Limited attention: the constraint underlying search image

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Recent models of predator search behavior integrate proximate neurobiological constraints with ultimate economic considerations. These models are based on two assumptions, which we have critically examined in experiments with blue jays searching for artificial prey images presented on a computer monitor. We found, first, that when jays had to switch between searching for two distinct prey types, they showed no reduction in detection rates compared to no-switching conditions, and second, that when jays divided attention between searching for two prey types at the same time, they had lower detection rates than when they focused attention on one prey type at a time. Our results suggest that limited attention strongly affects predator search patterns and diet choice, including the ubiquitous tendency to form search images. *Key words:* attention, blue jay, constraint, foraging, predator, prey, search image, switching. *[Behav Ecol 12:192–199 (2001)]*

The foraging behavior of predators searching for cryptic prey can strongly affect the fitness of both the predators and the prey, and consequently, the dynamics of populations and communities of animals and plants (e.g., Bond and Kamil, 1998; Hassell, 1978; Martin, 1988; Sutherland, 1996); hence ecologists must acquire a realistic understanding of predators' search patterns and their dynamics. In a series of papers, Dukas and colleagues (Dukas and Clark, 1995a, 1995b; Dukas and Ellner, 1993) attempted to integrate mechanistic neurobiological information with foraging theory in order to explain and predict how constraints on information processing together with economic considerations shape predators' foraging patterns. These models included two assumptions. First, the brain can effectively process only a limited amount of information at any given time. Substantial evidence indicating a very limited rate of information processing by the brain comes from neurobiological studies in humans and monkeys, which have employed either electrophysiological recording from individual neurons or brain imaging. These studies have revealed that focusing attention on a given task is associated with increased activation of the neurons processing this task, suppressed activity of other neurons, and enhanced behavioral performance on the attended task (e.g., Behrmann and Haimson, 1999; Corbetta et al., 1990; Desimone, 1998; Kastner et al., 1998; Spitzer et al., 1988).

The other assumption in the foraging models that include neurobiological constraints is that alternation among distinct tasks involves a period of reduced efficiency immediately following a switch. Some proximate reasons for such interference between distinct tasks are: (1) the mere passage of time devoted to one task is accompanied with the decay of memory of the other task, (2) the newly acquired information interferes with information already in memory, or (3) the old information already in memory interferes with the acquisition of new information. Extensive evidence for interference exists from human and animal studies conducted in the laboratory and in the field (Anderson, 1990, 1995; Duncan et al., 1994;

Spear and Riccio, 1994; Stanton, 1983; Wickens, 2000; Woodward and Laverty, 1992).

Optimality analyses including one (Dukas and Ellner, 1993) or two (Dukas and Clark, 1995a) of the neurobiological constraints just mentioned predict that animals should search only for a single cryptic food type at any given time while ignoring alternatives that are equally cryptic, rewarding and abundant, a behavioral pattern sometimes referred to as "search image" (Dukas, 1998; Tinbergen, 1960). This prediction is attractive because it allows integration within foraging theory of the somewhat separate research on perceptual biases affecting predator search. In the four decades since Lucas Tinbergen (1960) coined the term "search image," researchers have focused mostly on establishing whether search images do indeed exist (Dawkins, 1971a,b; Pietrewicz and Kamil, 1979; Reid and Shettleworth, 1992). Recent studies have indicated that selective attention is involved in search images (Blough, 1991; Langley, 1996). However, these studies, which aimed to establish the existence of search images, did not critically test for either the effect of limited attention or switching on predator searching behavior.

Here we present results of experiments designed to evaluate the costs of switching and divided attention using blue jays *(Cyanocitta cristata)* foraging for digital images of cryptic prey. We began with a quantification of the cost of switching, because this could provide us with the necessary knowledge for designing a well-controlled experiment measuring the cost of divided attention. In the first experiment, we predicted that because switching between distinct search tasks can decrease performance, increasing the rate of alternation between the tasks would decrease the overall rate of target detection. In the second experiment, we repeated the test for the effect of switching, this time comparing the extremes of no switching at all to switching at an average rate of one alternation every other trial. The second experiment also included another set of sessions, in which we compared target detection rate when jays had to either focus attention on searching for a single target type per display or divide attention between searching for two distinct target types per display. In that set of sessions, we predicted that dividing attention would decrease the frequency of target detection.

