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# INFORMATION PROCESSING AND PREY DETECTION[1]

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*Abstract.* We present a model to examine how foragers should divide attention among different potential prey types in order to maximize their net rate of energy intake. We define attention as the brain's capacity to process information simultaneously. Our model is based on neuropsychological studies suggesting first, that predators who divide attention among an increasing number of different prey types decrease their ability to detect any given type, and second, that this decrease is larger when prey items are more difficult to detect. Our model also incorporates the effects of search rate on foragers' probability to detect prey. The model predicts that foragers encountering cryptic prey should devote all attention to a single prey type. When encountering conspicuous prey, foragers should divide attention among the different prey types. For prey types that differ in conspicuousness but are equal in energy content, handling time, and density, foragers should give more attention to the more conspicuous prey if the conspicuousness values of all prey types are relatively small. However, when all prey are more conspicuous, foragers should devote more attention to the less conspicuous prey type. We suggest that our model may serve to explain and predict some of the foraging decisions of animals searching for cryptic or conspicuous prey, and especially studies on "search image" formation.

*Key words: divided attention; energy; foraging; information processing; maximizing energy intake; prey detection; search patterns.*

## INTRODUCTION

Psychological studies of humans and other animals demonstrate that the brain has a limited capacity for the amount of information it can process simultaneously. This capacity is usually associated with **attention** (Kahneman 1973, Schneider and Shiffrin 1977, Navon and Gopher 1979, Wickens 1984, Roitblat 1987, Posner and Peterson 1990, Eysenck and Keane 1990). Limited attention means that animals can process efficiently only a certain amount of information at one time. For example, foragers devoting more attention to predators devote less attention to prey and are less efficient at detecting prey, and vice versa (Lawrence 1985, Metcalfe et al. 1987, Milinski 1989).

The studies on attention suggest two important predictions about the performance of predators searching for prey. First, predators that divide their attention among an increasing number of different prey types would decrease their ability to detect any given prey type. Second, this decrease in detection ability would be larger when the different prey items are more difficult to detect. It seems, therefore, that in addition to

other decisions foragers must make (reviewed in Stephens and Krebs 1986, Kamil et al. 1987), foragers may have to decide how to divide their attention among different types of prey. Here we present a model that examines how foragers should divide their attention among different potential prey types in order to maximize their net rate of energy intake. The model predicts (a) how many prey types a forager should try to detect, and (b) how the forager should divide its attention among these prey types.

The problem of prey detection is faced by many kinds of foragers, including, for example birds, fish, and snakes searching for cryptic prey (Tinbergen 1960, Dawkins 1971, Pietrewicz and Kamil 1981, Guilford and Dawkins 1987, Metcalfe et al. 1987, Melcer and Chiszar 1989, Milinski 1989), predators searching for bird nests (Martin 1988*a*, *b*), egg-laying butterflies searching for host plants (Rausher 1978, Stanton 1983, Papaj and Prokopy 1989), and bees foraging for flowers (Dukas and Real, *in press*). Consequently, our model may help in explaining and predicting many of the foraging decisions animals make.

## THE MODEL

### *Searching for prey*

Our model is based on Gendron and Staddon's (1983) extension of the basic optimal diet model (Stephens and Krebs 1986:Chapter 2). In the basic model, the

forager is assumed to search for randomly distributed prey, and its net rate of energy gain is

$$R = \frac{\sum_{i=1}^{m} \lambda_i e_i}{1 + \sum_{i=1}^{m} \lambda_i h_i}, \qquad (1)$$

where $\lambda_i$ is the rate at which prey of type $i$ are captured (no. prey per unit of time); $e_i$ is the net energy gain from a type $i$ prey item; and $h_i$ is the handling time for a type $i$ prey item. Eq. 1 incorporates the "zero–one" rule, i.e., prey of a given type should either be consumed whenever encountered, or never consumed. The sums in Eq. 1 thus include only those prey types that are consumed.

Gendron and Staddon (1983) extended this model to include the effects of search rate $S$, defined as the area searched per unit time. First, the energy cost of searching is explicitly accounted for, assuming that the cost is a linear function of the search rate: search cost (energy per unit time) $= f + bS$, where $f$ and $b$ are species-specific positive constants. Second, the capture rate of type $i$ prey is expressed as

$$\lambda_i = SD_i P_{d,i}, \qquad (2)$$

where $D_i$ is the density (prey/area) of type $i$ prey, and $P_{d,i}$ is the probability of detecting a prey item of type $i$ that has been encountered. Here "encounter" refers to physical proximity, e.g., a prey item is "encountered" when it comes within the visual range of the predator. More prey items will be "encountered" when the predator uses a higher search rate, but these items must also be "detected" by the predator before they can be captured and consumed. Gendron and Staddon (1983, 1984) showed that $P_d$ is inversely related to the forager's search rate. With these extensions, net rate of energy gain becomes

$$R = \frac{S \sum_{i=1}^{m} D_i P_{d,i} e_i - (f + bS)}{1 + S \sum_{i=1}^{m} D_i P_{d,i} h_i}. \qquad (3)$$

As before, $e_i$ is the net energy gain from prey type $i$, which includes the energy cost of handling, $fh_i$. Eq. 3 is the basis for our model. To complete the model, we now specify how $P_{d,i}$ depends on prey conspicuousness and on the forager's search rate and allocation of attention.

*Attention, search rate, and prey detection*

The probability of detecting an encountered prey item $(P_d)$ is, by definition, directly related to the conspicuousness of this prey type. We define conspicuousness as the degree of dissimilarity between the prey and its surrounding background. This may be either the physical background, or other less preferred prey types.

