THE ROYAL SOCIETY

Behavioural and ecological consequences of limited attention

Reuven Dukas†

Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada V5A 1S6 (*dukas@mcmaster.ca*)

Ecological research in the past few decades has shown that most animals acquire and respond adaptively to information that affects survival and reproduction. At the same time, neurobiological studies have established that the rate of information processing by the brain is much lower than the rate at which information is encountered in the environment, and that attentional mechanisms enable the brain to focus only on the most essential information at any given time. Recent integration of the ecological and neurobiological approaches helps us to understand key behaviours with broad ecological and evolutionary implications. Specifically, current data indicate that limited attention affects diet choice and constrains animals' ability simultaneously to feed and attend to predators. Recent experiments also suggest that limited attention influences social interactions, courtship and mating behaviour.

Keywords: attention; cognition; foraging; mate choice; predation

1. INTRODUCTION

Limited attention means that the brain has a limited rate of information processing. Limited attention may constrain behaviour. For example, many animals must search visually for cryptic items such as food and predators. Looking for such items requires complex pattern recognition, which is computationally demanding. This means that although the visual field of most animals is between 180° to 360°, animals must somehow restrict the amount of visual information processed at any given time (Broadbent 1965; Milinski 1990; Dukas 1998; Kastner & Ungerleider 2000). Similar problems of information overload are known in the auditory, somatosensory and olfactory domains (Drevets *et al.* 1995; Mondor & Zatorre 1995; Nams 1997).

Because limited attention is closely related to all other components of animal cognition, it is relevant to briefly define these components. Throughout this review, cognition refers to all stages of information processing, from the reception of stimuli by the sensory organs to decisions executed by the nervous system. Constraint is defined as anything that prevents, delays, or increases the cost of attaining a certain ability. Perception is the translation of environmental signals into neuronal representations. Learning is the ability to acquire a neuronal representation of either a new association between a stimulus and an environmental state or a new motor pattern. Long-term memory consists of all passive memory representations of previously learned information. Working memory comprises a small set of currently active neuronal representations. Unlike attention, working memory has a time dimension: working memory refers to the information stored in an activated state for some short duration, while attention refers to the information processed at any given moment. An individual typically attends only to a subset of the information in working memory, and working memory contains a tiny fraction of the information stored in long-term memory (Baddeley 1986; Cowan 1993, 2001; McElree 2001). Finally, problem solving is a search for the best action given the known states of relevant environmental features.

Most sensory neurons respond selectively to specific information, such as colour, brightness contrast, or sound frequency. Furthermore, in most sensory modalities, an individual neuron has a receptive field corresponding to a circumscribed area of the perceived environment. Because the neurons preserve the spatial relations of peripheral receptors, the brain contains numerous orderly maps of its surroundings, in which nearby neurons correspond to nearby locations in the environment (Kandel *et al.* 1995; Kaas 1997). Selective attention means that the activity of neurons with the appropriate receptive fields and stimulus preferences is either enhanced or synchronized while other neurons are suppressed (Kastner & Ungerleider 2000; Fries *et al.* 2001; Treue 2001).

While handling difficult tasks, focusing attention on one attribute or location enhances neuronal and behavioural performance compared with dividing attention among several attributes or locations (Vandenberghe *et al.* 1997; Kastner & Ungerleider 2000). For example, human subjects who had to decide whether two successive images differed slightly in shape, colour or speed performed better when informed which single attribute could be different between the images than when told that the images could differ in any of the three attributes. Brain imaging indicated that the performance enhancement was associated with heightened neuronal activity of the specific brain region processing each attribute (Corbetta *et al.* 1990).

---

† Present address: Department of Psychology, McMaster University, 1280 Main Street West, Hamilton, Ontario L8S 4K1, Canada.

One contribution of 12 to a Theme Issue 'Information and adaptive behaviour'.

Phil. Trans. R. Soc. Lond. B (2002) **357**, 1539–1547
DOI 10.1098/rstb.2002.1063

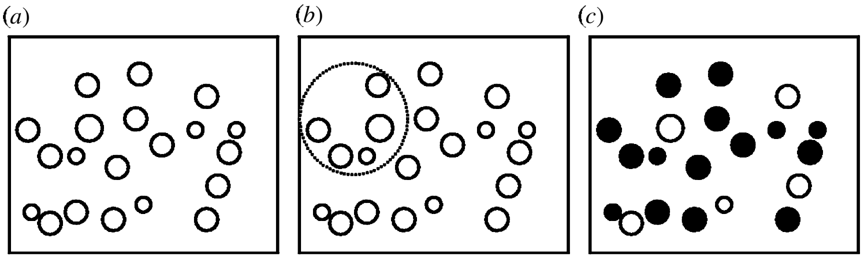

Figure 1. The effects of spatially- and stimulus-selective attention on target detection. All three panels contain the same target and background items at identical spatial configurations. The target is a circle that is larger than all other circles.
(*a*) Unfocused attention. (*b*) Spatially-selective attention: the target is inside the dotted circle (at the middle right side).
(*c*) Stimulus-selective attention: the target is a white circle (at the upper left side of the panel).

Two complementary means of information filtering are, first, focusing attention only on a small portion of the visual field at any given time (spatially-selective attention), and second, attending to one or a few relevant stimuli while ignoring other information (stimulus-selective attention). Figure 1 illustrates the effects of spatially- and stimulus-selective attention on target detection. All three panels contain the same target and background items at identical spatial configurations. The target is a circle that is larger than all other circles. For illustration purposes, the detection task is not very difficult, but the difficulty can readily be increased by reducing the difference between the target and background items and by adding many more background items. In figure 1*a*, finding the target can be somewhat difficult. In figure 1*b* (spatially-selective attention), marking the general area of the target allows a subject to focus spatial attention on the approximate target location. This can increase the probability of detection and decrease the detection latency compared with the search task in figure 1*a*. In figure 1*c* (stimulus-selective attention), a subject is told that the target is a white circle, which allows focusing attention only on the white circles. Again, this increases the probability of detection and decreases the detection latency compared with the search task in figure 1*a*.