METHODS

Subjects

The eight blue jays *(Cyanocitta cristata)* used in the experiments were captured as nestlings in Lincoln, Nebraska, USA,

approximately a year before the experiments and were hand raised in the laboratory. During the experiment, the jays were maintained at 80% of their *ad libitum* body weight with controlled daily feedings of turkey starter and Lefeber brand food pellets. The jays were housed in individual cages, with water available, at a constant room temperature of 27°C and on a 14:10 h light:dark cycle.

Apparatus
We trained and tested the jays in an operant chamber (approximately 50 × 50 × 50 cm) with opaque walls located in a small, darkened room. A white noise generator was played throughout the experiment to mask outside sounds. Stimuli were presented on a computer monitor embedded in the front wall of the chamber. A lamp mounted above the monitor provided dim light throughout the experiment. We attached a clear Plexiglas sheet to the front of the monitor by springs to prevent damage to the monitor and to the jays' beaks. An infra-red "touch screen" reported the location of each peck directed at the screen. A wooden perch was positioned approximately 10 cm from the touch screen and 15 cm above the chamber floor. Jays standing on the perch could readily peck at targets presented on the monitor screen and reach the food rewards, which were half pieces of mealworms (*Tenebrio molitor*), delivered via a Davis UF-100 universal feeder into a food cup mounted to the left of the lower left corner of the monitor. At the moment of reward delivery, a light above the food cup was turned on and fully illuminated the food cup for 3 s. All stimulus presentations, schedules of reward delivery and data recording were controlled by a personal computer programmed in Borland C.

Training
Prior to each experiment, we trained the jays to peck at targets presented among non-target background items on the computer monitor. In the final stage of training, we gradually increased the density of background items in order to create the desired highly cryptic conditions. In experiment 2, we also altered the background items to make them more similar to the target. During the final stage of training, we adjusted task difficulty individually for each jay in order to maintain the percentage of correct detection by each jay at approximately 65%. By the end of the training period for each experiment, the jays were familiar with the experimental protocol and were able to detect what we perceived as highly cryptic targets.

Experiment 1: the cost of switching

Methods
In this experiment we wished to quantify the cost of switching between two distinct search tasks by manipulating the frequency of switching events per session. Specifically, we expected switching to diminish searching performance and thus predicted that increasing the frequency of switches per session would result in reduced target detection rate.

We created two artificial prey images and backgrounds. Because bird color vision is different from that of humans (e.g., Jacobs, 1981), we used only monochromatic images. The images were an artificial caterpillar 15 pixels long and five pixels wide on a background of a random assortment of segments, and an artificial moth 20 pixels in maximum length and 17 pixels in maximum width on a background consisting of various components of the moth's body parts. Although the visual dimensions of the targets were slightly different, both were treated by the computer as being at the center of a 20 × 20 pixel virtual display corresponding to approximately 8 × 8 mm on the screen. (Faithful reproductions of the images and backgrounds used are technically unattainable in print format; hence the authors will provide electronic examples of the displays on request).

A 100-trial session consisted of 50 caterpillar displays and 50 moth displays. Half the displays of each target contained the target at a randomly chosen location and numerous background items, and the other half contained background items only. The jays had two distinct search tasks (searching for either a moth on its background, or for a caterpillar on its background) and we manipulated the frequency of switching between these tasks.

In nature, switching between searching for alternative prey types might occur over various temporal scales. To cover a wide range of possibilities, we compared jays' performances at three switching rates: low, moderate, and high. The low switching rate consisted of a single switch per session, occurring on a randomly chosen trial between the 45th and 55th trial. The moderate switching treatment involved 10 switches per session, with switching occurring randomly every 8 to 12 trials. Finally, the high switching treatment involved 50 switches occurring randomly every one to three trials. Our protocol simulated a natural situation of a forager alternating searching between two prey types each occurring in a distinct patch.

Each trial began with the presentation of a start signal, a red circle at the center of the blank monitor. Upon a single peck to the start signal, the display was presented. The display always contained background and a move signal consisting of a green circle at the center of the display; it also contained a prey item on 50% of the trials. A jay could do one of four things: (1) peck at the target ("correct detection"), (2) peck at the background ("false alarm"), (3) peck at the move circle ("correct rejection" on negative displays and a "miss" on positive displays), or (4) not peck at all. Correct detection resulted in the delivery of half a mealworm and 3 s feeding time followed by a 5 s intertrial interval. A peck at the background resulted in the termination of the trial without reward followed by a long intertrial interval of 30 s. A peck at the move key resulted in the termination of the trial followed by a 1 s intertrial interval. A trial that lasted for 30 s without any response ended with no reward and was followed by a long intertrial interval of 30 s.