In addition, we assume that $P_d$ is related to the amount of attention devoted to that particular prey type. At least two studies strongly suggest a nonlinear relation between $P_d$ and attention. Lindsey et al. (1968) found a nonlinear decrease in the detection ability of human subjects attending to an increasing number of stimuli. Dukas and Real (*in press*) found a similar nonlinear decrease in bumble bees' ability to detect rewarding flowers among nonrewarding ones when bumble bees attended to either one, two, or three rewarding floral types. Note that the above studies did not directly measure the relationship between $P_d$ and attention and this remains to be empirically determined. In addition, Gendron and Staddon (1984) found a nonlinear relation between $P_d$ and search rate.

Our equation for the relation between $P_d$ and attention is based on the assumption that increasing attention or decreasing search rate should have quantitatively similar effects on $P_d$ (Lindsey et al. 1968). Based on Gendron and Staddon (1984), we therefore expect that for a cryptic prey and very low search rate, $P_d$ remains low for small values of attention, but approaches one for the maximum level of attention. We assume that even cryptic prey can be found with maximum attention and unlimited time; therefore, $P_d$ reaches 1 with maximum attention even for cryptic prey. For conspicuous prey and very low search rate, $P_d$ increases rapidly with relatively small amount of attention, and asymptotically approaches 1 (Fig. 1A). For the model, we chose a simple mathematical expression having these properties,

$$P_{d,i} \propto a_i^{1/k_i}, \qquad (4)$$

where $a_i$ is the fraction of the predator's attention devoted to prey type $i$ ($0 \le a_i \le 1$, $\Sigma a_i \le 1$), and $k_i$ is the conspicuousness index of prey type $i$, $k > 0$. (The meaning of Eq. 4 is that with all factors except $a$ and $k$ held constant, $P_d$ is proportional to $a^{1/k}$.) A larger value of $k$ means more conspicuous prey, and therefore, a higher probability of detection at any given attention level. Prey type $i$ is cryptic in the qualitative sense described above if $k_i < 1$ in Eq. 4, and it is conspicuous if $k_i > 1$ (Fig. 1A). Note that we assume that foragers have complete knowledge about the appearance of the different prey types, and that prey types are different in all attributes of appearance. We do not consider explicitly the case of preferred prey types sharing one or more attributes, such as color. However, in such cases foragers may be able to attend to all types as if they were a single type, by attending to the shared attribute. Also, we do not consider here the possibility that qualitative differences within and between categories of attributes have different effects on the foragers. For example, foragers may search more easily for one color and one shape, than for two colors, or vice versa.

To model the effects of search rate on prey detection, we essentially follow Gendron and Staddon (1983).
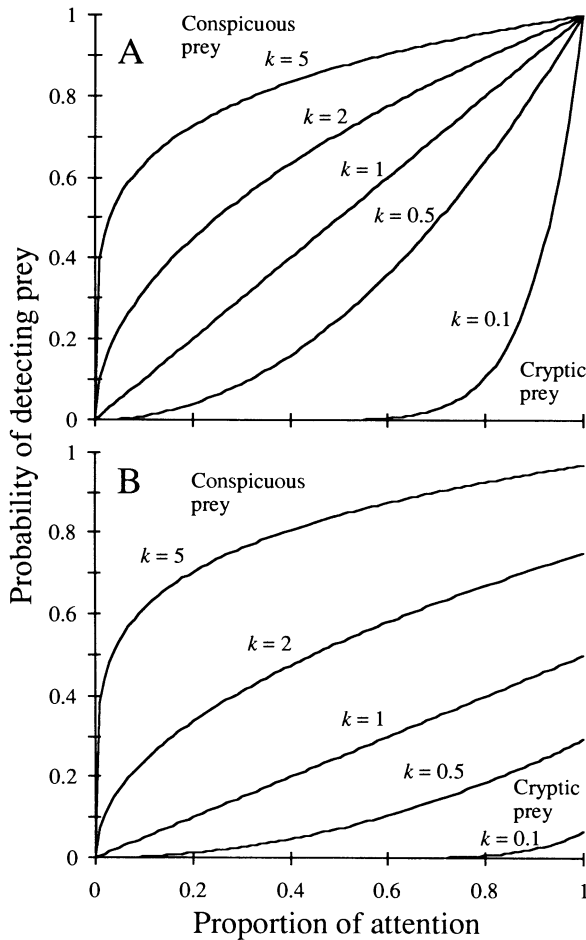
FIG. 1. (A) The probability of detecting an encountered prey item as a function of attention only (Eq. 4). Each curve represents prey with different conspicuousness ($k$). (B) The probability of detecting an encountered prey item as a function of attention (Eq. 6) with $(S/M) = 0.5$, i.e., search rate is half of the maximum possible search rate. Each curve represents prey with different conspicuousness ($k$).

Gendron and Staddon's (1984) experimental study with human subjects supports the hypothesis that the probability of detecting a cryptic prey increases nonlinearly as the search rate decreases. To describe their graphical model, Gendron and Staddon (1983, 1984) used the functional form

$$P_{d,i} = [1 - (S/M)^{k_i}]^{1/k_i}.$$

$M$ represents the maximum possible search rate, at which the predator cannot detect any prey regardless of how conspicuous they are. We are not specifically concerned with the effects of search rate, but based on Gendron and Staddon's work and other studies (Anderson 1981, O'Brien et al. 1990, Getty and Pulliam 1991, 1993) we know that search rate is an important component of a forager's strategy for dealing with prey. We therefore chose to include search rate in our model

for the probability of detection, using a simpler functional form that has the same qualitative behavior:

$$P_{d,i} \propto 1 - (S/M)^{k_i}. \tag{5}$$

Numerical solutions for a range of parameter values indicate that the change in functional form does not alter any of the qualitative predictions from our model. This equation, like Gendron and Staddon's, has the qualitative properties of decreasing from 1 at $S = 0$, to 0 at $S = M$. For conspicuous prey (large values of $k_i$), the detection probability remains high until the search rate is near the maximum. For cryptic prey (small values of $k_i$), the detection probability decreases rapidly when search rate increases from near 0.

