University of Nebraska - Lincoln
DigitalCommons@University of Nebraska - Lincoln

Papers in Behavior and Biological Sciences | Papers in the Biological Sciences

2000

The cost of limited attention in blue jays

Reuven Dukas
Simon Fraser University, rdukas@sfu.ca

Alan Kamil
University of Nebraska - Lincoln, akamil1@unl.edu

Follow this and additional works at: https://digitalcommons.unl.edu/bioscibehavior

Part of the Behavior and Ethology Commons

Dukas, Reuven and Kamil, Alan, "The cost of limited attention in blue jays" (2000). *Papers in Behavior and Biological Sciences*. 54.
https://digitalcommons.unl.edu/bioscibehavior/54

This Article is brought to you for free and open access by the Papers in the Biological Sciences at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Papers in Behavior and Biological Sciences by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

Published in *Behavioral Ecology* 11:5 (2000), pp. 502-506. Copyright © 2000 International Society for Behavioral Ecology.
Published by Oxford University Press. Used by permission.

Submitted September 1, 1999; revised December 28, 1999; accepted January 6, 2000.

The cost of limited attention in blue jays

Reuven Dukas and Alan C. Kamil

Nebraska Behavioral Biology Group, School of Biological Sciences, University of Nebraska–Lincoln, Lincoln, NE 68588-0118, USA

Corresponding author – R. Dukas: Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada; email rdukas@sfu.ca

Abstract

Experiments with fish and birds suggest that animals are unable to simultaneously allocate sufficient attention to tasks such as the detection of an approaching predator while searching for cryptic prey. We quantified the effects of limited attention on performance in controlled laboratory settings and report here the first direct evidence that attending to a difficult central task simulating foraging deters a bird's ability to detect a peripheral target, which could be a predator. Our results fill a gap between ecological and neurobiological studies by illustrating that, although attention is an efficient filtering mechanism, limited attention may be a major cause of mortality in nature.

Keywords: attention, blue jays, *Cyanocitta cristata*, survival, vigilance.

Neurobiological research on humans and monkeys indicates that attentional mechanisms direct the brain's limited computational resources to the most relevant information, filtering out less important information. Consequently, subjects that pay more attention to a central difficult task compensate by devoting less attention to a secondary task (Desimone, 1998; Desimone and Duncan, 1995; Hillyard et al., 1998; Kastner et al., 1998). For example, Rees et al. (1997) instructed human subjects to focus on a linguistic task appearing at the center of a computer display, which also included moving stimuli at its periphery. Behavioral measures and brain imaging revealed that the subjects devoted less attention to the moving stimuli when the linguistic task was difficult (detecting bisyllabic words) than easy (detecting uppercase letters). If the mechanisms of attention studied in humans and monkeys are shared by other species, the issue of limited attention is of critical relevance for ubiquitous behaviors such as diet choice and balancing tasks that must be carried out simultaneously, such as food search and predator avoidance (Dukas, 1998b; Dukas and Ellner, 1993; Milinski, 1990).

A number of studies are consistent with the hypothesis that limited attention constrains forager performance. Some of these studies documented a change in foraging behavior after exposure to model predators (Metcalfe et al., 1987; Milinski and Heller, 1978). Such change could be caused by reduced attention to food when more attention was devoted to predator avoidance. For example, Milinski (1984) reported that after exposure to a model of an avian predator, three-spined sticklebacks preferred to forage at daphnia swarms of lower density, and that such swarms allowed them higher detection rates of approaching predators. Indeed, Godin et al. (1988) documented higher mortality rates of fish hunting for daphnia at higher densities. Alternatives to limited attention, however, such as fear-induced physiological changes (Lima, 1998), or reduced visibility at higher food density, may also account for the above results. Another category of studies consists of reports that animals engaged in feeding, playing, or fighting are either less likely to respond to an approaching predator or respond to the predator at a shorter distance than when not engaged in other activity (Blumstein, 1998; Brick, 1998; Krause and Godin, 1996). A likely alternative in these cases is a lower motivation to immediately respond to the predator (Ydenberg and Dill, 1986). All these studies, however, are highly suggestive and invite a more controlled set of experiments.