The experiment was conducted with a randomized blocks design. Each of the three treatments was tested once in random order within each 3-day block for a total of 10 blocks. The first trial in each session consisted of a randomly chosen display type (caterpillar or moth), counterbalanced within treatments and across blocks. That is, for each treatment, 5 days began with caterpillar and the other 5 days started with moth. In subsequent trials, display type remained the same until the first switch, at which the display type was alternated; then the display type was identical until the subsequent switch (10 and 50 switches) or the session end (one switch). Each display had a 0.5 probability of containing a single prey item.

At the end of each 3-day block throughout the experiment, we monitored the average proportions of correct detection by each jay. If detection by a jay exceeded 70% for either prey type, we decreased that prey conspicuousness by increasing the background density for that jay. This way we could maintain the perceived prey conspicuousness approximately constant between jays and throughout the experiment. Note that we had to adjust difficulty in order to counteract learning by the jays and maintain the key experimental condition of a search for cryptic prey. The adjustment did not compromise our statistical tests because it was carried out between blocks. That is, experimental treatments within a block were always carried out under identical difficulty, allowing us to conduct a comparison between treatments within blocks.

We calculated the detection rate of each target type as the number of targets detected per session over the total time
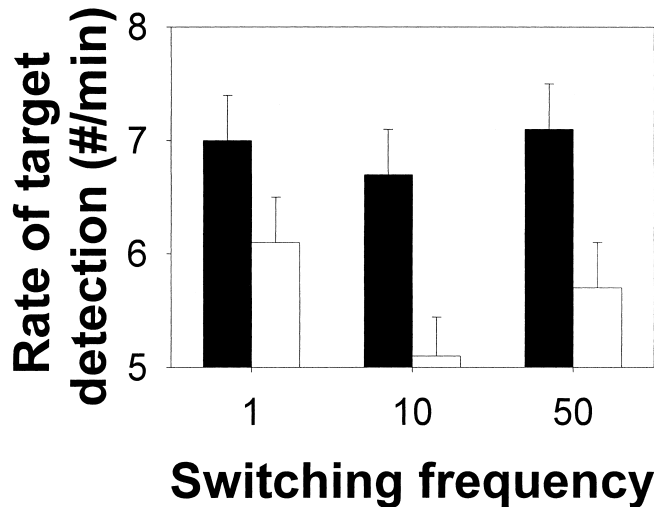
Figure 1
Averages (+ SE) of target detection rates in Experiment 1. The black and white bars depict the caterpillar and moth targets respectively.

Table 1
The protocol of Experiment 2

Session type	Start signal	Display consisting of	
		Target type	Background type
A/A	A	A	A
B/B	B	B	B
A/A‖B/B	A	A	A
	or	or	or
	B	B	B
A/($A + B$)	A	A	$A + B$
B/($A + B$)	B	B	$A + B$
A/($A + B$)‖B/($A + B$)	A + B	A	$A + B$
	or	or	or
	A + B	B	$A + B$

Each trial began with the presentation of a start signal, which, in all sessions but A/($A + B$)‖B/($A + B$), indicated which target would appear in the following display. The targets are depicted in plain upper case letters, and the background is represented in italic to indicate that a target was highly cryptic against its corresponding background.

spent searching for that target type. The results were analyzed with a repeated measures ANOVA, which included switching frequency (three values), target type (two values) and block number (10) as fixed factors, and jay (four individuals) as a random factor.

Results
There was no significant effect of the switching frequency on target detection rate. That is, the jays detected targets at similar rates during sessions with 1, 10 or 50 switches (repeated measures ANOVA, $F_{2,6} = 1.4$, $p > .3$, Figure 1). The caterpillar was detected at a higher rate ($p < .006$), but the interaction between switching frequency and target type was not significant ($p > .1$). The jays slightly varied in their behavior across treatments ($F_{6,54} = 2.7$, $p < .05$ for the jay by treatment interaction). A power analysis (Cohen, 1988) revealed that the power to detect moderate (20%) differences in detection rate was close to one, as indeed indicated by the highly significant effect of target type.

We examined performance in detail in the trials immediately before and after a switch. Switching had no effect on the frequency of correct pecks ($p > .1$), but it had a strong effect on response latency only in the single-switch treatment, with latency being the shortest just before switching, longest in the first two trials after switching, and then rapidly decreasing. The effect of switching on response latency was not significant for the whole data set ($p > .1$), but highly significant for a data set containing only the single switch treatment ($F_{5,15} = 8.1$, $p < .001$). Overall, switching in the single switch treatment resulted in increased search latencies in the two trials following the switch, adding about 6.5 s to search duration. This amounted to less than 1% of the average total search duration of approximately 715 s for the 100-trial session.

