

Causes and Consequences of Limited Attention

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Key Words

Attention · Cognition · Diet · Foraging · Predation · Search image

Abstract

This review focuses on the evolutionary causes and consequences of limited attention, defined as the restricted rate of information processing by the brain. The available data suggest, first, that limited attention is a major cognitive constraint determining animals' search for cryptic food, and, second, that limited attention reduces animals' ability to detect predators while involved in challenging tasks such as searching for cryptic food. These two effects of limited attention probably decrease animal fitness. Furthermore, a simulated evolutionary study provides empirical support for the prediction that focused attention by predators selects for prey polymorphism. The neurobiological mechanisms underlying limited attention have been widely studied. A recent incorporation of that mechanistic knowledge into an ecological model suggests that limited attention is an optimal strategy that balances effective yet economical search for cryptic objects. The review concludes with a set of testable predictions aimed to expand the currently limited empirical knowledge on the evolutionary ecology of limited attention.

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Introduction

Many animals, from tiny insects to large-brained mammals, are capable of perceiving numerous stimuli through several sensory organs, integrating that information with knowledge already stored in memory, and acting upon that knowledge in ways that enhance fitness [Anderson, 1990; Cheney and Seyfarth, 1990; Seeley, 1996; Altmann, 1998; Dukas, 1999a; Dukas and Bernays, 2000]. Although animal cognitive abilities are remarkable, they are not unlimited. A few cognitive constraints that limit performance are low learning rate, imperfect long-term memory, limited working memory capacity and limited attention.

Attention is a well established research discipline in the fields of human psychology and neurobiology [Broadbent, 1965; Kastner and Ungerleider, 2000]. Only recently, however, behavioral ecologists have closely examined attention and its consequences for animal behavior, ecology and evolution. This review will focus on that recent work. Specifically, I will begin with a few definitions of key terms and then briefly summarize the vast neurobiological literature on attention. The main body of the review will focus on four questions: (1) Does limited attention affect animal behavior? (2) Does limited attention affect ecological and evolutionary interactions? (3) Does limited attention affect fitness? And, (4) why is attention limited? I will conclude by presenting a set of testable hypotheses regarding the evolutionary ecology of limited attention.

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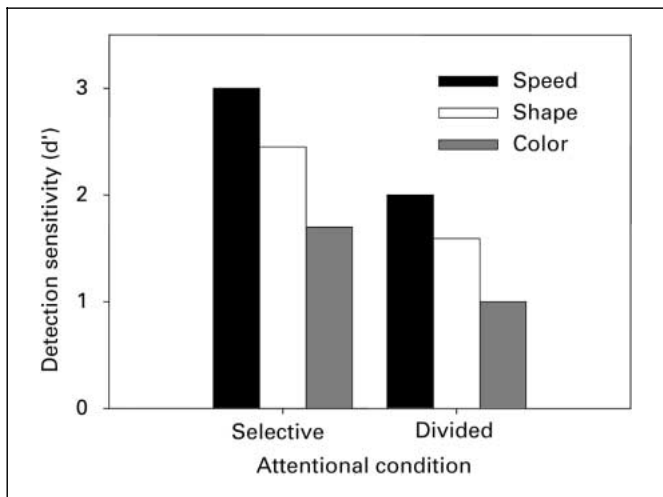


Fig. 1. Sensitivity (d'), which is a corrected measure of the frequency of correct detection, was significantly higher under the selective than divided attention condition ($p < 0.001$). Data from Corbetta et al. [1990b].

Definitions

Cognition may be defined as all stages of information processing, from the reception of stimuli by the sensory organs to decisions executed by the brain. 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 new information, which may be a new association between a stimulus and an environmental state, a new association between a stimulus and behavioral pattern, or a new motor pattern. Long-term memory consists of passive representations of information already learned. Working memory comprises a small set of the active neuronal representations. Finally, attention refers to the neuronal representation(s) activated at any given time. Limited attention means that the brain can process a very restricted amount of information at any given time. In other words, the brain has a limited rate of information processing. Although working memory and attention are tightly linked, working memory refers to the information stored in an activated state for some short time, whereas 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 only contains a tiny fraction of the information in long-term memory [Baddeley, 1986; Cowan, 1993, 2001; McElree, 2001].