Limited attention may affect all major categories of animal activity, including foraging, anti-predatory behaviour, mating and social interactions. Whereas the focus on foraging in this review reflects the current literature bias, the shorter sections devoted to activities other than foraging clearly indicate promising avenues for further research.

2. EFFECTS OF LIMITED ATTENTION ON FORAGING

(a) *Search rate and habitat choice*

At any given time, animals can either attend to a large portion of the visual field and coarsely perceive their surroundings, or focus on a narrow angle to extract fine details. The focus of attention can rapidly shift in angle width and spatial position, with the constraint that there be a negative correlation between the angle width and level of detail per degree of the visual field (Eriksen & Yen 1985; Van Essen *et al.* 1991; Connor *et al.* 1997). Because searching for conspicuous targets can be successful even with no perception of fine details, such a search can be conducted with a wide attentional angle, allowing a search of a large area per unit time. By contrast, searching for a cryptic target, which requires attention devoted to minute details, must be conducted with a narrow attentional angle covering only a small area per unit time. In other words, whereas an easy search task allows for a high search rate, an effective search for cryptic targets requires a low search rate, even if the latter means a lower encounter rate with potential prey (see Gendron & Staddon 1983).

Drift-feeding fishes provide an excellent model system for studying the effect of limited attention on food search because they stay stationary while letting the current bring drifting food to them. Hughes & Dukas (2003) modelled how limited attention would affect the area searched by a drift-feeding fish at any given time under different stream conditions. The model has five components: (i) a library from which a fish can choose the shape and size of its search area; (ii) an equation that predicts the probability that a prey organism will be detected while it is in a 'cell' within the fish's search area; (iii) a procedure for predicting the distribution of prey detection locations; (iv) a method for predicting the fish's net rate of energy intake; and (v) a way to predict which of the available search areas a fish will select from the library in order to maximize its net rate of energy intake. The model's predictions are in close agreement with experimental data showing a narrowing of the search angle by Arctic grayling when either current velocity or prey crypticity are increased (O'Brian & Showalter 1993). When the current velocity increases, a larger volume of water passes by the fish per unit time. Narrowing the search angle compensates for the increase in rate of water flow, allowing the maintenance of some optimal water volume searched per unit time. Similarly, increased prey crypticity favours a narrower attentional focus, which allows the fish to maintain a higher probability of prey detection than with a wider angle (figure 2; Hughes & Dukas 2003). This means that factors increasing prey crypticity, such as increased turbidity due to environmental degradation, may decrease the fish feeding rate, and consequently, alter growth rate and habitat choice (Metcalfe *et al.* 1997). Such environmental variables may also influence anti-predatory behaviour, an issue examined below. Critical tests are necessary to verify that limited attention is indeed a key constraint influencing the searching behaviour of drift-feeding fishes.

(b) *Diet choice*

Attending selectively to the visual attributes of specific prey can increase the probability of detection compared with spreading attention over distinct attributes of different prey types. Tinbergen (1960) was perhaps the first ecologist to suggest that something akin to limited atten-

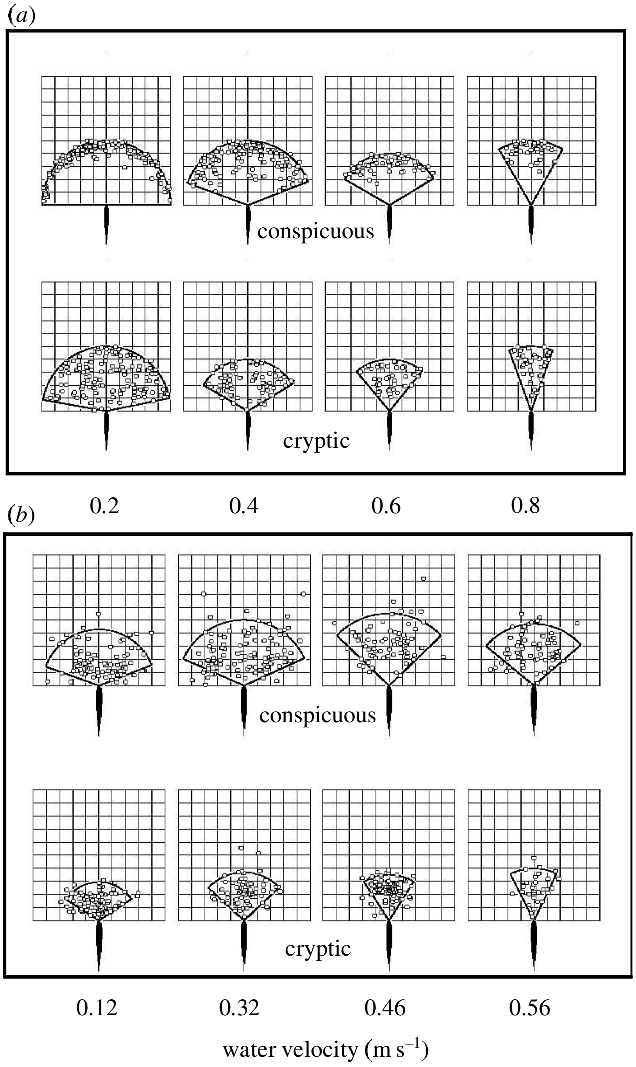

Figure 2. The effects of current velocity and prey conspicuousness on the angle of search for food items by drift-feeding fishes. Each panel consists of eight grids with a spacing of 10 cm. Each grid represents the area upstream from the fishes, which is shown at the bottom centre of the grid. The small squares are prey items at the location of detection. The simulations in (*a*) are based on a prey model that incorporates the effects of limited attention to predict the locations at which simulated prey items would be detected by the fishes. (*b*) This depicts empirical data for Arctic grayling from O'Brian & Showalter (1993). The simulations and empirical data are in qualitative agreement: both show a decrease in search angles with increased water velocity and with a change from conspicuous to cryptic prey. Both panels are modified from Hughes & Dukas (2003).