Consider a blue jay perching on a tree trunk and directing its gaze toward the bark in search for cryptic insects (Endler, 1984; Sargent, 1976). The blue jay has the visual ability to simultaneously detect approaching predators while foraging (Fite and Rosenfield-Wessels, 1975; Martin, 1986), but such detection may be hindered due to limited attention, at least when the foraging task is difficult and attention-demanding. We simulated such a foraging scenario under controlled laboratory conditions to quantify the importance of limited attention. Specifically, we predicted that jays would have a higher probability of detecting peripheral targets when engaged in an easy than in a difficult central search task.

Methods

Subjects

The five blue jays (*Cyanocitta cristata*) used in the experiment were captured as nestlings in Lincoln, Nebraska, USA, approximately 1 year before the experiment 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 h:10 h light: dark cycle. Before the experiments, we trained the jays to peck at targets presented on a computer monitor. By the end of the training period jays were familiar with the experimental protocol and stabilized in their performance.

Apparatus

We trained and tested the jays in an operant chamber (approximately 50 x 50 x 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 house light 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 infrared 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 mon-

itor screen and reach the food rewards. The rewards were half pieces of mealworms (*Tenebrio molitor*), which were 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.

Experiment 1: central task difficulty

Protocol

Our goal was to create two levels of central task difficulty. We wanted to achieve this goal by presenting a target among either a small or large number of nontarget background items, which were isolated pieces of the target, placed at randomly chosen locations on every trial (Figure 1d). In experiment 1 we tested whether we could indeed alter the difficulty of the search task by changing the number of these distracters included in the displays. In this preliminary experiment, the display consisted of a red central circle, a monochromatic target, the central target (a caterpillar 15 pixels long and 5 pixels wide) shown at a random location within the central circle, and a known number of background items (Figure 1; see below). The target caterpillar appeared inside the circle in randomly determined 50% of the trials (positive trials), with the remaining trials being negative. Display duration was varied randomly between 50 to 500 ms, with each duration presented 10 times in a 100-trial daily session. There were 3 types of daily sessions, in which the central circle contained 1, 5, or 10 background items. The jays were trained to peck at the target during positive trials and to avoid pecking during negative trials. The experiment was conducted with three jays, each jay performing four blocks, with each session type presented once in random order within a 3-day block.

Results

A larger number of background items was associated with a lower frequency of correct responses. The percentages of correct responses were 81.00 ± 2.50, 67.00 ± 3.20, and 56.50 ± 1.75 with 1, 5, and 10 background items, respectively (repeated-measures ANOVA on arcsine-transformed proportions, $F_{2,4}$ = 30.7, p <.005). The results of this experiment indicated that we could indeed alter the central task difficulty by modifying the number of background items in the central circle.

Experiment 2: the cost of limited attention

Protocol

Each daily session consisted of 50 trials. A jay initiated each trial by pecking a red circle at the center of the monitor (Figure 1). After a brief delay, a display was presented for 500 ms. All displays consisted of a red central circle, two red peripheral ellipses, and a monochromatic target, either a central target (a caterpillar 15 pixels long and 5 pixels wide) shown at a random location within the central circle with probability 0.5, or a peripheral target (a moth 20 pixels in maximum length and 17 pixels in maximum width) shown at a random location inside the left or right ellipse with probability 0.25 for each side (Figure 1). We did not use simulated predators because these can have uncontrolled behavioral effects unrelated to attention, such as fear or reduced motivation to feed (Lima, 1998), which we wished to eliminate. Direct observations of the jays confirmed that they faced the center of the screen during display presentations and