The Neurobiology of Limited Attention

The neurobiology of attention has been studied mostly through electrophysiological recordings of single neurons in monkeys and imaging of large neuronal populations in humans using either positron emission tomography (PET) or functional magnetic resonance imaging (fMRI). Similar conclusions about attention have been reached with the different techniques and subject species: when subjects face a difficult detection task involving a few highly cryptic distinct stimuli, focusing attention on a given stimulus is correlated with enhanced response and sharpened selectivity of the neurons that process that stimulus, and a diminished activity of the neurons processing other stimuli. Simultaneous behavioral tests reveal that the probability of detecting the given stimulus is increased while the probability of detecting other stimuli is decreased [Moran and Desimone, 1985; Spitzer et al., 1988; Heinze et al., 1994; Drevets et al., 1995; Kastner and Ungerleider, 2000]. For example, human subjects, who had to decide whether two successive images differed slightly in shape, color or speed, performed better when informed which single attribute would be different between the images than when told that the images could differ in any of the three attributes (fig. 1). Brain imaging indicated that the performance enhancement was associated with heightened neuronal activity of the specific brain region processing each attribute [Corbetta et al., 1990a, b].

Although the exact neurobiological mechanisms that underlie limited attention are not well understood, it is easy to obtain an intuitive understanding of limited attention. An enormous rate of information processing is required for reconstructing a scene such as one's visual environment. Hence only a small proportion of the information available at any given time can be processed by the part of the nervous system devoted for vision. For example, in primates, the eyes can receive the raw information constituting the surrounding visual scene, but the optical nerve already transmits only 2% of the information captured by the retinas. Most importantly, even though approximately 60% of the primate neurocortex is devoted to vision, the visual cortex processes only 1% of the information transmitted by the optical nerve at any given time [Van Essen et al., 1991, 1992; Van Essen and Anderson, 1995; Barton, 1998]. That is, even though the rate of visual information processing by the cortex is only about 0.02% of the raw visual information, this amounts to a rather high information flow requiring a large volume of nervous system and resulting in the superb visual abili-

ty characterizing primates. Still, much of one's visual environment remains unprocessed at any given time and this necessary neglect may affect individual behavior and fitness.

Does Limited Attention Affect Animal Behavior?

Behavioral Experiments

The section above indicated that humans and monkeys perform better on difficult target detection tasks when focusing rather than dividing attention. Is this true for other species as well? The most direct evidence for the effect of limited attention on target detection comes from controlled laboratory studies with blue jays (*Cyanocitta cristata*) [Dukas and Kamil, 2001]. The blue jay protocol was originally developed in the 1970's [Pietrewicz and Kamil, 1977, 1979] and has been used extensively ever since for testing hypotheses in animal behavioral ecology and cognition. In the limited attention experiment, the blue jays were trained to search for and peck at two types of targets presented at random locations on a computer monitor equipped with infrared sensors which reported the peck location. The background consisted of randomly placed items, which made the two target types appear cryptic (fig. 2) and the conspicuousness of each target type could be adjusted by altering the number and dimensions of the background items.

The experiment commenced once the jays were well experienced at searching for and pecking at the cryptic targets. Once a day, each 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 randomly generated background. A single peck at the display terminated the trial. A peck at the target was rewarded with half a mealworm, and the next trial was presented after 3 s. A peck at the background resulted in a 15 s delay followed by the presentation of the next trial. Finally, when the jays did not peck at all, the trial was terminated after 15 s, with the next trial presented after 1 s.

There were six types of sessions presented in random order within each of 16 blocks. Three of the sessions were devoted to measuring the cost of switching between searching for the two target types. These sessions, as well as additional experiments, indicated no cost of switching, which will not be discussed further here [see Dukas and

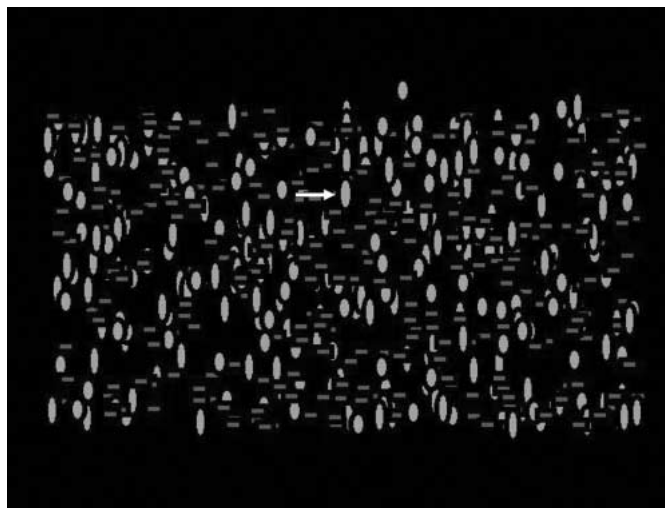


Fig. 2. An example illustrating one of the two targets (marked with an arrow) and the randomly generated background items used in Dukas and Kamil [2001].