To model the joint effects of search rate and attention on the probability of detecting prey, we simply use the product of Eq. 4 and Eq. 5:

$$P_{d,i} = (1 - (S/M)^{k_i})a_i^{1/k_i}. \tag{6}$$

For a given search rate, $P_d$ increases as a function of attention, and has higher values for more conspicuous prey (Fig. 1B). By using the multiplicative model, Eq. 6, we are assuming that there is no interaction between search rate and attention, and that the total amount of attention devoted for foraging is constant regardless of the search rate. Substituting Eq. 6 into Eq. 3 gives our model's expression for net energy gain,

$$R = \frac{S \sum_{i=1}^{m} D_i[1 - (S/M)^{k_i}]a_i^{1/k_i}e_i - (f + bS)}{1 + S \sum_{i=1}^{m} D_i[1 - (S/M)^{k_i}]a_i^{1/k_i}h_i}. \tag{7}$$

Any prey type with $a_i = 0$ is not consumed, so we allow the sums in Eq. 7 to run over all potential prey types in the environment. The forager's diet then consists of those prey types for which $a_i > 0$.

## RESULTS

We assume that foragers will choose their search rate ($S$), and the fraction of attention devoted to each prey type ($a_i$) in order to maximize their net rate of energy intake $R$, given by Eq. 7. We also assume that foragers have a complete knowledge about the appearance of the different prey types and that it is easy to manipulate prey after detection. Prey manipulation is discussed by Hughes (1979), McNair (1981), Waser (1986), Lewis (1986), and Croy and Hughes (1991).

We present the results for the optimal allocation of attention only, because optimal search rate has already been discussed elsewhere (Gendron and Staddon 1983, 1984). Allowing the forager to choose the optimal search rate does not directly affect either the optimal number of prey types or the optimal allocation of attention. However, it makes our model more realistic because it allows foragers to adjust search rate as a function of prey conspicuousness; for example, foragers can decrease search rate when prey becomes more cryptic.

This has an indirect effect on the optimal allocation of attention, because changes in search rate affect the relative detectability of prey types at any given levels of attention (Eq. 6).

In addition to the analytical solutions, we also examined numerical examples of the model. In the numerical examples, the parameter values for energy expenditure and prey are for Northern Bobwhite quails foraging for pellets composed of flour and lard (Gendron and Staddon 1983, Gendron 1986). For our analytical results, we assume that either $h_i/e_i$ is the same for all prey types, or else that the handling times $h_i$ are negligibly small. "Small" here means that the forager spends most of its time looking for prey, and relatively little time handling prey that it has captured. In terms of our model, the technical assumption is that

$$S \sum_{i=1}^{m} D_i P_{d,i} h_i \ll 1$$

in the denominator of Eq. 3. The detection probabilities $P_{d,i}$ and the parameter combination $SD_i h_i$ are both dimensionless, so whether or not this assumption is satisfied is independent of the units used (e.g., whether handling times are measured in seconds or hours).

### Prey types with identical parameter values

First, we consider the simplest case, in which all prey types have the same parameter values ($k$, $D$, $e$, and $h$). Thus each prey type has a distinct appearance from the other prey types, but all types are equally difficult to detect, equally abundant, and equally rewarding if captured. It can be shown (Appendix 1) that when all potential prey types are equally cryptic ($k_i < 1$), the optimal diet consists of a single prey type only, and when all potential prey types are equally conspicuous ($k_i > 1$), the optimal diet consists of all prey types.

Using Eq. 7, we compared the net rate of energy intake of a forager using the optimal allocation of attention and two possible alternative allocations of attention. When all three prey types are cryptic ($k = 0.5$), the forager's net rate of energy intake is either two or three times higher when attending to only one prey type than to either two or three prey types, respectively (Fig. 2A, B). When all three prey types are relatively conspicuous ($k = 2.0$), the forager's net rate of energy intake is higher when attending to all three prey types compared to either only one or two prey types (Fig. 2A, C).

### Prey types with different conspicuousness

Here we consider another case, where all prey types have the same energy content, handling time, and density; however, the prey types differ in their conspicuousness. When all prey types are cryptic ($k_i < 1$), the optimal strategy is to attend only to the prey types with the highest $k$ value (Appendix 1; Fig. 3, example a). When all prey types are conspicuous ($k_i > 1$), the op-
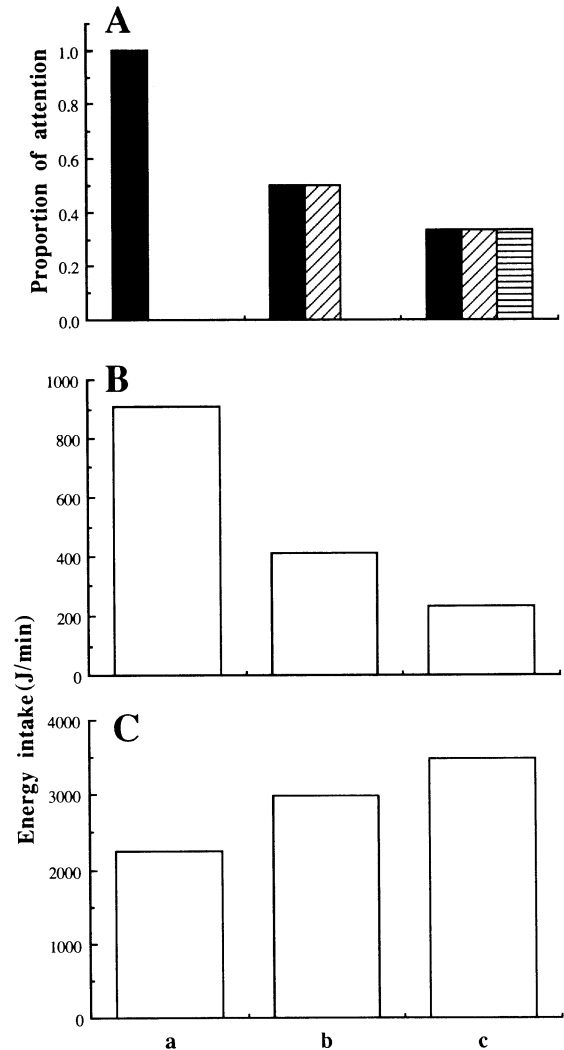