Experiment 2: the partial costs of divided attention and switching

In Experiment 1, each target type was presented on a unique background, which informed the jays which single target to search for. Hence the jays could always focus attention on searching for a single target at a time. In contrast, in Experiment 2 we wished to compare target detection rate in sessions where jays were informed which of the two target types to

search for versus sessions where they were not informed and hence had to divide attention between searching for either type. Because this test of the effects of divided attention had to include target switching, we included measurement of the cost of switching in this experiment. This allowed us to separately assess costs of both switching and divided attention. Even though we expected no switching costs based on our previous experiment, the measurement of switching costs in this experiment was a necessary control.

Methods
We used two new pairs of targets and backgrounds: (1) target A was a white vertical ellipse 24 pixels high and 8 pixels wide, with a background consisting of numerous white ellipses shorter or narrower than the target, and (2) target B was a brown horizontal bar 12 pixels wide and 4 pixels high, with a background consisting of numerous brown bars shorter or narrower than the target. Although the visual dimensions of the targets were different, the targets were treated by the computer as being at the center of a sensitive area of identical size. (Faithful reproductions of the images and backgrounds used are technically unattainable in this publication format; hence the authors will provide electronic examples of the displays on request.) In this experiment, the ''start signal'' for each trial consisted of the target(s) that could appear in the subsequent display, presented at the center of a red circle (see below).

The experiment consisted of two subtests, one quantifying the effect of switching alone and the other measuring the combined effects of divided attention and switching. Overall, there were six session types. The features of each type are detailed below and referred to throughout using a code summarized in Table 1. One set of three session types was designed to quantify the cost of switching. Each trial of these sessions began with the presentation of the start signal, which contained the single target type that would appear in the subsequent display. The display always included a single target, which appeared on its corresponding background (Table 1). In session types A/A (target A, background A) and B/B (target B, background B), a single target type appeared in both the start signals and displays of all 50 trials. In session type A/A‖B/B (target A, background A; or target B, background B) each trial consisted of either a start signal containing target

A followed by a display containing target A with its matching background, or a start signal containing target B followed by a display containing target B with its matching background. Each trial type appeared equally often and in random order. During these three session types, both the start signal initiating each trial and the background informed the jays which single target to search for. Hence the jays could always focus attention on searching for this target only. The jays did not switch between targets in sessions A/A and B/B, but they often switched between targets in session $A/A\|B/B$. Thus a comparison of the detection rates during session $A/A\|B/B$ with those during sessions A/A and B/B would reveal any cost of switching.

The other three session types were designed to measure the cost of divided attention, although switching costs could not be ruled out. In trials of these sessions, a single target always appeared on a mixed background consisting of numerous white ellipses shorter or narrower than target A, and numerous brown bars shorter or narrower than target B (Table 1). In session type $A/(A + B)$ (target A, background $A + B$) and session type $B/(A + B)$ (target B, background $A + B$), a single target type appeared in all the start signals and displays of all 50 trials. In session type $A/(A + B)\|B/(A + B)$ (target A, background $A + B$; or target B, background $A + B$) the start signal always included the two targets, and each of the two targets appeared in the display of half the trials in random order. During $A/(A + B)$ and $B/(A + B)$ sessions, the start signal initiating each trial informed the jays which target would be found in the display. Hence the jays could always focus attention on searching for this target only. In contrast, in $A/(A + B)\|B/(A + B)$ sessions, the start signal indicated that either target may appear in the following display. Thus the jays always had to divide attention between searching for either target. A comparison of the detection rates between $A/(A + B)\|B/(A + B)$ sessions and the $A/(A + B)$ and $B/(A + B)$ sessions would reveal the combined costs of divided attention and switching, and the relative contribution of divided attention could be measured by subtracting the cost of switching evaluated in sessions A/A, B/B, and $A/A\|B/B$.

Once a day, a jay performed a single session consisting of 50 trials. Each trial began with the presentation of the "start signal" at the center of the blank screen. Pecking at the start signal prompted the presentation of the display depicting a single cryptic target at a randomly chosen location and a background. A single peck at the display terminated the trial. A peck at the target was rewarded with half a mealworm, with the following trial presented after 3 s. A peck at the background resulted in 15 s delay. Finally, when jays did not peck at all, the trial was terminated after 15 s, with the next trial presented after 1 s.