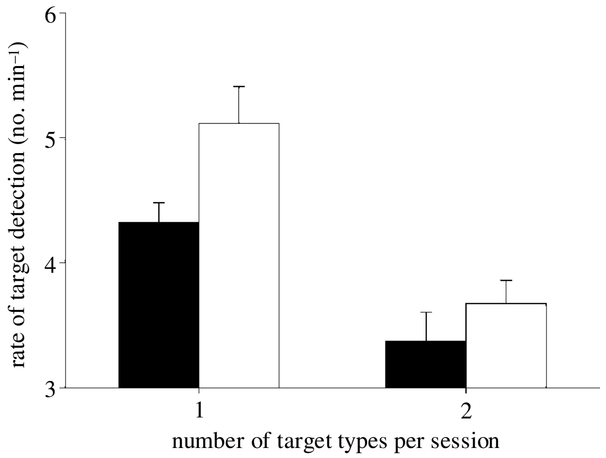

Figure 3. The rate of target detection by blue jays in sessions in which either they searched for only one of two cryptic targets, or they searched for the two targets at the same time. The black and white bars depict the two target types. The target-detection rate was significantly lower when the jays divided attention between the two target types ($p < 0.001$). From Dukas & Kamil (2001), with permission.

tion affects birds searching for cryptic insects: '...the intensity of predation depends to a great extent on the use of specific searching images. This implies that the birds perform a highly selective sieving operation on the visual stimuli reaching their retina. ...There is some reason to believe that the birds can use only a limited number of different searching images at the same time' (p. 332). Later, MacArthur (1972) clarified that 'such a search image will still be proper economic behaviour if ...the bird is incapable of simultaneously remembering that both beetles and green caterpillars are good to eat, or if the struggle to remember hampers his search' (p. 63). Several experiments over the past few decades are in agreement with the search image hypothesis (e.g. Dawkins 1971; Pietrewicz & Kamil 1979; Reid & Shettleworth 1992; Bond & Kamil 1999), although the term itself has been controversial, in part, because of misunderstandings of the cognitive mechanisms involved.

At least four cognitive traits: learning, long-term memory, working memory and attention, are typically involved in a search for cryptic prey. First, an animal has to recognize that a certain food type is palatable and nutritious, and learn the features distinguishing it from its surrounding background, including unacceptable food items. Second, the animal has to maintain long- and short-term representations of that information. Some studies indicate that interfering activities, including searching for alternative food types, may disrupt the memory about how to find a certain food (Anderson 1995; Dukas & Clark 1995; Wickens 2000). However, experiments with blue jays searching for cryptic targets do not support the memory-interference hypothesis (Dukas & Kamil 2001).

Finally, both spatially-selective attention and stimulus-selective attention influence search for cryptic food. Spatially-selective attention would affect search rate, an issue discussed above (§ 2a). The modification of search rate is not a mutually exclusive alternative to stimulus-selective attention. Animals searching for highly cryptic prey would typically adopt a low search rate and focus attention on a single prey type (see Reid & Shettleworth 1992; Dukas & Ellner 1993; Plaisted & Mackintosh 1995). The effect of stimulus-selective attention was quantified in recent laboratory experiments with blue jays searching for familiar cryptic digital targets. When the jays had to divide attention between searching for two target types simultaneously, they showed a 25% lower target-detection rate than when they were allowed to focus attention on one target type at a time (figure 3; Dukas & Kamil 2001). That is, an unfocused search for highly cryptic prey is less efficient than a focused search for one prey type at a time. Experiments with pigeons also indicate the importance of stimulus-selective attention in searching for cryptic targets (Blough 1991; Langley 1996).

In summary, limited attention is a key constraint underlying searching for cryptic food. When the search task is very difficult and each of the cryptic food types has a distinct appearance, limited attention may necessitate a selective search for one food type at a time. When a few distinct prey types are equally cryptic and profitable but different in abundance, it is optimal to attend selectively to the most common type (Dukas & Ellner 1993). Such selective searching may be labelled 'search image'. It is probably most appropriate to define search image as a selective search for a particular cryptic prey type, which involves an increased probability of detecting that type and a reduced probability of detecting other distinct prey types. Perhaps the most common instances of search image are cases in which predators learn to focus their attention on the cryptic prey type that they have detected most frequently in their recent feeding. This means that animals searching for cryptic prey may show frequency-dependent predation, focusing on the common prey type while overlooking rare prey types. Possible implications of such behaviour are discussed in § 6.

(c) *Host–plant specialization in insects*

The section on diet choice indicated that limited attention can explain animals' tendencies to search for one food type at any given time. Limited attention may partially explain why insect herbivores have a restricted diet even when they are not limited by deterring secondary compounds (Bernays 2001). Recent experiments indicate that specialist insects forage more efficiently than closely related generalists (Jans & Nylin 1997; Bernays & Funk 1999), and that generalist species forage more efficiently when they feed on items of just one food type than when they feed on several types (Bernays 1998, 1999). For example, Bernays & Funk (1999) compared the speed and accuracy of host finding between specialist and generalist populations of the aphid *Uroleucon ambrosiae*. Populations of this species from Eastern USA are highly specific to the host plant *Ambrosia trifida* (Asteraceae), whereas those from the South Western USA feed on a variety of taxa from the Asteraceae in addition to *A. trifida,* their preferred host. First, a larger proportion of specialists than generalists found an *A. trifida* plant from a distance of 1 m in a wind tunnel. Second, a larger proportion of specialists than generalists reached *A. trifida* placed between two non-host plants. Third, the specialists were more persistent than the generalists in their initial probing attempts into the host-plant tissue. Fourth, the specialists spent a greater proportion of the 12 h trials feeding than the generalists. Finally, after spending 24 h in an enclosure containing *A. trifida*, the optimal host, and three sub-optimal host species from the Asteraceae, a higher fraction of specialists than generalists settled on *A. trifida.*

It appears that insects that handle less information perform better than ones that deal with more information and that this, together with other advantages of specialization, can explain the restricted diet of many phytophagous insects. Because limited attention has been studied mostly in vertebrates, further experiments are necessary to critically identify the mechanisms limiting information processing in insects and their relevance for diet specialization.