FIG. 2. (A) Three alternatives (a, b, c) for the proportion of attention given to prey types 1 (■), 2 (▨), 3 (▤). (B) The resulting net rate of energy intake obtained for each of the three alternatives when all three prey types are equally cryptic ($k = 0.5$). (C) The resulting net rate of energy intake obtained for each of the three alternatives when all three prey types are equally conspicuous ($k = 2.0$). All three prey types have the same net energy content of 125.52 J/prey, the same density of 4 prey/m², and handling time of 0.01 min/prey. The values of the constants for energy expenditure are $f = 20$, and $b = 1.6$.

timal strategy is to devote attention to all prey types. However, there is a distinct change in the optimal allocation of attention as prey become increasingly more conspicuous (Appendix 2; Figs. 3 and 4A). When all prey types have small conspicuous values (for example $1 < k_i < 2$), the optimal strategy is to allocate attention to all prey types, with more attention given to prey with higher $k$ values (Fig. 3, examples b and c). In other words, the forager should devote more attention to the *most* conspicuous prey types. However, when prey types become more conspicuous ($k_i \gg 1$), the optimal strat-
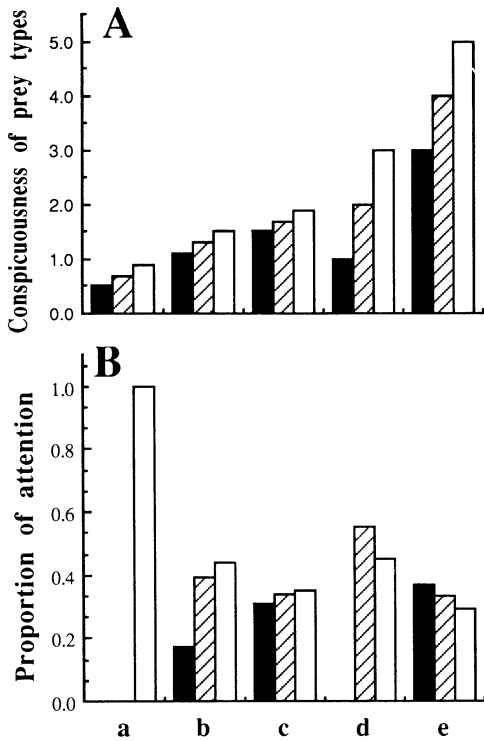
FIG. 3. (A) Five examples for the conspicuousness of prey types 1 (■), 2 (▨), 3 (□). (B) The optimal proportion of attention given to each of the three prey types for each of the five examples. See legend of Fig. 2 for other prey parameters.

egy is to allocate more attention to the *less* conspicuous prey types (Fig. 3, example e, Fig. 4A).

Another case is where foragers encounter a mixture of cryptic and conspicuous prey types. In this case, the optimal strategy is to attend to all conspicuous types $(k_i > 1)$, and to at most one of the cryptic types (Fig. 3, example d, Fig. 4A). The relative allocation of at-

tention to these types is discussed in Appendix 1 (see Eqs. A.4 and A.5).

### Prey types with different energy content or density

Here all prey types have the same conspicuousness index and handling time, but they differ in their energy content or density. When $k_i$ are below one, the optimal strategy is to attend only to the prey with the highest product $D_i e_i$ (Fig. 5, example a; Appendix 1). For conspicuous prey $(k_i > 1)$, the optimal strategy (Appendix 1) is to allocate attention to all prey types with

$$a_i/a_j = (D_i e_i/D_j e_j)^{k/(k-1)}. \tag{8}$$

Since $\Sigma a_i = 1$, the optimal attention given to prey type $i$ is

$$a_i = \frac{(D_i e_i)^{k/(k-1)}}{\displaystyle\sum_{j=1}^{m} (D_j e_j)^{k/(k-1)}}. \tag{9}$$

More attention is given to the prey with the higher product $D_i e_i$ (Fig. 4B).

For $k$ near 1, attention is disproportionately concentrated on the more rewarding prey types. Examples b–e in Fig. 5 illustrate that small differences in energy content produce relatively large differences in attention for $k = 2$. In examples b and e, the optimal attentions for the least rewarding prey type are only 2.4% and 0.5%, respectively; it is technically in the diet, but effectively the forager would be ignoring it. As $k$ decreases towards 1 in Eq. 9, the fraction of attention devoted to the prey type with the highest value of $D_i e_i$ goes to 1, and the attention devoted to all other prey types goes to 0. Fig. 6 shows how this occurs in an example with two prey types. Thus, while the number of prey types in the optimal diet changes at $k = 1$ (all prey types for $k > 1$, but only one prey type for $k <$