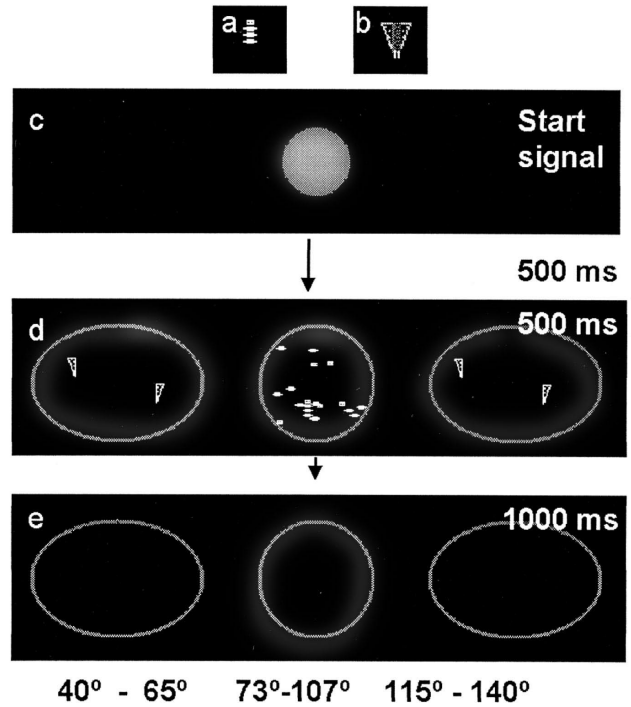

Figure 1. The two target types used: **(a)** a central target (caterpillar), which was displayed at a randomly chosen location within the central circle at a probability of 0.5, and **(b)** a peripheral target (moth), which was presented inside one of the two peripheral ellipses at a probability of 0.25 for each ellipse. The experiment consisted of two session types, center easy and center difficult. The session types differed only in the number of background items inside the central circle **(d)**. A jay initiated a trial by pecking at the start signal **(c)**. After 500 ms, the display, which contained a randomly chosen target and background items at randomly chosen locations, was presented for 500 ms (d). Then all items were cleared, except for the red circle and ellipses, which remained for additional 1000 ms **(e)**. A correct response consisted of a peck inside the circle or ellipse that contained a target. The visual angles, as perceived by the jays, are depicted below panel (e).

that they did not move their heads from one side of the monitor to the other during the brief display presentations.

During the experiment, the circle and two ellipses always contained nontarget background items, which were isolated pieces of the targets, placed at randomly chosen locations on every trial (Figure 1d). The number of background items inside the central circle was small during center easy sessions and large during center difficult sessions. The number of background items inside the peripheral ellipses was small and constant across all sessions (Figure 1d). After the brief presentation of the display, the target and background items were cleared, but the three red circles remained for additional 1000 ms (Figure 1e). Thus, a jay had a total of 1500 ms to peck at the monitor. A single peck terminated the trial. A peck directed at the circle or ellipse containing the target ("correct detection") was rewarded with half a mealworm. A peck at a wrong circle or ellipse resulted in three beeps followed by a delay of 1 min. Jays attempted to avoid such delays, which served as mild punishment (Kamil et al., 1993). If a jay did not peck at all, the next trial followed after 5 s delay. The experiment consisted of 12 2-day blocks, each containing the 2 session types in random order. Five jays were used.

We predicted that during center easy sessions, jays would use a broad focus of attention toward much of the monitor, and during center difficult sessions, they would direct a narrow focus