The experiment was conducted with a randomized blocks design. Each of the six treatments was tested once in random order within each 6-day block, with a total of 16 blocks. At the end of each 6-day block throughout the experiment, we monitored the average proportions of correct detection by each jay. If detection exceeded 65% for either prey type, we decreased that prey conspicuousness by increasing the similarity of the background items to the target. This way we could maintain prey conspicuousness approximately constant throughout the experiment. Note that, as in Experiment 1, this adjustment, which allowed us to maintain the required cryptic conditions in spite of jay learning, did not compromise the statistical tests, because the changes in difficulty only occurred between blocks and we tested for treatment effects within blocks. We calculated the detection rate of each target type as the number of targets detected per session over the total time spent searching in trials consisting of that target type. The results were analyzed with repeated measures AN-
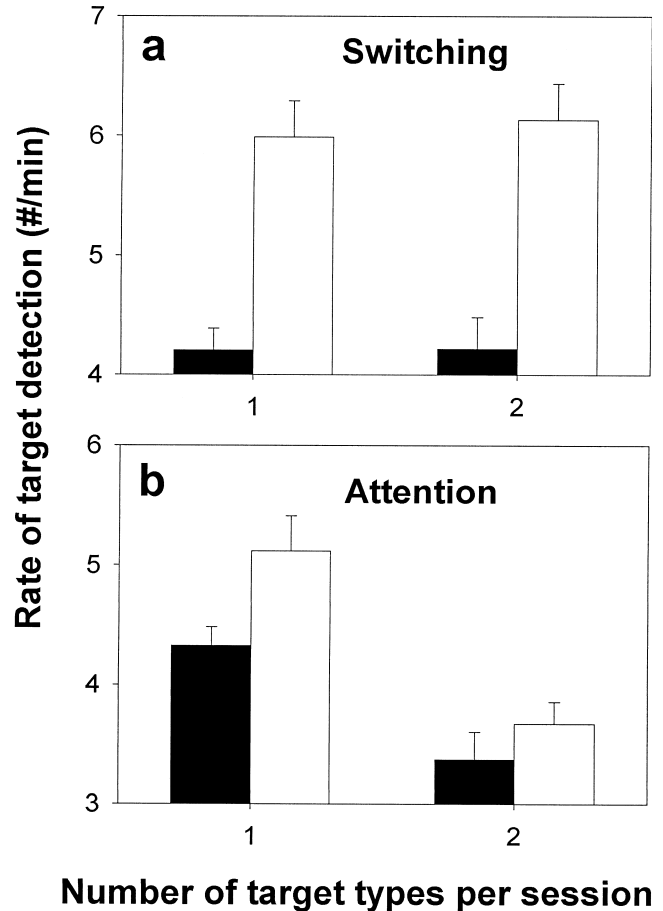

Figure 2
Averages (+ SE) of target detection rates in Experiment 2. (a) Depicts results from the three sessions that tested for the effect of switching. The jays switched between searching for one or another target type between trials in session $A/A\|B/B$ but searched for a single type in session A/A and session B/B (Table 1). (b) Shows results from the other three sessions, which tested for the effect of divided attention. The jays divided attention between searching for two target types in session $A/(A + B)\|B/(A + B)$ but focused attention on searching for a single type in session $A/(A + B)$ and session $B/(A + B)$ (Table 1). The black and white bars depict target A and B respectively.

OVA's, which, for each of the subtests, included the number of target types per session (one or two), the target type (A or B), and block number (a total of 16) as fixed factors, and jay identity (eight individuals) as a random factor. Note that we compared jay performance only within each subtest of three sessions because the background difference between the two subtests (A or B in the first three sessions, and A + B in the other three sessions) was an obvious reason for differences in performance between the two subtests.

Results
The target detection rate in session $A/A\|B/B$, when the target types were presented in random order each on their unique background, was very similar to target detection rates in sessions A/A and B/B, when all of the trials of a session consisted of a single target type on its unique background (repeated measures ANOVA, $F_{1,7} = 0.3$, $p > .5$, Figure 2a). The pattern of similar performance between treatments was persistent across jays ($F_{7,105} = 1.8$, $p > .05$ for the jay by treatment interaction).