FIG. 4. (A) An example for the optimal allocation of attention for two prey types with different conspicuousness. Prey type 1 is fairly conspicuous ($k = 2$), and the conspicuousness of prey type 2 varies from 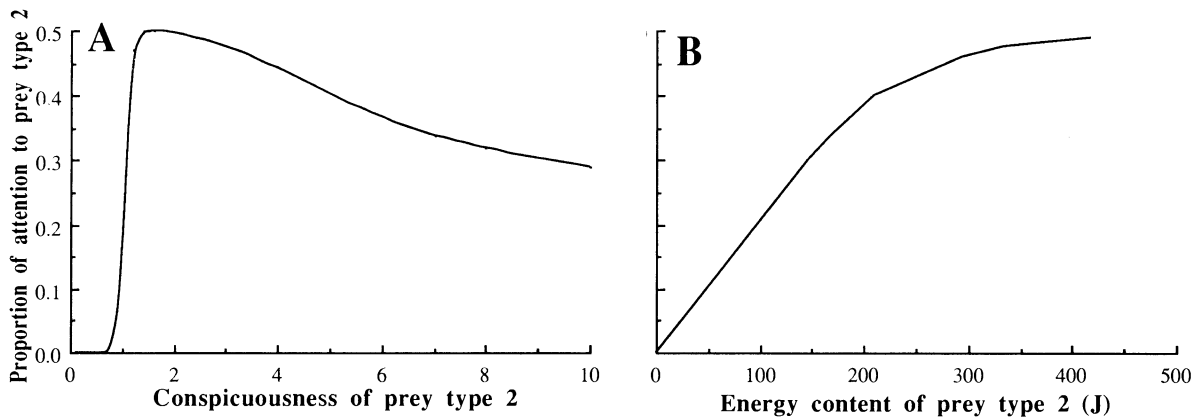very cryptic to very conspicuous. (B) An example for the optimal allocation of attention for two prey types with different caloric content. Both prey types are fairly conspicuous ($k = 2$). Prey type 1 has energy content of $e = 125.52$ J/prey, and the energy content of prey type 2 varies. See legend of Fig. 2 for other prey parameters.
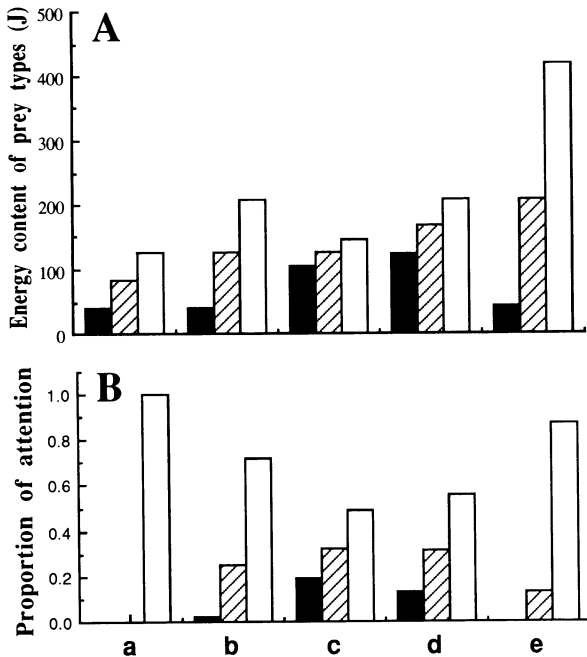
FIG. 5. (A) Five examples for the energy content of prey types 1 (■), 2 (▨), 3 (□). (B) The optimal proportion of attention given to each of the three prey types for each of the five examples. In example a, all three prey types have the same conspicuousness, $k = 0.5$; in the other four examples, all three prey types have the same conspicuousness, $k = 2$. See legend of Fig. 2 for other prey parameters.

1), the amount of attention devoted to each prey type is a continuous function of $k$, without any jumps, over the entire range of possible $k$ values ($k > 0$). In Appendix 2 we show that this conclusion remains true for prey types with unequal values of $k_i$.

## DISCUSSION

### The optimal allocation of attention

Our model predicts that a predator encountering several cryptic prey types should devote all of its attention to a single type in order to maximize its net rate of energy intake (Fig. 2A, B). This prediction is based on the relation between the probability of detecting prey ($P_d$) and attention, with no further assumptions about controversial concepts such as "search image" (Tinbergen 1960, Dawkins 1971, Lawrence and Allen 1983, Guilford and Dawkins 1987, 1989a, b). The model also predicts that when prey are conspicuous, a predator should divide its attention among several prey types (Fig. 2A, C). In this case, the division of attention among several prey types does not reduce by much the probability of detecting prey of each type. At the same time, the effective density of prey items increases, because the predator attends to more prey per unit area. Another interesting prediction of the model is that a predator feeding on a less conspicuous prey type and

a very conspicuous one should devote more attention to the less conspicuous prey (Figs. 3 and 4A). The reason for this is that the marginal increase in $P_d$ with increasing attention is higher for the less conspicuous prey than for the more conspicuous one.

Our model does not contradict previous discussions of "search image," which usually mention problems of selective attention to prey (Lawrence and Allen 1983). However, our approach to the problem of prey detection is based on clear psychological (e.g., Kahneman 1973, Wickens 1984) and neurological evidence (Spitzer et al. 1988, Corbetta et al. 1990, Posner and Peterson 1990), and our assumption about the relation between attention and prey detection can easily be tested empirically as we describe below. Following Gendron and Staddon (1983, 1984), we also included the effect of search rate on the probability of detecting prey. Recently, search rate was suggested as an alternative explanation for all previous studies that attempted to demonstrate "search image" (Guilford and Dawkins 1987, 1989a, b). Based on the neuropsychological studies cited above, we believe a model such as ours, that integrates both attention and search rate, can serve to predict and explain many of the foraging decisions of animals searching for cryptic or conspicuous prey.

Another prediction of our model is that foragers searching for cryptic prey should switch to an alternative prey type when its density increases above a threshold value. This is in contrast to the standard optimal diet model which predicts no change in diet when the density of nonconsumed prey types increases (Stephens and Krebs 1986). Similar predictions, of predators switching to an alternative prey when the density of this prey increases, were made by Hughes (1979), McNair (1981), and Staddon and Gendron
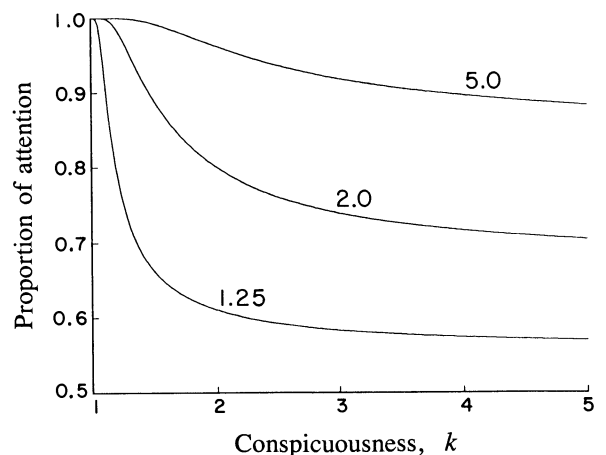


FIG. 6. Optimal allocations of attention as prey conspicuousness ($k$) decreases towards 1 for two prey types with equal conspicuousness (Eq. 9). The graph shows the fraction of attention given to prey type 1 when $D_1e_1 > D_2e_2$, for different values of the ratio $D_1e_1/D_2e_2$, where $D$ is prey density and $e$ is the net energy gain from prey.