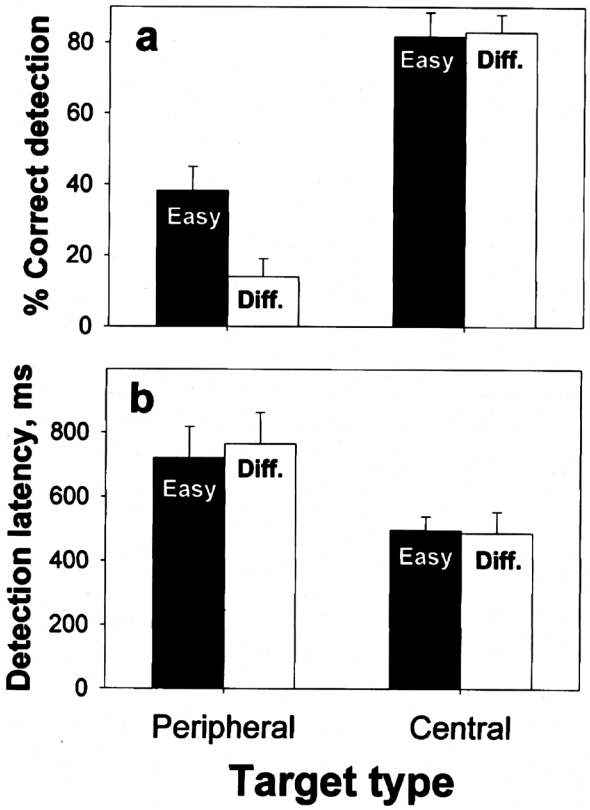

Figure 2. (a) The percentage of correct detection (mean + 1 SE) of the peripheral target was significantly higher during the center easy (shaded bars) than center difficult (open bars) sessions, but correct detection of the central target was similar in either session type. **(b)** The average detection latency of the peripheral target was similar during the center easy (shaded bars) and center difficult (open bars) conditions. Detection latency of the central target was also similar during the center easy and center difficult conditions.

of attention toward the central circle because the central circle was the location most likely to contain a target. Thus we predicted that the frequency of peripheral target detection would be lower in the center difficult than center easy sessions.

Results

The jays correctly detected 38% of the peripheral targets during the center easy sessions but only 14% during the center difficult sessions (repeated-measures ANOVA on arcsine-transformed proportions, $F_{1,4} = 112$, $p < .001$; Figure 2a). In contrast, the frequency of correct detections of the central target was 81.7% during the center easy condition, virtually identical to the 82.9% observed during center difficult sessions ($F_{1,4} = 0.02$, $p > .8$; Figure 2a), suggesting that by allocating more attention to the central circle, jays were able to maintain a high detection frequency of the central target.

Incorrect detections consisted of wrong pecks, meaning that the jays pecked at a circle not containing the target, and no pecks, meaning that the jays did not peck at all during the brief display presentation. It is relevant to report the distribution of these distinct categories. Incorrect detections of peripheral targets consisted of 66% ± 1.9% wrong pecks and the rest no pecks during center easy sessions and 82% ± 1.6% wrong pecks and the rest no pecks during center difficult sessions. Incorrect detections of central targets consisted of 65% ± 2.4% wrong pecks and the rest no pecks during center easy sessions and 57% ± 2% wrong pecks and the rest no pecks during center difficult sessions.

An alternative explanation for our results is that jays required a shorter search time for scanning the central circle and thus spent more time scanning the peripheral ellipses during the center easy than during center difficult sessions. This possibility is not supported by the latency data, as the time required for correct detection of a central target (measured from display onset) was similar during the center easy and center difficult sessions ($F_{1,4} = 0.02$, $p > .8$; Figure 2b). The latency for correct detection of a peripheral target was also similar under either session type ($F_{1,4} = 0.07$, $p > .8$; Figure 2b).

Discussion

Our results demonstrate that limited attention constrains a forager's ability to notice peripheral targets, which could be approaching predators, when involved in challenging foraging tasks. These results suggest that in nature, foragers engaged in more difficult food-detection tasks may incur higher rates of predation. Alternatively, in habitats with higher predation risk, foragers may allocate more attention to predator detection and less attention to food search (see Dukas, 1998b; Dukas and Ellner, 1993; Milinski, 1990). This may result in reduced food intake, and consequently, lower fitness due to a decrease in growth rate and body condition (Lima, 1998). Our findings are consistent with previous experiments (Godin and Smith, 1988; Krause and Godin, 1996; Lawrence, 1985; Metcalfe et al., 1987; Milinski, 1984; Milinski and Heller, 1978), all suggesting that foragers under challenging conditions could not devote sufficient attention to the dual task of searching for food and detecting predators. As we mentioned in the introductory section, these studies did not consist of critical tests for the effect of limited attention. Our results are also in agreement with studies in pigeons, where results have indicated that selective attention affects subjects' food searching behavior (Blough, 1969, 1991; Langley, 1996; Riley and Leith, 1976). For example, Vreven and Blough (1998) documented a decrease in target detection accuracy by pigeons when the number of either potential targets or nontargets increased. We have augmented previous studies by critically evaluating the possible role of limited attention for the ubiquitous task of finding food and detecting predators at the same time while controlling for alternatives.