(d) *Predator confusion*

Eighty years ago, Miller (1922, p. 123) suggested that 'it is easier to hit a single bird than one of a dozen. The number of possibilities in the latter case distracts the attention from any one individual, and in consequence all are likely to escape.' There are two ways of refining the above hypothesis. First, a predator must divide its attention among many of the visible members of a swarm, and the consequent cost of divided attention is a reduced probability of capture. This possibility is unlikely because it is well established that animals can selectively attend to a small subset of the available visual information (see § 1). Second, it is difficult for a predator to select the target of focused attention out of numerous members of a swarm because they all appear identical. Experimental data and human experience indeed indicate that the cognitive task of selecting a target within a moving swarm of apparently identical items is more demanding than that of feeding on either isolated prey or a group of visually distinct individuals. For example, Landeau & Terborgh (1986) presented largemouth bass with shoals of eight silvery minnows containing between one and seven blue-painted individuals. The bass's capture rate was twice as high when the shoals had one or two odd individuals of either colour (for example, either two blue and six brown minnows, or six blue and two brown minnows). This experiment indicates that oddity eliminates the confusion caused by the need to select for a single fish among several similar individuals, but it does not fully eliminate the possibility of other effects of the odd individuals on shoal behaviour and coherence, which may increase predation.

Although several studies indicate that predators have difficulty in dealing with swarming prey (e.g. Godin & Smith 1988; Milinski 1984, 1990), the predator-confusion hypothesis requires further critical tests. For instance, it is not clear why a predator cannot 'lock-in' on an individual at the swarm's edge, where target selection seems easier. Some species, such as flocks of shorebirds, apparently prevent such possible predator strategy by employing a flight pattern with frequent, abrupt directional changes. Finally, one must control for the possibility that a predator attempts to avoid injury due to collision with swarm members other than its selected target. While it is obvious that a raptor aiming for the centre of a flying bird-flock may incur severe injury, the effect of even slight eye damage to a predator attacking a fish school may not be negligible. In short, neither neurobiological nor ecological data currently provide critical support for the predator-confusion hypothesis, and this issue requires further critical tests.

3. EFFECTS OF LIMITED ATTENTION ON COURTSHIP

Limited attention has not been widely studied in the domain of courtship and mate choice. Nevertheless, the sections below illustrate the possible importance of limited attention in structuring courtship behaviour and sexually selected traits.

(a) *Selective attention*

The fact that an animal has the sensory capacity to perceive certain information does not necessarily imply that it actually attends to that information while searching for a mate, choosing among potential mates, or watching courtship displays. It is known that animals only attend to a small fraction of the information available at any given time; hence female bias in directing attention to some stimuli may select for certain male courtship patterns. This idea is a variation of the sensory exploitation hypothesis (Ryan 1990; Endler 1992).

Selective attention has recently been employed to explain the structured choruses produced by calling males of various acoustic insects and amphibians. Females in at least some of these species selectively attend to and pursue the first call of a sequence, hence favouring males that produce the leading call. A strategy for increasing the probability of producing the leading call is to refrain from calling immediately after another call. This strategy, however, would drastically reduce a male's call frequency in choruses consisting of numerous individuals. To overcome this limitation, the males selectively attend to, and refrain from calling after, their closest neighbours only, a compromise allowing them to produce a high rate of leading calls among their immediate neighbours (Greenfield *et al.* 1997; Snedden *et al.* 1998; Greenfield & Rand 2000).

(b) *Attracting, focusing and sustaining attention*

Unlike feeding situations, where foragers actively seek prey, courtship settings may involve females engaged in non-mating tasks. In such conditions, the males might have to alert the females to their presence by somehow attracting the females' attention. This can be done, for example, by using abrupt movements, which attract the attention of most animals. Typically, animals would direct their eyes towards the moving object, which may be a prey or predator, in order to inspect it closely with the highest-resolution portion of their retinas (Ingle 1982). It has been argued that males in many species have adopted courtship patterns consisting of high-velocity motion patterns because such movements attract female attention (Fleishman 1992; Persons *et al.* 1999).

Richards (1981) suggested that the initial few notes in the song of many passerines, which have a narrower frequency range and wider temporal spacing than the rest of the song, are structured for high detectability, while the rest of the song is more complex but less conspicuous at a distance. In other words, the initial notes serve to attract the attention of potential listeners, who then focus on the remainder of the song.

Finally, in addition to initially attracting a female's attention, courtship displays may have been selected to keep the female's focus on the male. It is possible that the continuous movement typical of many courtship displays serves to keep the female's attention (see Endler 1992). Additional critical tests are necessary to establish the effects of limited attention on courtship.

4. ATTENDING TO MORE THAN ONE TASK AT THE SAME TIME

Animals must commonly handle more than one task at a time. An ubiquitous example is searching for food while avoiding predators. Other situations include attending to predators while playing, courting, or fighting (Blumstein 1998; Brick 1998) and dividing attention between searching for food and monitoring group members that may have found food (see Giraldeau & Caraco 2000). Limited attention may strongly affect the simultaneous execution of two or more tasks.

