some behavioral data in agreement with our model already exists, but it would need to be augmented with explicit information on head direction. For example, blackbirds spent longer time scanning the environment for predators while feeding on conspicuous than cryptic food (Lawrence, 1985). How did the blackbirds use the extra vigilance time? Did they reduce scan angle under the better feeding conditions as the model predicts (Figure 2, middle versus low regions)?

In summary, our analysis indicates that limited attentional capacity and successive allocation of focused attention may constitute an optimal strategy that balances the need to process large information flows with the economic costs of building and maintaining brain tissue.

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