Our experiments are relevant for many species and foraging scenarios that allow simultaneous search for food and predators. Examples include fish foraging in open water and birds feeding on tree trunks or branches. Moreover, our experiments are also relevant for the food search periods by animals such as ground-feeding birds, which alternate between head-down postures used for food search, and head-up positions used for scanning the environment for predators. Although earlier studies assumed that such ground-feeding birds cannot detect predators while in the head-down position, it is now established that they can (Lima and Bednekoff, 1999). However, the ability to detect approaching predators while focusing attention on food may be low, at least when the feeding task is difficult.

We designed our experiment to critically test for the effect of limited attention, while compromising on some aspects of natural foraging situations. First, we used two target types rather than food and a predator. An image of a predator or severe punishment could dramatically alter the jays' behavior, which we wanted to avoid. One might argue that our results documenting reduced ability to notice a peripheral target associated with

reward under more difficult central task conditions would not be replicated when the peripheral target is associated with predation. There are two aspects to such possible criticism. First, it is feasible that under demanding situations jays can simply allocate more attention to handle dual tasks. This is probably possible to some extent. However, the fact that all animals studied so far do not usually possess larger attentional capacities suggests that there is some cost associated with increasing the amount of information they process at the same time. One possible cost is a higher rate of exhaustion under such demanding information load (Dukas, 1998b; Dukas and Clark, 1995b). This idea requires empirical evaluation as outlined in Dukas and Clark (1995b).

Another line of criticism is that jays would always allocate more attention to the periphery if they anticipate predation rather than merely another feeding opportunity. This is a likely scenario, but it would probably require the jays to devote less attention to the central task. In general, jays and other species would probably alter the optimal allocation of attention between feeding and predator avoidance in response to short-term requirements and information about predation risk, with the changes in allocation of attention being correlated with changes in performance on the associated tasks. An experiment by Metcalfe et al. (1987) indicating that juvenile salmon showed reduced ability to select optimal food items after exposure to predators accords with the possibility that the fish devoted more attention to predator avoidance and less attention to food after perceiving the predator. As we mentioned in the Introduction, however, such an experiment does not exclude the likely alternative of fear-induced physiological changes, which diminish foraging performance.

Another somewhat unnatural aspect of our protocol is that we were concerned with static visual targets even though foragers are also sensitive to abrupt movement. Some animals also are highly responsive to other stimuli, such as smell or sound, to increase the probability of detecting approaching predators. Nevertheless, our approach is highly relevant for many natural situations because predators typically attempt to minimize detection by moving slowly, quietly, and against the wind. Moreover, predators may attempt to capture an animal while it focuses attention on food, as indicated by the animal's body posture and behavior. As we demonstrated here, when an animal focuses attention on food, even relatively salient stimuli may go unnoticed.

In line with the neurobiological research on attention, we have focused on information that must be processed at the same time. Foragers can partially mitigate the negative effect of limited attention by alternating between periods in which most attention is devoted to food and intervals in which most attention is directed toward scanning the environment for predators. Such behavioral patterns have been addressed by studies on antipredator vigilance, although these studies usually focus on species such as ground-feeding birds, where feeding and predator vigilance periods can partially be identified by the head-down and head-up positions respectively (Lima and Bednekoff, 1999; Lima and Dill, 1990; Pulliam, 1973).