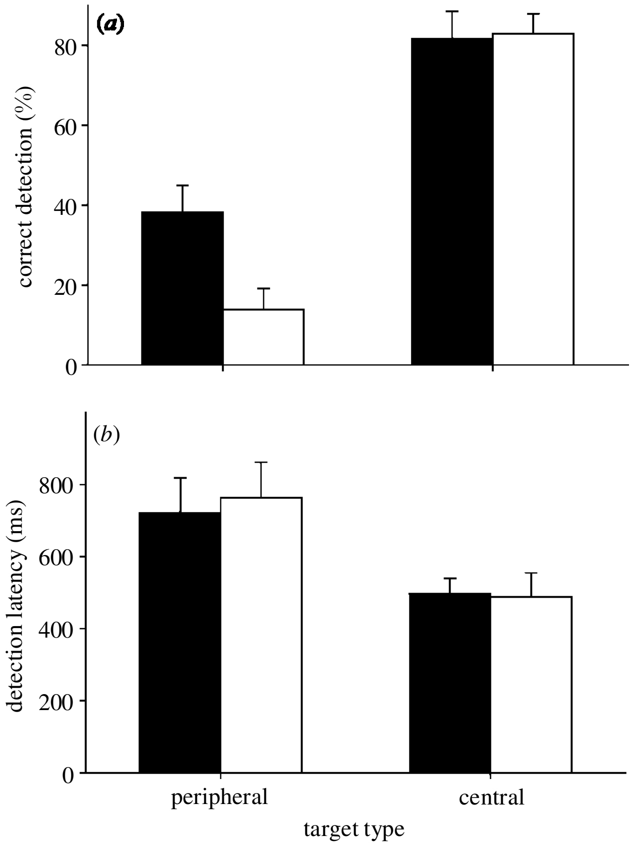

Figure 4. (*a*) Results from a laboratory experiment with blue jays searching for cryptic digital targets agree with the prediction that limited attention diminishes detection performance under challenging search conditions. The percentage of correct detection (mean + 1 s.e.) of the peripheral target was significantly higher during the 'centre easy' (filled bars) than 'centre difficult' (open bars) sessions ($p < 0.001$), but correct detection of the central target was similar in either session type. (*b*) The alternative that the jays had access time to switch their eyes or attention to the peripheral targets under the centre easy condition is not supported by the latency data. The average detection latency of the peripheral target was similar during the centre easy (filled bars) and centre difficult (open bars) conditions. Detection latency of the central target was also similar during the centre easy and centre difficult conditions. From Dukas & Kamil (2000), with permission.

A difficult food-search task would require a narrower focus of spatial attention than an easy task. Hence searching for highly cryptic food may limit an animal's ability to notice predators simultaneously approaching at the periphery of the visual field. In a controlled laboratory experiment testing that prediction, blue jays that had to detect cryptic targets at the centre of the visual field were three times less likely to discover peripheral targets than when they were required to detect conspicuous targets at the centre of the visual field (figure 4). That is, even though the two experimental treatments (easy- and difficult-central detection) involved identical visual fields, identical conspicuousness of the peripheral targets and identical frequencies of target appearances within the visual field, the difficult-central detection treatment required more attention to be devoted to the centre of the visual field; this resulted in a much reduced frequency of detecting the peripheral targets than during the easy-central detection treatment (Dukas & Kamil 2000).

The results of the blue jay experiment are in agreement with data indicating increased probability of predation in fishes engaged in more challenging feeding tasks (Milinski 1990; Krause & Godin 1996). That is, whereas the laboratory jay study critically assessed the effect of limited attention but did not have predators, the fish studies quantified the effect of predators but did not critically test for the effect of limited attention. Together, these studies indicate that limited attention is a plausible cause of predation in nature.

The above discussion does not suggest that animals cannot conduct two tasks simultaneously. Rather, it indicates that performance on one or two tasks performed simultaneously may be compromised if the combined attentional requirements are high. It is probably impossible to predict *a priori* whether performance on simultaneous tasks would suffer due to limited attention. For example, there is some evidence that when the two tasks involve two different sensory systems rather than one (e.g. auditory and visual rather than two auditory tasks), performance may be less affected (Duncan *et al.* 1997). Similarly, one might predict that some animals possess specialized adaptations that enhance their performance on dual tasks. Finally, there are various ways of coping with limited attention in order to reduce its negative effects on performance. Two of these tactics are discussed in the next section.

5. COPING WITH LIMITED ATTENTION

(a) *Learning what to attend to*

Animals searching for cryptic targets, such as camouflaged food or concealed predators, may sometimes have to attend successively to a small area at a time, ultimately covering the whole visual field. In many cases, however, experience may indicate that certain spatial locations are more likely to harbour a target than other sites, so attention can be concentrated on these areas, allowing an increased probability of early detection and overall time saving. Tests with humans indeed indicate that they optimize the spatial distribution of attention, focusing more on locations where they are more likely to find targets (Shaw & Shaw 1977).

Efficient use of limited attention based on experience is a possible advantage of territoriality. For example, territorial animals may learn to pay more attention to routes used by predators and to abrupt movements at unexpected locations compared with movements at sites where plant movement occurs in windy weather. That is, in addition to merely learning about locations either rich in food or dangerous due to predator activity, animals may learn to selectively attend to locations and stimuli that are most likely to affect fitness. This filtering of information based on experience may significantly reduce information overload due to limited attention. The effect of experience on the spatial and temporal distribution of attention can readily be tested with non-human animals using a protocol similar to that of Shaw & Shaw (1977).

(b) *Proficiency can reduce attentional requirements*

Many tasks that are attention-demanding when executed by novices may require little attention after extensive learning. Hence, experts on that task may be able to conduct another task at the same time with little or no interference. For example, beginners would typically fully focus on operating an automobile, negotiating traffic and navigating, while experienced drivers may rely on 'automatic pilot' for these tasks while devoting most attention to a conversation with a passenger. Similarly, people who learn how to read focus initially on the letters and words. After acquiring good reading skills, readers identify letters and words with little attention, and thus can devote most attention to comprehension, which is much improved compared with that of novices (e.g. LaBerge & Samuels 1974; Logan 1988).

The changes in attentional requirements with skill acquisition have, to our knowledge, been studied only in humans, but they are probably relevant for other species as well. This indicates, for example, that an animal devoting 5 minutes to handling a novel food may be less likely to notice an approaching predator than an animal spending the same length of time on familiar food.