The target detection rates were much lower in session A/$(A + B)\|$B/$(A + B)$, when the two target types were presented in random order on a mixed background, than during sessions A/$(A + B)$ and B/$(A + B)$, when only a single prey type was presented on a mixed background each session type ($F_{1,7} = 76$, $p < .001$, Figure 2b). Overall, the jays detected targets at an average rate of 3.5 ± 0.2 (mean $\pm$ SE) per min spent searching in session A/$(A + B)\|$B/$(A + B)$; this was 25% lower than the average rate of target detection of 4.7 ± 0.2 in sessions A/$(A + B)$ and B/$(A + B)$. The pattern of lower performance in session A/$(A + B)\|$B/$(A + B)$ than in sessions A/$(A + B)$ and B/$(A + B)$ was persistent across jays ($F_{7,105} = 1.4$, $p > .1$ for the jay by treatment interaction).

DISCUSSION

Experiment 1 indicated no cost of switching. Similarly, there was no cost of switching in the sessions of Experiment 2 when the different target types were presented on the start key and had a target-specific background. However, in the other sessions of Experiment 2, target detection rates were much lower when the jays had no cues, either on the start key or in the background, that would allow them to direct their attention towards a specific target. Thus, our results agree with the prediction that dividing attention between searching for two distinct cryptic target types at any given time causes lower detection rate (Figure 2b) and we can reject the hypothesis that switching between searching for alternative targets alone reduces detection performance (Figures 1 and 2a). Although one might be tempted to identify hints of cost of switching in Experiment 1, we should emphasize that we failed to find significant effects of switching in additional detailed analyses. Moreover, there was not even a slight sign of switching cost in Experiment 2 (Figure 2a), which was the most elaborate and with a high statistical power due to the use of eight jays and 96 daily sessions. The issue of costs of switching and divided attention is highly relevant for optimal foraging decisions (Dukas and Clark, 1995a; Dukas and Ellner, 1993). However, here we did not allow the jays to choose between alternative foraging strategies. Rather, we forced the jays to switch or divide attention in certain sessions but not in others because we wished to measure costs of switching and divided attention.

Our conclusion about the detection cost of divided attention is based on the assumption that in A/$(A + B)\|$B/$(A + B)$ sessions, when either target A or B could appear and there was no cue of any sort indicating which target might be present, the jays indeed divided attention between simultaneously searching for the two target types. We do not possess direct neuronal information to substantiate this assumption. Thus it is possible that the jays did one of the following two alternatives. First, they could always focus attention first on one type and then switch to the other, a behavior that should have resulted in a lower detection latency for one target type. The results do not agree with this option, as the average trial duration was similar for the two target types in A/$(A + B)\|$B/$(A + B)$ sessions: 9.1 ± 0.19 s and 8.9 ± 0.18 s for targets A and B respectively. Individual analyses revealed that all eight jays showed a similar pattern of just slightly better performance on target B than A. A second alternative is that the jays rapidly alternated between searching for targets A and B; for example, they may have searched for target A for 1 s and then focused on searching for target B for 1 s, and so on. We consider this alternative to be close to true simultaneous division of attention, because an analysis with a temporal resolution of 2 s would not distinguish between the two. Moreover, Duncan et al. (1994) found that, in human subjects, it takes about half a second to effectively switch attention between

distinct visual tasks. This suggests that rapid switching of attention (at least in humans) is inefficient due to time loss.

Kono et al. (1998), in a study that focused on search image more than selective attention, also tested the effects of background signaling on detection. They used two moth species (*Catocala relicta* and *C. ilia*) which rest on different tree species and were always shown on their species-typical substrate. When the display presented to blue jays only contained a single type of tree, and therefore could only contain a specific moth, performance was no better than when both tree types were shown. There are a number of methodological differences between Kono et al. (1998) and this study, which might account for the difference in results. One difference particularly worth further study is that Kono et al. (1998) always used the same cue as the start signal. It is possible that most of the effects of divided attention that we observed in this study were due to the lack of information on the start signal during A/$(A + B)\|$B/$(A + B)$ sessions compared to the presence of explicit information allowing focused attention in sessions A/$(A + B)$ and B/$(A + B)$.

In sum, the jays' reduced performance in A/$(A + B)\|$B/$(A + B)$ sessions is best explained by limited attention. Because our inference about limited attention was based on behavioral information, we briefly discuss below relevant neurobiological data.