Elaborate research on attention has been conducted only on humans and monkeys. Experiments using direct electrophysiological recordings or brain imaging have unambiguously established that focusing more attention on a task is associated with enhanced activity of the neurons processing information related to that task and improved behavioral performance on the task. At the same time, the processing of information associated with a secondary task is suppressed, and, consequently, performance on the secondary task is reduced (Desimone, 1998; Desimone and Duncan, 1995; Hillyard et al., 1998; Kastner et al., 1998; Rees et al., 1997). It is clearly advantageous to filter out unimportant information and focus only on the relevant, but attention cannot be perceived only as an efficient filtering mechanism, because animals often encounter a larger amount of relevant information than they can process at the same time. Under such conditions, attentional mechanisms allow allocation of attention to what is perceived as the most important tasks. Sometimes, however, animals may fail to attend to peripheral information, which may be an approaching predator.

We have recently replicated our results indicating that limited attention constrains foraging performance in another study using a distinct protocol (Dukas and Kamil, manuscript in preparation). While our empirical results and earlier formal theoretical research (Dukas and Clark, 1995a,b; Dukas and Ellner, 1993) bring the idea of constraints on information processing closer to behavioral ecology, this issue is well established in the cognitive sciences (Behrmann and Haimson, 1999; Desimone and Duncan, 1995). Still, integrating issues such as limited attention within behavioral ecology invites the question, why is attention limited? We can confidently answer that the limitation in question is not either within the sensory system or specific to the visual modality. For example, at a cocktail party, we tend to focus our attention on one conversation at a time, even though our ears can receive sounds from numerous conversations.

Although many neurobiological studies (see Behrmann and Haimson, 1999, for the latest ones) have focused on the mechanisms of attention, the question of what determines optimal attentional capacity has not been explicitly addressed. At some superficial level, it is easy to accept the notion that there must be a ceiling on the amount of information that can be processed at any given time. Information processing requires enormous computation by neurons; hence the number of neurons and limitations on the number of interconnections among neurons must allow only for some finite amount of information to be processed at the same time. Due to limited knowledge, we cannot at this time go further than this general argument. More explicit analyses of optimal cognitive abilities would require data not yet available about the cost associated with cognitive ability and the physiological and phylogenetic constraints involved (see Dukas, 1998b, 1999).

In sum, at any given time, the information received by sensory systems may far exceed an animal's processing ability (Desimone, 1998). As a result, some relevant information must be left unprocessed, even if this results in heightened risk of predation or inefficient foraging. In this context, the functional significance of attentional mechanisms would be to filter out some information, allowing focus on the information expected to have the greatest effect on fitness (Dukas, 1998b; Dukas and Ellner, 1993). This is an example of how cognitive abilities can be central to ecological concerns, and why ecological insight is relevant for cognitive science. An important issue for future research at the interface of cognition and ecology (Balda et al., 1998; Dukas, 1998a, 1999; Shettleworth, 1998) is identifying the neurobiological, computational, and phylogenetic mechanisms that have shaped limited attentional capacity.

Acknowledgments—We thank A. Bond, C. Cink, N. Ternus, C. Smith, M. Belik, B. Gibson, and M. Sinsel for assistance and comments on the manuscript, L. Bernays, K. Cheng, and D. Westneat for comments, and the National Institutes of Health for financial support.

References

Balda RP, Pepperberg IM, Kamil AC, 1998. Animal cognition in nature. London: Academic Press.

Behrmann M, Haimson C, 1999. The cognitive neuroscience of visual attention. Curr Opin Neurobiol 9: 158-163.

Blough DS, 1969. Attention shifts in a maintained discrimination. Science 166: 125-126.

Blough P, 1991. Selective attention and search images in pigeons. J Exp Psychol Anim Behav Process 17: 292-298.

Blumstein DT, 1998. Quantifying predation risk for refuging animals: a case study with golden marmots. Ethology 104: 501-516.

Brick O, 1998. Fighting behaviour, vigilance and predation risk in the cichlid fish *Nannacara anomala*. Anim Behav 56: 309-317.

Desimone R, 1998. Visual attention mediated by biased competition in extrastriate visual cortex. Phil Trans R Soc Lond B. 353: 1245-1255.

Desimone R, Duncan J, 1995. Neural mechanisms of selective attention. Annu Rev Neurosci 18: 193-222.