6. EVOLUTIONARY PERSPECTIVES: DIVERGENCE, POLYMORPHISM AND SPECIATION

In the section on diet choice (§ 2b), I discussed the possibility that limited attention would cause animals searching for cryptic prey to show frequency-dependent predation, focusing on the common prey type while overlooking rare types. This may lead to divergent selection on the visual appearance of coexisting cryptic taxa (Clark 1962). That mechanism has been invoked to explain the dissimilarity in the visual appearance of coexisting cryptic moth species subjected to bird predation (Ricklefs & O'Rourke 1975) and leaf-shape variation among *Passiflora* species attacked by *Heliconius* butterflies (Gilbert 1975). Neither the moth nor the *Passiflora* systems have been studied in the level of detail necessary to elucidate the exact role of predators and herbivores, respectively. Nevertheless, another butterfly–host system examined by Rausher (1978) suggests that a visually selective search by butterflies for their host plant selected for a change in plant leaf shape.

The pipevine swallowtail butterfly (*Battus philenor*) uses two host *Aristolochia* species in east Texas. The most common species, *A. reticulata,* has the broad, ovate leaves characteristic of the genus, whereas the sympatric, rare *A. serpentaria* has long, narrow leaves. *Aristolochia serpentaria* also begins producing leaves one to two weeks later in the spring than *A. reticulata*. Ovipositing female swallowtails use leaf shape as a visual cue to locate and land on possible host plants, which are then inspected with tarsal chemoreceptors. The females readily learn to associate chemical cues in the leaf with its shape (Papaj 1986). It appears that early in the spring, the butterflies learn to focus their search on the broad leaves of the common host, which lowers the probability of discovering the rare, narrow-leaf host. Whereas learning appears to be the central cognitive mechanism determining the selective search for broad leaves, it is possible that selective attention reduces the chance that the butterflies would discover the host with narrow leaves (Rausher 1978). Further tests are necessary to quantify the role of selective attention in this system.

Overall, there is no evidence that selective attention by a single predator species has been responsible for patterns of divergent appearance in any taxa. Feasible alternatives for the apparent divergence include chance and the activity of a few predators with distinct perceptual abilities. Nevertheless, divergent selection on the appearance of sympatric prey species sharing a predator is theoretically feasible (Abrams 2000) and requires experimental tests.

Limited attention of a predator searching for cryptic prey may also lead to divergent selection intraspecifically, generating and maintaining individuals that are visually distinct from common conspecifics. Such individuals may have higher fitness if overlooked by their predator (Clark 1962; Allen 1988). To demonstrate that polymorphism is maintained by a predator focusing on a common morph while overlooking rare ones, a few conditions must exist. First there has to be only a single predator. The alternative of two or more predators with different sensory capacities is highly feasible (Endler 1988; Abrams 2000). For example, Losey *et al.* (1997) studied the causes of polymorphism in the pea aphid, *Acyrthosiphon pisum*, which has red and green morphs. They found that the wasp parasitoid, *Aphidius ervi* preferentially attacked the green morph, while ladybird beetles, *Coccinella septempunctata* preyed more often on the red morph. Losey *et al.* (1997) demonstrated that the aphid polymorphism could be maintained by balanced selection from its two natural enemies.

Second, the different morphs must occur within the same microhabitats. The alternative that distinct morphs have evolved and been maintained because each appears cryptic on visually distinct backgrounds is very likely. For example, predation experiments with wild scrub jays indicated that the unstriped green morph of the walking stick, *Timema cristinae*, is most cryptic on its preferred host plant, *Ceanothus spinosus*, while the striped green morph is most cryptic on its preferred plant, *Adenostoma fasciculatum* (Sandoval 1994). Finally, the predator must indeed take a higher proportion of the more common morph. Bond & Kamil (1998) conducted a long-term laboratory experiment with blue jays searching for three digital images. The starting image frequencies were identical and the combined size of the three image populations was kept constant. At the end of each predation session, each image multiplied asexually in proportion to its surviving population. Initially, the blue jays preferred the two images that they found less cryptic, reducing the proportions of their populations to about 12.5% each. Then the blue jays preferentially targeted the most common, albeit most cryptic image. That is, the jays focused on the common target while overlooking the rare, visually distinct targets even though the jays had been highly effective at detecting these targets earlier.

In summary, the behavioural evidence indicates that predators' selective attention on the most common prey morph may help to maintain prey polymorphism. It is not clear, however, whether any documented case of polymorphism in nature is indeed maintained due to frequency-dependent predation by a single predator. Other ecological conditions mentioned earlier in this section may be responsible for the observed polymorphism, and experimental studies are necessary to evaluate the relative role of each mechanism. Regardless of the exact mechanism, if divergent selection in appearance due to predation is coupled with assortative mating, reproductive isolation and speciation may occur. This theoretically feasible idea requires empirical testing.

7. CONCLUSIONS AND PROSPECTS

The integration of neurobiological and ecological research helps us to understand how limited attention influences several foraging and anti-predatory behaviours and indicates the possible importance of selective attention in courtship, mate choice and social behaviour. Most notably, current data indicate that limited attention affects diet choice and constrains animals' ability simultaneously to feed and attend to predators. The field is now ripe for critically evaluating the ecological and evolutionary effects of limited attention. Does selective attention by a predator cause divergent selection in the visual appearance of co-occurring cryptic prey species? Is there a clear case where polymorphism is maintained by a single predator focusing on the most common morph? If so, what are the dynamics of frequency-dependent selection over prey generations? We know most about attention in the visual domain, but neurobiological and behavioural studies indicate similar effects of attention in the auditory, somatosensory and olfactory domains (Drevets *et al.* 1995; Mondor & Zatorre 1995; Nams 1997). The evolutionary and ecological effects of limited attention in these areas are yet to be explored.

I thank L. Bernays, C. Clark, L Chittka, S. Dall, L. Dill and D. Osorio for comments on the manuscript. My work was supported by NSERC operating grants to C. W. Clark, A. Ø. Mooers and B. D. Roitberg.

REFERENCES

Abrams, P. A. 2000 Character shifts of prey species that share predators. *Am. Nat.* **156**, S45–S61.

Allen, J. A. 1988 Frequency-dependent selection by predators. *Phil. Trans. R. Soc. Lond.* B **319**, 485–503.

Anderson, J. R. 1995 *Learning and memory*. New York: Wiley.