Clark, 1995; Dukas and Kamil, 2001]. In the other three sessions, we compared the overall target detection rate when the jays either focused attention on searching for one target type, or divided attention between searching for the two target types. In session A, the start signal in all trials consisted of a circle containing target A, and the following images in all 50 trials contained target A. That is, the start signal informed the jays to search for target A, and their experience throughout the session also indicated that only target A was present. In session B, the start signal in all trials consisted of a circle containing target B, and the following images in all 50 trials contained target B. Again, the jays had two types of information indicating that only target B would be present. Finally, in session A or B, the start signal in all trials consisted of a circle containing both target A and target B. Twenty five trials contained target A whereas the other 25 trials contained target B, with the two trial types presented in random order. Here, both the start signal and the jays' experience throughout the session indicated that the jays had to search for either target on each trial. In short, in session A and session B the jays could focus attention on searching for a single target type, but in session A or B the jays had to divide attention between searching for either target type.

The target detection rates were much lower when the jays had to divide attention between searching for the two target types in session A or B than when they could focus attention on searching for a single target type in session A

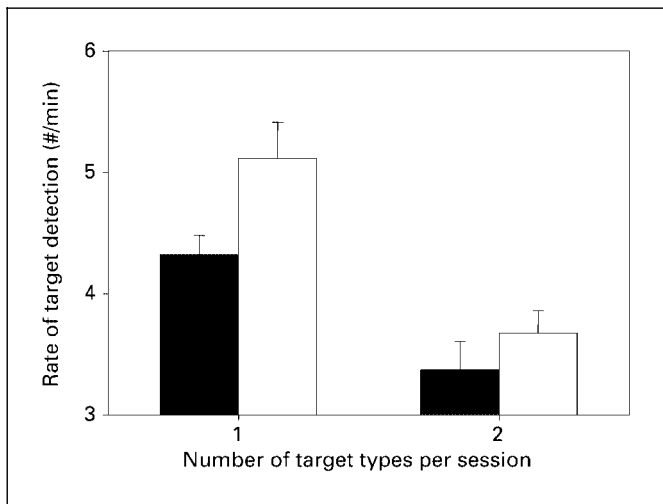


Fig. 3. The rate of target detection by blue jays in sessions in which either they searched for only one of two cryptic targets, or they searched for the two targets at the same time. The black and white bars depict the two target types. Target detection rate was significantly lower when the jays divided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

and session B (fig. 3). Overall, the jays detected targets at an average rate of 3.5 ± 0.2 (mean \pm SE) per minute spent searching in session A or B, which was 25% lower than the average rate of target detection of 4.7 ± 0.2 in session A and session B. In short, limited attention prevented the jays from performing well on two concurrent difficult search tasks, a result in agreement with the extensive literature on limited attention in humans and monkeys [Desimone and Duncan, 1995; Kastner and Ungerleider, 2000].

Theory of Prey Choice

The empirical results on the effect of limited attention on target detection rate in the blue jays indicate that limited attention might alter the predictions of optimal foraging models that only consider energy and time factors. Consider the classical prey model for the simple case of a forager encountering items of a few distinct prey types that are equally abundant and have equal energy content and handling time. In this case, the prey model predicts that the forager should feed on all prey types [Charnov, 1976; Stephens and Krebs, 1986]. Incorporating limited attention into the prey model, however, alters the model's predictions, which now also depend on prey conspicu-ness, defined as the degree of dissimilarity between a prey item and its surrounding background. That is, conspicu-