The neurobiology of limited attention

The neurobiology of attention has been studied most directly through electrophysiological monitoring of individual neurons in monkeys (Moran and Desimone, 1985; Spitzer et al., 1988). More recently, two types of brain imaging, positron emission tomography (PET), and functional magnetic resonance imaging (fMRI), have been widely used to monitor attention in large populations of neurons (Corbetta et al., 1990; Drevets et al., 1995; Heinze et al., 1994). For example, Corbetta et al. (1990) instructed human subjects to report whether the moving bars in two successive briefly presented computer displays were identical. In the focused attention treatment, the subjects had been told what visual attribute may differ between the bars on each display (color, shape, or velocity). In the divided attention treatment, the subjects had only been told that the bars could differ in one of the three attributes. Through the employment of PET, Corbetta et al. (1990) found that focusing attention on a single attribute was correlated with increased neuronal activation in the area of the visual cortex that processes this attribute compared to the divided attention treatment. Correspondingly, subjects' performance on the discrimination task was higher in the focused than divided attention treatment. In short, hundreds of studies using numerous protocols have all identified neuronal correlates of limited attention, and research is now focused on the mechanisms underlying the selective allocation of attention to the most relevant information (Behrmann and Haimson, 1999; Desimone, 1998; Desimone and Duncan, 1995; Hillyard et al., 1998). The neurobiological research, however, implicitly assumes that attention is an efficient mechanism allowing animals to focus only on relevant information. This notion overlooks the ecological reality, that limited attention can be costly, an issue we discuss below.

Limited attention: the constraint underlying search image

Limited attention implies that the amount of information foragers process at any given time can strongly affect their feeding success. Indeed we have documented here that jays detected targets at a lower rate when they were forced to divide attention between searching for two target types than when

they could focus attention on a single target (Figure 2b). Hence from a cognitive perspective, it is advantageous to focus attention on a single difficult task at any given time. However, in an environment where a few types of visually distinct food types of identical conspicuousness, quality, and density are randomly distributed, focusing attention on searching for only a single food type means that the effective density of food is reduced, because the other food types are overlooked. Thus the benefit from selective attention must be sufficiently large to compensate for the effective decrease in food density. A formal model of this foraging problem, which includes a parameter for limited attention (Dukas and Ellner, 1993), indicates that when food is highly cryptic, focusing attention on one type while ignoring others is indeed optimal. Hence this model offers a likely explanation of foragers' tendencies to use search images when searching for cryptic food. Our results are in agreement with the model because we have documented a cost of dividing attention during search for highly cryptic targets. In other words, limited attention is the only identified neurobiological mechanism that has been shown theoretically (Dukas and Ellner, 1993) and empirically (Experiment 2) to explain observational and empirical studies on search images.

Several previous studies on search image discussed the possible role of selective attention (e.g., Bond, 1983; Dawkins, 1971b; Langley et al., 1996; Reid and Shettleworth, 1992). Most notably, Blough (1989) compared pigeon performance in sessions in which subjects were either informed or uninformed which of two targets would appear among non-targets in a computer display. The information about target identity was provided either with a visual cue preceding each trial, or by presenting one target type in all trials within a single session. Either type of information resulted in a slight (5–10%) increase in response latencies compared to sessions where no information was provided. The targets used, however, were rather conspicuous, as indicated by the approximately 85% correct detections and 1 s response latencies. The sessions in which the pigeons were either informed or uninformed prior to the trial which target to search for were similar to our sessions with mixed backgrounds in Experiment 2, in which we documented large costs of divided attention (Figure 2b) while ruling out the possible effect of switching costs (Figure 2a). This strongly suggests that with the use of highly cryptic targets, our results will be replicated with pigeons as well as other species.

While we believe that limited attention is the central feature explaining search image, other factors, especially learning, are likely to be involved in various field settings. In many cases, items of the same food type are clustered in time and space. Indeed foragers possess behavioral mechanisms, such as reducing movement distance and increasing turning angle, which help them exploit patchily distributed food (Dukas and Real, 1993a; Hassell, 1978; Price and Reichman, 1987). Hence in a realistic natural setting, where a forager has only limited knowledge of the available cryptic food items, learning about one type, which appears to be common at a certain time and place, may be followed with a period of focused search for this type.

Is switching costly?

Our prior expectation of significant costs of switching between tasks was mostly based on human studies, which indicate that the learning of one item of information may interfere with the later recall of another item learned previously or subsequently (reviewed in Anderson, 1990, 1995; Baddeley, 1986). Our experiments, however, addressed alternation between well-learned tasks, which had been known for weeks or months prior to testing. It is possible that a well-practiced switching assignment would have little or no cost. Although one might argue that well practiced switching would incur costs in tasks that are sufficiently difficult, the fact is that the level of difficulty we employed was sufficient to reveal large costs of divided attention, but not switching (Figure 2). Unfortunately, we cannot provide a meaningful comparison of the difficulty of search tasks in our experiments and in the field.