Baddeley, A. 1986 *Working memory*. Oxford University Press.

Bernays, E. A. 1998 The value of being a resource specialist: behavioral support for a neural hypothesis. *Am. Nat.* **151**, 451–464.

Bernays, E. A. 1999 When host choice is a problem for a generalist herbivore: experiments with the whitefly, *Bemisia tabaci*. *Ecol. Entomol.* **24**, 260–267.

Bernays, E. A. 2001 Neural limitations in phytophagous insects: implications for diet breadth and evolution of host affiliation. *A. Rev. Entomol.* **46**, 703–727.

Bernays, E. A. & Funk, D. J. 1999 Specialists make faster decisions than generalists: experiments with aphids. *Proc. R. Soc. Lond.* B **266**, 151–156. (DOI 10.1098/rspb.1999.0615.)

Blough, P. 1991 Selective attention and search images in pigeons. *J. Exp. Psychol. Anim. Behav. Processes* **17**, 292–298.

Blumstein, D. T. 1998 Quantifying predation risk for refuging animals: a case study with golden marmots. *Ethology* **104**, 504–516.

Bond, A. B. & Kamil, A. C. 1998 Apostatic selection by blue jays (*Cyanocitta cristata*) searching for virtual prey produces balanced polymorphism. *Nature* **395**, 594–596.

Bond, A. B. & Kamil, A. C. 1999 Searching image in blue jays: facilitation and interference in sequential priming. *Anim. Learn. Behav.* **27**, 461–471.

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

Broadbent, D. E. 1965 Information processing in the nervous system. *Science* **150**, 457–462.

Clark, B. 1962 Balanced polymorphism and the diversity of sympatric species. In *Taxonomy and geography* (ed. D. Nichols), pp. 47–70. Oxford: Systematics Associations.

Connor, C. E., Preddie, D. C., Gallant, J. L. & Van Essen, D. C. 1997 Spatial attention effects in macaque area V4. *J. Neurosci.* **17**, 3201–3214.

Corbetta, M., Miezin, S., Dobmeyer, G. L., Shulman, G. L. & Petersen, S. E. 1990 Attentional modulation of neural processing of shape, color, and velocity in humans. *Science* **248**, 1556–1559.

Cowan, N. 1993 Activation, attention, and short-term memory. *Memory Cogn.* **21**, 162–167.

Cowan, N. 2001 The magical number 4 in short-term memory: a reconsideration of mental storage capacity. *Behav. Brain Sci.* **24**, 87–185.

Dawkins, M. 1971 Perceptual changes in chicks: another look at the 'search image' concept. *Anim. Behav.* **19**, 566–574.

Drevets, W. C., Harold, B., Videen, T. O., Snyder, A. Z., Simpson, J. R. & Raichie, M. E. 1995 Blood flow changes in human somatosensory cortex during anticipated stimulation. *Nature* **373**, 249–252.

Dukas, R. 1998 Constraints on information processing and their effects on behavior. In *Cognitive ecology* (ed. R. Dukas), pp. 89–127. University of Chicago Press.

Dukas, R. & Clark, C. W. 1995 Searching for cryptic prey: a dynamic model. *Ecology* **76**, 1320–1326.

Dukas, R. & Ellner, S. 1993 Information processing and prey detection. *Ecology* **74**, 1337–1346.

Dukas, R. & Kamil, A. C. 2000 The cost of limited attention in blue jays. *Behav. Ecol.* **11**, 502–506.

Dukas, R. & Kamil, A. C. 2001 Limited attention: the constraint underlying search image. *Behav. Ecol.* **12**, 192–199.

Duncan, J., Sander, M. & Ward, R. 1997 Restricted attentional capacity within but not between sensory modalities. *Nature* **387**, 808–810.

Endler, J. A. 1988 Frequency-dependent predation, crypsis and aposomatic coloration. *Phil. Trans. R. Soc. Lond.* B **319**, 505–523.

Endler, J. A. 1992 Signals signal conditions and the direction of evolution. *Am. Nat.* **139**, S125–S153.

Eriksen, C. W. & Yen, Y. Y. 1985 Allocation of attention in the visual field. *J. Exp. Psychol. Hum. Percep. Perform.* **11**, 583–597.

Fleishman, L. J. 1992 The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *Am. Nat.* **139**, S36–S61.

Fries, P., Reynolds, J. H., Rorie, A. E. & Desimone, R. 2001 Modulation of oscillatory neuronal synchronization by selective visual attention. *Science* **291**, 1560–1563.

Gendron, R. P. & Staddon, J. E. R. 1983 Searching for cryptic prey: the effects of search rate. *Am. Nat.* **121**, 172–186.

Gilbert, E. L. 1975 Ecological consequences of a coevolved mutualism between butterflies and plants. In *Coevolution of animals and plants* (ed. E. Gilbert & P. H. Raven), pp. 210–240. Austin, TX: University of Texas Press.

Giraldeau, L.-A. & Caraco, T. 2000 *Social foraging theory. Monographs in behavior and ecology*. Princeton University Press.

Godin, J. G. J. & Smith, S. A. 1988 A fitness cost of foraging in the guppy. *Nature* **333**, 69–71.

Greenfield, M. D. & Rand, A. S. 2000 Frogs have rules: selective attention algorithms regulate chorusing in *Physalaemus pustulosus* (Leptodactylidae). *Ethology* **106**, 331–347.

Greenfield, M. D., Tourtellot, M. K. & Snedden, W. A. 1997 Precedence effects and the evolution of chorusing. *Proc. R. Soc. Lond.* B **264**, 1355–1361. (DOI 10.1098/rspb.1997.0188.)

Hughes, N. F. & Dukas, R. 2003 A model of prey detection by drift-feeding fish. (In preparation.)

Ingle, D. J. 1982 Organization of visuomotor behaviors in vertebrates. In *Analysis of visual behavior* (ed. D. J. Ingle, M. A. Goodale & R. J. W. Mansfield), pp. 67–109. Cambridge, MA: MIT Press.