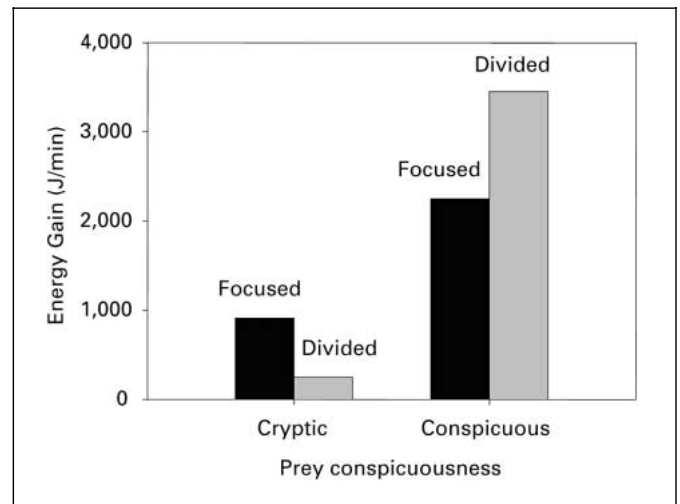


Fig. 4. The net rate of energy intake of a simulated forager encountering items of three distinct food types with identical conspicu-ness. The simulation was run for each of the four combinations of conspicuosity (cryptic or conspicuous prey) and attention (focused or divided attention). That is, the forager could either focus attention on searching for one food type during the session or divide attention among all three types at the same time. All three food types had identical density, net energy content, and handling time. Data from Dukas and Ellner [1993].

ous prey appears distinct against the background whereas cryptic prey looks similar to its surroundings. For conspicuous prey, the attentive prey model makes predictions similar to the ones of the basic prey model: the foragers should search for all prey types. For cryptic prey, however, the attentive prey model predicts that the forager should search only for items of a single prey type and ignore all other types [Dukas and Ellner, 1993].

The predictions of the attentive prey model for the settings just described (items of a few distinct prey type of equal density, energy content and handling time) are intuitively appealing: while searching for conspicuous prey types, it is best to divide attention among all the available types. This strategy would not be hindered by limited attention and the forager can take all the available prey items it encounters. With cryptic prey, however, dividing attention between more than one prey type reduces detection due to limited attention (fig. 3). Although focusing on a single prey type means that the forager bypasses other equally rewarding types, simulations indicate that this strategy results in a higher net rate of energy intake (fig. 4).

Search Image

Since Lukas Tinbergen [1960] first introduced the term 'search image', researchers have attempted to provide clear evidence that animals indeed selectively search for a certain prey type due to some perceptual biases [Dawkins, 1971; Pietrewicz and Kamil, 1979; Blough, 1991; Reid and Shettleworth, 1992; Bond and Kamil, 1999]. The integration of neurobiological, cognitive and behavioral-ecological data in the past decade allows us to go beyond description and conclude that search image is an optimal strategy that should be adopted by animals feeding on cryptic food due to limited attention [Dukas and Ellner, 1993]. Search image can best be defined as a selective search for one out of a few available distinct prey types, which involves increased probability of detecting that type and decreased probability of detecting any of the other types. Although selective attention due to limited attention plays a central role in search image, other cognitive traits including learning, long-term memory and working memory must also be involved because the forager has to acquire and update knowledge about the locally available food types and their relative profitability.

Search Rate

In addition to attending selectively to certain stimuli, animals must also choose what area of the visual field to attend to at any given time. That is, because of limited attention, attending to a large angle would allow an animal only coarse perception, but attending to a narrow angle would enable the animal to detect fine details [Eriksen and Yen, 1985; Connor et al., 1997]. The visual system of many animals also has a strong influence on the perception of minute details because only the fovea allows very fine discrimination [Van Essen and Anderson, 1995; Wandell, 1995]. However, the information bottleneck determining the focus of attention appears to be limited attention rather than visual constraints. For example, in primates, the information attended to at any given time is less than 1% of the information received by the eyes [Van Essen et al., 1991; Van Essen and Anderson, 1995].

Many animals must move through the environment in search of food while trying to avoid predators. The visual focus of attention adopted by an animal while scanning its surroundings for either food or concealed predators can influence its rate of movement. For example, as first suggested by Gendron and Staddon [Gendron and Staddon, 1983; Gendron, 1986], search rate, defined as the area searched per unit time, is lower when animals look for cryptic than conspicuous food. The pattern of movement itself may also be affected by limited attention. Many ani-

mals intersperse their movement with short pauses [O'Brian et al., 1990]. One explanation for such pauses is that they are required for paying sufficient attention to crucial information such as the route ahead, obstacles, food, or predators [Kramer and McLaughlin, 2001].