Other behavioral consequences of limited attention

Limited attention can have other effects on behavior besides the issue of searching for cryptic food addressed here. First, in addition to selectively attending to relevant items or visual attributes such as certain colors and shapes, animals may also modify the area they attend to at any given time as a function of the difficulty of a given search task: the attentional scope can be wide for easy search tasks but narrow for difficult tasks (Desimone and Duncan, 1995; Dukas, 1998; Eriksen and Yen, 1985; LaBerge, 1983). Narrowing the focus of attention implies that a smaller area is searched per unit time, that is, the search rate is reduced. Thus limited attention also provides a neurobiologically based explanation for the observation that animals reduce search rate when the difficulty of a search task is increased (Gendron, 1986; Gendron and Staddon, 1983). The ability to modify the spatial focus of attention, however, does not eliminate the need to selectively attend to a certain target or visual attribute when the search task is difficult (Dukas and Ellner, 1993). That is, the suggestion that alteration of search rate can explain observations on search image (Guilford and Dawkins, 1987) is in disagreement with neurobiological data, behavioral observations, and theory (Behrmann and Haimson, 1999; Bond, 1983; Dukas and Ellner, 1993; Moran and Desimone, 1985; Plaisted and Mackintosh, 1995; Reid and Shettleworth, 1992).

Second, another effect of limited attention is that when animals focus attention on a difficult foraging task, they may be less likely to notice approaching predators (Godin and Smith, 1988; Krause and Godin, 1996; Milinski, 1984; Milinski and Heller, 1978). This prediction was critically tested by Dukas and Kamil (2000) who found that when blue jays were engaged in an easy central search task they were three times more likely to detect briefly presented peripheral targets than when engaged in a difficult central task. This suggests that limited attention could be a major cause of mortality in nature.

Third, many flower visitors tend to restrict visits to the flowers of one species while bypassing equally rewarding alternatives (Waser, 1986). This behavior, which appears similar to search image, may be caused, at least in part, by limited attention (Chittka et al., 1999; Dukas and Real, 1993b). Finally, limited attention could explain why many insect herbivores have a restricted diet even when they are not limited by deterring secondary compounds. One explanation for this diet specialization is that the insect herbivores can make faster and better feeding decisions when they focus attention on foraging for a single plant species only (Bernays and Wcislo, 1994). Recent experiments indeed indicate that specialist insects forage more efficiently than closely related generalists (Bernays and Funk, 1999; Jans and Nylin, 1997), and that generalist species forage more efficiently when facing items of one type rather than a few food types (Bernays, 1998, 1999). These studies clearly indicate a role of some cognitive limitation in favoring specialization, but the exact mechanisms are yet to be critically examined. In sum, limited attention appears to have a few ecologically important effects on animal behavior.

This conclusion warrants further analyses of the factors underlying limited attention.

Why is attention limited?

Neurobiologists focusing on mechanisms take as a given that the brain can effectively process only a limited amount of information at any given time. In contrast, ecologists addressing questions on the adaptive value of a trait cannot accept a constraint as a given, unless it is directly derived from some fundamental laws of physics or chemistry. Hence it is relevant to ask ''why is attention limited?'' At the neurobiological level, it is established that the recognition of visual patterns is computationally demanding and cannot be performed at the maximal possible resolution across the entire visual field (Maunsell, 1995; Van Essen et al., 1992). That is, the brain does not possess the computational power to process all the information provided by the sensory organs at any given time. The underlying reasons for this limited power have not been elucidated. The cause may simply be a limited number of neurons, but it may involve less studied issues concerning some limitation on the integration of signals from numerous neurons. From a functional perspective, we may assume that attentional capacity is at some optimal level determined by certain costs and benefits (see Dukas, 1999), although various fundamental constraints may be important as well. For example, one may argue that attentional capacity reflects a trade-off between the marginal cost of maintaining additional neuronal tissue and the marginal benefit from the added attentional span. An illuminating approach would be to search, based on relevant ecological knowledge, for species differences in attentional capacities.

In sum, by integrating proximate neurobiological knowledge with foraging theory, we believe we have provided a realistic account of search image: a prey model that includes a limited attention parameter predicts that predators searching for cryptic prey should focus on a single prey at a time while ignoring equally cryptic, rewarding and abundant alternatives (Dukas and Ellner, 1993). Here and in a companion article (Dukas and Kamil, 2000), we have shown that limited attention is indeed a relevant trait that can explain search image and other ecologically important behaviors.

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