(1983). In Hughes' (1979) and McNair's (1981) models, learning to recognize or handle prey was a function of prey density, so higher density of a certain prey type increased its actual ranking. Higher prey density in the model of Staddon and Gendron (1983) caused the predator to decrease its mistaken attempts to attack prey, and therefore increased its probability of prey capture.

In our model, we assumed that foragers have a perfect knowledge about the appearance of the several prey types in their diet. However, it may be that detecting one prey type interferes with the memory about the appearance of another prey type. This is a problem of memory constraint (Lewis 1986, Waser 1986), that may become more severe when prey become relatively more difficult to detect (Staddon 1983). Stanton (1983) found that egg-laying female *Colias* butterflies made more mistaken landings on nonhost plants after they had foraged for nectar on flowers. This suggests that in these butterflies, searching for flowers interferes with the memory for host plants. Fortunately, it is possible to separate experimentally possible effects of memory interference from the effects of division of attention. For example, subjects may be trained and later tested for their ability to detect a single familiar prey type in the morning, and another familiar prey type in the afternoon. Here subjects devote all attention to one prey type at a time on a predicted schedule. A reduction in the probability of detecting each prey type at the beginning of each period will suggest memory interference.

### The relation between attention and prey detection

We assumed a nonlinear relation between attention and prey detection, that is concave for cryptic prey and convex for conspicuous prey. We based this assumption on the experiment on search rate by Gendron and Staddon (1984). However, the exact relation between attention and prey detection can be estimated more directly. For example, subjects may be tested for their ability to detect visually items of a single "prey" type while simultaneously attending to a listening task. The proportion of attention allocated to each of the two tasks can be manipulated by changing the relative payoff associated with a correct response to each task (Norman and Bobrow 1975, Navon and Gopher 1979, Sperling 1984). Therefore, one can construct a graph of the probability of detecting a single prey for different levels of attention and for prey types of different conspicuousness.

Similar experiments may be conducted with animals whose attention is divided between prey capture and predator avoidance. For example, Metcalfe et al. (1987) found that salmon (*Salmo salar*) made more mistaken attacks on inedible food pellets under higher predation risk. They suggested that fish devoted less attention to prey when predation risk increased (see also Lawrence 1985, Milinski 1989). Note, however, that looking in the direction of food may restrict the ability of the forager to watch for predators. This is at least in part a problem of physical reception of stimuli, and not only a problem of attention.

### Ways of testing the model

A basic prediction of the model is that foragers encountering several equally rewarding food types should (a) search for a single type if food types are cryptic, and (b) search for all types if food types are conspicuous. This prediction can be tested with a variety of species, using two differently colored food types. The same food types will be cryptic when put on a similarly colored background, and conspicuous when put on contrasting background. For example, green and orange food types may be (a) cryptic on background made of patches of green and orange, and (b) conspicuous when put on background made of patches of blue and red (see Dawkins 1971). The relative conspicuousness of each food type must be quantified in a preliminary experiment. This can be done by allowing a forager to search for food items of a single type and monitoring the proportion of items detected at a given time. Alternatively, the proportion of correct pecks at food items vs. incorrect ones may be recorded.

In each of the two experimental conditions (cryptic or conspicuous food types), one forager at a time will encounter equal numbers of each of the two food types. First, foragers will learn to recognize the food types and increase their probability of detecting food items (or proportion of correct pecks). Only after foragers reach asymptotic performance in detecting food items, will the proportion of items of each type that are consumed be monitored. Foragers are expected to consume only a single food type when the two types are cryptic, and both food types when they are conspicuous. Variations of this experiment may be used to test other predictions of our model.

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# APPENDIX 1

Here we derive the analytic results stated in the text. Without loss of generality, we choose units for search rate so that the maximum search rate, $M$, is equal to 1. Suppose that the search rate $S$ is given, but attentions $a_i$ may vary. Then if the handling times $h_i$ are small (as we assume in the text), or if $h_i/e_i$ is the same for all prey types $i$, then maximization of $R$ as a function of the $a_i$ is equivalent to maximizing

$$r = \sum_{i=1}^{m} D_i P_{d,i} e_i. \tag{A.1}$$

As $h_i \downarrow 0$ the denominator in $R$ becomes constant, and $r$ is the only term in the numerator that depends on the $a_i$; whereas if $h_i/e_i \equiv C$ for all $i$, then $R = (Sr - f - bS)/(1 + CSr)$ which is an increasing function of $r$. From here on, we assume there-

fore that the optimal $a_i$ maximize $r$ conditional on the value of $S$.

Consider any two prey types $i$ and $j$ ($i \neq j$) with $a_i + a_j = \alpha > 0$, $1 \leq i, j \leq m$. The contribution to $r$ from these prey types is

$$g(a_i) = D_i e_i (1 - S^{k_i}) a_i^{1-k_i} + D_j e_j (1 - S^{k_j})(\alpha - a_i)^{1-k_j}. \quad \text{(A.2)}$$

Differentiating,

$$g'(a_i) = (D_i e_i / k_i)(1 - S^{k_i}) a_i^{1-k_i-1}$$
$$- (D_j e_j / k_j)(1 - S^{k_j})(\alpha - a_i)^{1-k_j-1}. \quad \text{(A.3)}$$

If both prey types are conspicuous ($k > 1$), then $g'(a_1)$ approaches $+\infty$ as $a_1 \to 0$ and $-\infty$ as $a_1 \to \alpha$; hence both $a_1$ and $a_2$ must be in the optimal diet. If both prey types are cryptic ($k < 1$), then differentiating Eq. A3 shows that $g'' < 0$; hence $g$ is maximized either at $a_i = 0$ or at $a_i = \alpha$, and a diet containing both $a_i$ and $a_j$ cannot be optimal.