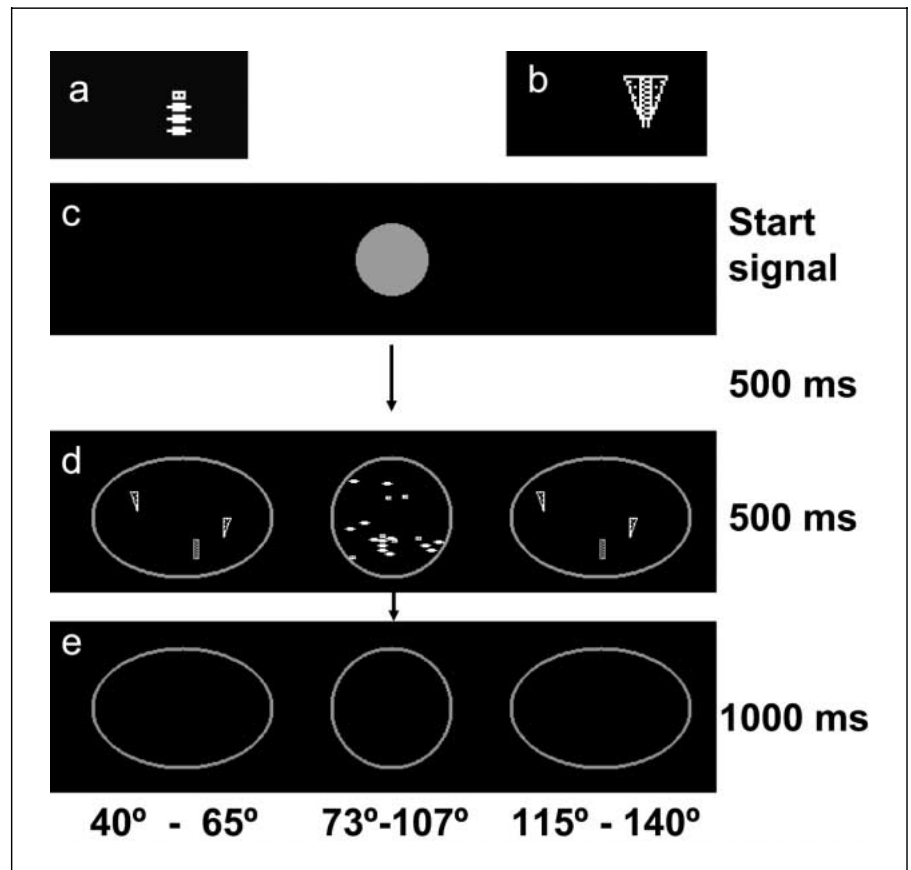
Does Limited Attention Affect Fitness?

The experimental data (fig. 3) suggest that limited attention may reduce fitness due to a reduction in feeding rate. Such an effect, however, may be difficult to quantify because it may only translate into reduced body reserves, which can potentially influence future survival or reproduction. It is easier to measure costs of limited attention if they affect the probability of noticing approaching predators. A few experiments with fish have indeed suggested that this might be the case [Milinski and Heller, 1978; Milinski, 1984; Metcalfe et al., 1987; Godin and Smith, 1988]. For example, Kraus and Godin [1996] compared guppies' responses to an approaching cichlid predator when the guppies were either feeding or resting. In either condition, the guppies were in a similar horizontal posture and identical visual surroundings. Still, the guppies responded to the predator at a shorter distance while feeding than resting. One possibility for this difference is that the guppies paid less attention to their surroundings when feeding than resting. However, it is also possible that the guppies noticed the predator at a similar distance under either condition but decided to respond later while feeding than resting because the cost of feeding interruption is higher than the termination of resting [Ydenberg and Dill, 1986].

To test whether limited attention decreases a forager's ability to notice peripheral targets, which may be approaching predators, we simulated a realistic foraging scenario under controlled laboratory conditions [Dukas and Kamil, 2000]. Imagine a blue jay searching for cryptic insects on a tree trunk [Sargent, 1976; Endler, 1984]. The blue jay has the visual ability to simultaneously detect predators approaching from the periphery while focusing on the trunk because its visual field is approximately 300° [Fite and Rosenfield-Wessels, 1975; Martin, 1986]. Such detection, however, may be hindered by limited attention, at least when the search task is difficult and, hence, attention-demanding.