Jans, K. & Nylin, S. 1997 The role of female search behaviour in determining host plant range in plant feeding insects: a test of the information processing hypothesis. *Proc. R. Soc. Lond.* B **264**, 701–707. (DOI 10.1098/rspb.1997.0100.)

Kaas, J. H. 1997 Topographic maps are fundamental to sensory processing. *Brain Res. Bull.* **44**, 107–112.

Kandel, E. R., Schwartz, J. H. & Jessell, T. M. 1995 *Essentials of neural science and behavior*. Norwalk, OH: Appleton & Lange.

Kastner, S. & Ungerleider, L. G. 2000 Mechanisms of visual attention in the human cortex. *A. Rev. Neurosci.* **23**, 315–341.

Krause, J. & Godin, J. G. J. 1996 Influence of prey foraging posture on flight behavior and predation risk: predators take advantage of unwary prey. *Behav. Ecol.* **7**, 264–271.

LaBerge, D. & Samuels, S. J. 1974 Toward a theory of automatic processing in reading. *Cogn. Psychol.* **6**, 293–323.

Landeau, L. & Terborgh, J. 1986 Oddity and the 'confusion effect' in predation. *Anim. Behav.* **34**, 1372–1380.

Langley, C. M. 1996 Search images: selective attention to specific visual features of prey. *J. Exp. Psychol. Anim. Behav. Processes* **22**, 152–163.

Logan, G. D. 1988 Toward an instance theory of automatization. *Psychol. Rev.* **95**, 492–527.

Losey, J. E., Ives, A. R., Harmon, J., Ballantyne, F. & Brown, C. 1997 A polymorphism maintained by opposite patterns of parasitism and predation. *Nature* **388**, 269–272.

MacArthur, R. H. 1972 *Geographical ecology*. Princeton University Press.

McElree, B. 2001 Working memory and focal attention. *J. Exp. Psychol. Learn. Memory Cogn* **27**, 817–835.

Metcalfe, N. B., Valdimarsson, S. K. & Fraser, N. H. C. 1997 Habitat profitability and choice in a sit-and-wait predator: juvenile salmon prefer slower currents on darker nights. *J. Anim. Ecol.* **66**, 866–875.

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* (ed. R. N. Hughes), pp. 721–737. Berlin: Springer.

Miller, R. C. 1922 The significance of the gregarious habit. *Ecology* **3**, 122–126.

Mondor, T. A. & Zatorre, R. J. 1995 Shifting and focusing auditory spatial attention. *J. Exp. Psychol. Hum. Percept. Perform.* **21**, 387–409.

Nams, V. O. 1997 Density-dependent predation by skunks using olfactory search images. *Oecologia* **110**, 440–448.

O'Brian, W. J. & Showalter, J. J. 1993 Effects of current velocity and suspended debris on the drift feeding of Arctic greylings. *Trans. Am. Fisheries Soc.* **122**, 609–615.

Papaj, D. R. 1986 Conditioning of leaf-shape discrimination by chemical cues in the butterfly, *Battus philenor*. *Anim. Behav.* **34**, 1281–1288.

Persons, M. H., Fleishman, L. J., Frye, M. A. & Stimphil, M. E. 1999 Sensory response patterns and the evolution of visual signal design in anoline lizards. *J. Comp. Physiol. Sensory Neural Behav. Physiol.* **184**, 585–607.

Pietrewicz, A. & Kamil, A. C. 1979 Search image formation in the blue jay (*Cyanocitta cristata*). *Science* **204**, 1332–1333.

Plaisted, K. C. & Mackintosh, M. J. 1995 Visual search for cryptic stimuli in pigeons: implications for the search image and search rate hypotheses. *Anim. Behav.* **50**, 1219–1232.

Rausher, M. D. 1978 Search image for leaf shape in a butterfly. *Science* **200**, 1071–1073.

Reid, P. J. & Shettleworth, S. J. 1992 Detection of cryptic prey: search image or search rate? *J. Exp. Psychol. Anim. Behav. Processes* **18**, 273–286.

Richards, D. G. 1981 Alerting and message components in songs of rufous-sided towhees. *Behaviour* **76**, 223–249.

Ricklefs, R. & O'Rourke, K. 1975 Aspect diversity in moths: a temperate–tropical comparison. *Evolution* **29**, 313–324.

Ryan, M. J. 1990 Sexual selection, sensory systems and sensory exploitation. *Oxf. Surv. Evol. Biol.* **7**, 157–195.

Sandoval, C. P. 1994 Differential visual predation on morphs of *Timema christinae* (Phasmatodeae: Timemidae) and its consequences for host range. *Biol. J. Linn. Soc. Lond.* **52**, 341–356.

Shaw, M. L. & Shaw, P. 1977 Optimal allocation of cognitive resources to spatial locations. *J. Exp. Psychol. Hum. Percept. Perform.* **3**, 201–211.

Snedden, W. A., Greenfield, M. D. & Jang, Y. 1998 Mechanisms of selective attention in grasshopper choruses: who listens to whom? *Behav. Ecol. Sociobiol.* **43**, 59–66.

Tinbergen, L. 1960 The natural control of insects on pinewoods I. Factors influencing the intensity of predation by songbirds. *Archives Neerlandaises de Zoologie* **13**, 265–343.

Treue, S. 2001 Neural correlates of attention in primate visual cortex. *Trends Neurosci.* **24**, 295–300.

Vandenberghe, R., Duncan, J., Dupont, P., Ward, R., Poline, J. B., Bormans, G., Michiels, J., Mortelmans, L. & Orban, G. A. 1997 Attention to one or two features in left or right visual field: a positron emission tomography study. *J. Neurosci.* **17**, 3739–3750.

Van Essen, D. C., Olshsusen, B., Anderson, C. H. & Gallant, J. L. 1991 Pattern recognition, attention, and information bottlenecks in the primate visual system. *SPIE Conf. Visual Information Processing: From Neurons to Chips* **1473**, 17–28.

Wickens, C. D. 2000 *Engineering psychology and human performance*. Upper Saddle River, NJ: Prentice-Hall.