Dukas R, 1998a. Cognitive ecology: the evolutionary ecology of information processing and decision making. Chicago: University of Chicago Press.

Dukas R, 1998b. Constraints on information processing and their effects on behavior. In: Cognitive ecology (Dukas R, ed). Chicago: University of Chicago Press; 89-127.

Dukas R, 1999. Costs of memory: ideas and prediction. J Theor Biol 197: 41-50.

Dukas R, Clark CW, 1995a. Searching for cryptic prey: a dynamic model. Ecology 76: 1320-1326.

Dukas R, Clark CW, 1995b. Sustained vigilance and animal performance. Anim Behav 49: 1259-1267.

Dukas R, Ellner S, 1993. Information processing and prey detection. Ecology 74: 1337-1346.

Endler JA, 1984. Progressive background matching in moths and a quantitative measure of crypsis. Biol J Linn Soc Lond 22: 187-231.

Fite KV, Rosenfield-Wessels S, 1975. A comparative study of deep avian foveas. Brain Behav Evol 12: 97-115.

Godin JGJ, Smith SA, 1988. A fitness cost of foraging in the guppy. Nature 333: 69-71.

Hillyard SA, Vogel EK, Luck SJ, 1998. Sensory gain control (amplification) as a mechanism of selective attention: electrophysiological and neuroimaging evidence. Phil Trans R Soc Lond B 353: 1257-1270.

Kamil AC, Misthal RL, Stephens DW, 1993. Failure of simple optimal foraging models to predict residence time when quality is uncertain. Behav Ecol Sociobiol 4: 350-363.

Kastner S, De Weerd P, Desimone R, Ungerleider LG, 1998. Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. Science 282: 108-111.

Krause J, Godin JGJ, 1996. Influence of prey foraging posture on flight behavior and predation risk: predators take advantage of unwary prey. Behav Ecol Sociobiol 7: 264-271.

Langley CM, 1996. Search images: selective attention to specific visual features of prey. J Exp Psychol Anim Behav Process 22: 152-163.

Lawrence SE, 1985. Vigilance during easy and difficult foraging tasks. Anim Behav 33: 1373-375.

Lima SL, 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Adv Study Behav 27: 215-291.

Lima SL, Bednekoff PA, 1999. Back to the basics of anti-predatory vigilance: can non-vigilant animals detect attack? Anim Behav 58: 537-543.

Lima SL, Dill LM, 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68: 619-640.

Martin GR, 1986. The eye of a passeriform bird, the European starling (*Sturnus vulgaris*): eye movement amplitude, visual fields and schematic optics. J Comp Physiol A 159: 545-557.

Metcalfe NB, Huntingford FA, Thorpe JE, 1987. Predation risk impairs diet selection in juvenile salmon. Anim Behav 35: 931-933.

Milinski M, 1984. A predator's costs of overcoming the confusion-effect of swarming prey. Anim Behav 32: 1157-1162.

Milinski M, 1990. Information overload and food selection. In: Behavioral mechanisms of food selection (Hughes RN, ed). Berlin: Springer-Verlag; 721-737.

Milinski M, Heller R, 1978. Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.). Nature 275: 642-644.

Pulliam HR, 1973. On the advantage of flocking. J Theor Biol 38: 419-422.

Rees G, Frith CD, Lavie N, 1997. Modulating irrelevant motion perception by varying attentional load in an unrelated task. Science 278: 1616-1619.

Riley DA, Leith RC, 1976. Multidimensional psychophysics and selective attention in animals. Psychol Bull 83: 138-160.

Sargent TD, 1976. Legion of night: the underwing moths. Amherst: University of Massachusetts Press.

Shettleworth SJ, 1998. Cognition, evolution, and behaviour. Oxford: Oxford University Press.

Vreven D, Blough PM, 1998. Searching for one or many targets: effects of extended experience on the runs advantage. J Exp Psychol Anim Behav Process 24: 98-105.

Ydenberg RC, Dill LM, 1986. The economics of fleeing from predators. Adv Study Behav 16: 229-249.