These conclusions hold at any potentially optimal search rate ($0 < S < 1$), so we can conclude that the optimal diet includes all conspicuous prey types and at most one cryptic prey type. If prey types $i$ and $j$ are both in the diet ($a_i, a_j > 0$), then setting Eq. A.3 equal to 0 gives the relative attention to each,

$$\frac{a_i^{(1-1/k_i)}}{a_j^{(1-1/k_j)}} = \frac{D_i e_i (1 - S^{k_i})/k_i}{D_j e_j (1 - S^{k_j})/k_j}. \quad \text{(A.4)}$$

Now we apply these to the cases considered in the text.

1. *Identical parameter values.*—If $k > 1$, Eq. A.4 gives $a_i = a_j$ for all $i$ and $j$, so attention is divided evenly among all $m$ prey types ($a_i \equiv 1/m$). If $k < 1$ any diet consisting of only one prey type is optimal ($a_i = 1$, $a_j = 0$ for $j \neq i$).

2. *Differences in conspicuousness only.*—If all prey are cryptic ($k_i < 1$) the optimal diet contains only one prey type. Since (in this special case) the values of $D_i$, $e_i$ and $h_i$ are the same for all prey types, clearly the least cryptic prey type should be chosen. If all $k_i > 1$, it follows from Eq. A.4 that

$$a_i = \{\lambda(1 - S^{k_i})/k_i\}^{k_i/(k_i-1)} \quad \text{(A.5)}$$

for some constant $\lambda$ determined by the constraint $\Sigma\, a_i = 1$. We cannot solve Eq. A.5 analytically, but an asymptotic analysis (Appendix 2) confirms our numerical result that most attention is given to the most conspicuous prey when all $k_i$ are just slightly $>1$, but to the least conspicuous prey when all $k_i$ are large.

3. *Different energy content or density.*—If $k > 1$ (where $k$ is the common value of $k_i$) all prey types are in the diet, and Eq. A.4 reduces to Eq. 8, which gives the optimal allocation of attention. If $k < 1$, again only one prey type is in the diet; if type $i$ is chosen, the value of $r$ is $r_i = S(1 - S^k)D_i e_i$, so the prey type with the highest value of $D_i e_i$ should be chosen and all other prey types ignored. Thus the forager's preference among cryptic prey depends on the density of all prey types, and can switch if nonpreferred prey become more abundant or preferred prey become less abundant.

## APPENDIX 2

Here we derive the asymptotic behavior of the optimal attentions $a_i$ for conspicuous prey as $k_i \to 1$ and $k_i \to +\infty$. The main results are Eq. A.14, A.16, and A.17, which give the approximate solutions. Prey types may differ in any of the parameters $\{D_i, e_i, k_i\}$, but as in the text we assume that handling times are all negligible relative to search times. The approximate solutions confirm that two numerical results described in the paper are general properties of the model: (1) when all $k_i$ are near 1, more attention is given to the most conspicuous prey, while for $k_i \gg 1$, more attention is given to the least conspicuous prey, all else being equal; (2) the optimal attentions $a_i$ change continuously at $k = 1$, despite the change in the number of prey items in the optimal diet, unless $D_i e_i$ is the same for all prey types.

Consider first $k_i \to 1$. Let $k_i = 1 + \epsilon\gamma_i$, with $\gamma_i > 0$ and $\epsilon$ decreasing to 0 from above, and prey types numbered so that $k_1 \leq k_2 \leq \ldots k_m$. Only $O(\epsilon)$ terms are used in our approximations and we tacitly omit higher order terms from equations. With handling times neglected, the net rate of energy gain is

$$R = \sum_{i=1}^{m} D_i e_i a_i^{1-k_i} S(1 - S^{k_i}) - (f + bS). \quad \text{(A.6)}$$

The optimal search rate $S$ satisfies $\partial R/\partial S = 0$, which can be written as

$$\sum_{i=1}^{m} (w_i/W)(1 - (k_i + 1)S^{k_i}) = b/W, \quad \text{(A.7)}$$

where $w_i = D_i e_i a_i^{1-k_i}$ and $W = \sum_{i=1}^{m} w_i$. Since the left-hand side of Eq. A.7 is a weighted average, the optimal $S$ must be between $S_1$ and $S_m$, where $1 - (k_i + 1)S_i^{k_i} = b/W$; that is, $S_i = \{(1 - b/W)/(k_i + 1)\}^{1/k_i}$. Thus as $\epsilon \to 0$ the optimal $S$ approaches $S_0 = (1 - B)/2$, where $B$ is the limiting value of $b/W$, and we can set $S = S_0 + \epsilon\sigma$ to first order in $\epsilon$ (i.e., we assume $S$ has this behavior in order to find solutions of this

form). If $B > 1$, the energy cost of search is so high that the optimal strategy as $k_i \to 1$ is to remain immobile rather than forage for prey, so we assume $B < 1$.

From Eq. A.4, the optimal attentions $a_i$ have the form

$$a_i = \{\lambda_i D_i e_i (1 - S^{k_i})/k_i\}^{k_i/(k_i-1)} \quad \text{(A.8)}$$

with $\lambda_i$ implicitly determined by the constraint $\Sigma\, a_i = 1$. Then standard Taylor expansions applied to $S^{k_i}$, and a good deal of algebra, give

$$a_i = \{\lambda_i D_i e_i (1 - \epsilon\beta_i)\}^{1+1/\gamma_i} \quad \text{(A.9)}$$

where

$$\beta_i = \gamma_i + \frac{4\sigma}{(1 - B^2)} + \frac{2\gamma_i \ln S_0}{1 + B}. \quad \text{(A.10)}$$

For fixed $x$ and $y > 0$,

$$(1 + \epsilon x)^{1/\epsilon y} = \exp\{x/y\}\left(1 - \epsilon\frac{x^2}{2y}\right), \quad \text{(A.11)}$$

to first order in $\epsilon$. Applying this to Eq. A.9 gives

$$a_i = \exp\{-\beta_i/\gamma_i\}\{\lambda_i D_i e_i\}^{1+1/\gamma_i}\left\{1 - \epsilon\left(\beta_i + \frac{\beta_i^2}{2\gamma_i}\right)\right\}. \quad \text{(A.12)}$$

We now need to distinguish two cases. First, suppose that $D_i e_i$ is the same for all prey types, but $k_i$ may differ. Then $D_i e_i$ can be absorbed into $\lambda_i$ in Eq. A.12. Letting $\epsilon \to 0$ and using Eq. A.11, the constraint $\Sigma a_i = 1$ therefore implies that $\lambda_i = 1 + \delta\epsilon$, where $\delta$ is the unique solution to $\sum_{i=1}^{m} \exp\{(\delta - \beta_i)/\gamma_i\} = 1$. The optimal attentions are then

$$a_i = \exp\{(\delta - \beta_i/\gamma_i\} + O(\epsilon). \quad \text{(A.13)}$$

Using the definitions of $\beta_i$ and $\gamma_i$, Eq. A.13 can be re-written as

$$a_i = \exp\left\{C - \frac{\lambda}{k_i - 1}\right\} + O(\epsilon), \quad \text{(A.14)}$$

where $C = -\dfrac{2}{1 + B}\left(\ln\dfrac{1 - B}{2} + \dfrac{1 + B}{2}\right)$ and $\lambda$ is a constant implicitly defined by the constraint $\Sigma\, a_i = 1$. $C$ is a positive for all possible values of $B(0 \le B \le 1)$, hence $\lambda$ must be positive to keep $a_i \le 1$. Consequently, $a_i$ is an increasing function of $k_i$ in this case, as we set out to show.

Second, suppose that $D_i e_i$ varies among prey types. Since $a_i = O(1)$ as $\epsilon \to 0$, Eq. A.12 implies that $\lambda_i D_i e_i$ can be no larger than $1 + O(\epsilon)$; and since $\Sigma\, a_i = 1$, there must be at least one prey type $j$ for which $\lambda_i D_j e_j = 1 + O(\epsilon)$. This prey type must have the largest value of $D_i e_i$ (or else some $a_i$ would grow without bound as $\epsilon \to 0$). Setting $\lambda = (1 + \epsilon\delta)/D_j e_j$, substituting into Eq. A.12, and using Eq. A.11, the optimal attentions are

$$a_i = \left(\frac{D_i e_i}{D_j e_j}\right)^{k_i/(k_i - 1)} \exp\{(\delta - \beta_i)/\gamma_i\}(1 - O(\epsilon)). \quad \text{(A.15)}$$

As the $k_i$ decrease to 1, the first term on the right-hand side of Eq. A.15 dominates, so attention becomes concentrated on the prey type(s) with the highest value of $D_i e_i$; for all other prey types the optimal attention goes to 0. Hence if there is a single prey type $j$ such that $D_j e_j > D_i e_i$ for all $i \ne j$, then $a_j$ must $\to 1$ and therefore $\delta = \beta_j$. Using this in Eq. A.15 and simplifying, the optimal attention for $i \ne j$ is given asymptotically by

$$a_i \sim \left(\frac{D_i e_i}{D_j e_j}\right)^{k_i/(k_i - 1)} \exp\left\{\left(1 + \frac{2 \ln S_0}{1 + B}\right)\left(\frac{k_j - k_i}{k_i - 1}\right)\right\} \quad \text{(A.16)}$$

with $B = b/D_j e_j$ in this case since $a_j \to 1$, and $S_0 = (1 - B)/2$.

If the variation in $D_i e_i$ is small but not zero (specifically $D_i e_i = F(1 + \epsilon f_i)$, $F > 0$), similar results can be obtained, also with the inclusion that more attention is given to more conspicuous prey.

Now we consider the case of $k_i \gg 1$. To obtain approximate solutions, we assume that each $k_i \to \infty$ such that $\rho_1 < k_i/k_j < \rho_2$ for fixed positive constants $\rho_1$ and $\rho_2$, and all $i, j$. Since $S_i^{k_i} \le 1/(1 + k_i)$, the optimal search rate $S$ satisfies $S^{k_i} \le 1/(1 + k_1)^{\rho_1}$; hence $S^{k_i} \to 0$ and $(1 - S^{k_i})^{k_i/(k_i - 1)} \to 1$. Therefore in the general solution Eq. A.8 we must have $(\lambda D_i e_i/k_i)^{k_i/(k_i - 1)} = O(1)$ as $k_i \to \infty$; hence

$$(\lambda D_i e_i/k_i)^{k_i/(k_i - 1)} = (\lambda D_i e_i/k_i)(\lambda D_i e_i/k_i)^{1/(k_i - 1)}$$

$$= (\lambda D_i/k_i)(1 + o(1)).$$

Substituting these in Eq. A.8 gives $a_i = (\lambda D_i e_i/k_i)(1 + o(1))$ as $k_i \to \infty$, which implies that

$$a_i \sim (D_i e_i/k_i) / \sum_{j=1}^{m} (D_j e_j/k_j). \quad \text{(A.17)}$$

Thus $a_i$ is a decreasing function of $k_i$ (more attention is given to the less conspicuous prey types) and an increasing function of $D_i e_i$.