The blue jays were trained to detect two types of digital prey, a caterpillar, which could appear in the central circle at a probability of 0.5, and a moth, which could appear in either of the peripheral ellipses at a probability of 0.25

Fig. 5. The procedure used by Dukas and Kamil [2000]. The two target types were (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 an additional 1,000 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. From Dukas and Kamil [2000].



each (fig. 5). For ethical and practical reasons, we used the moth target rather than a predator to simulate the peripheral target. There were two types of sessions, easy and difficult, created by manipulating the background in the central circle. The caterpillar was conspicuous in the center easy condition and cryptic in the center difficult condition. The moth conspicuousness was identical in either session type. We reasoned that the jays would focus more attention on the central circle than the peripheral ellipses, because the probability of detecting a target was twice as high in the center than in either periphery [Dukas and Kamil, 2000]. We also predicted that attention to the periphery would be lower under the center difficult than center easy condition and that this change in the focus of attention would result in a higher detection rate of the peripheral target during the center easy than center difficult condition.

Indeed, the blue jays detected three times more peripheral targets under the center easy than center difficult condition while maintaining similar detection frequencies for the central target under either condition (fig. 6a). This

result agrees with our prediction. Moreover, the latencies for detection of the central target were similar under either condition and the latencies for detection of the peripheral target were similar under either condition (fig. 6b). This does not agree with the alternative that the jays had more time to switch attention from the center to the periphery under the easy than difficult sessions. In sum, the blue jay results, along with the ecological and neurobiological studies discussed earlier, suggest that animals engaged in a challenging task such as searching for cryptic food are less likely to notice approaching predators. Hence limited attention probably contributes to animal mortality in nature.

Does Limited Attention Affect Ecological and Evolutionary Interactions?

Limited attention may cause a forager searching for cryptic food to focus on one food type while overlooking others. If the forager selectively attends to only one of sev-

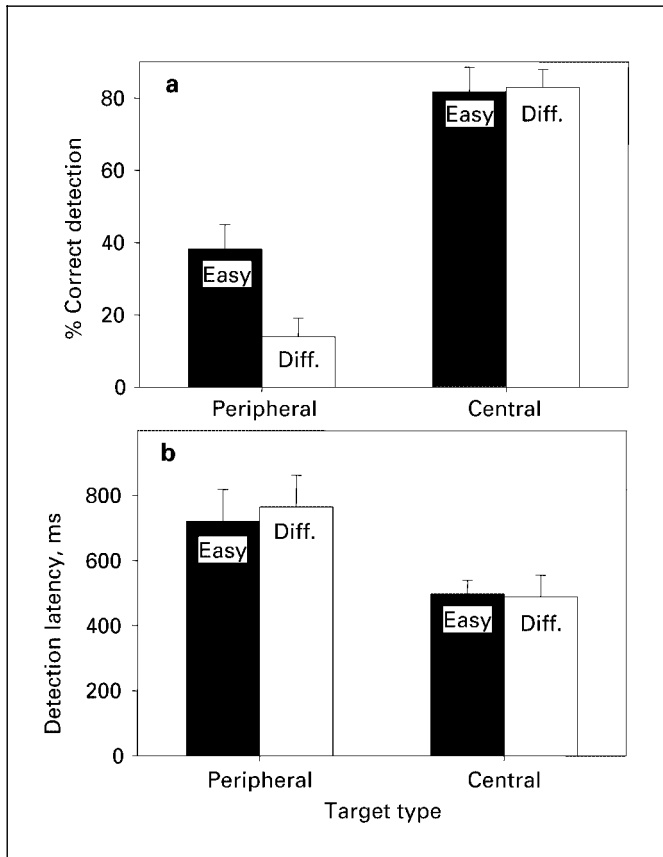


Fig. 6. a The percentage of correct detection (mean +1 SE) of the Peripheral Target was significantly higher during the Center Easy (dark bars) than Center Difficult (light bars) sessions, but correct detection of the Central Target was similar in either session type. **b** The average detection latency of the Peripheral Target was similar during the Center Easy (dark bars) and Center Difficult (light bars) conditions. Detection latency of the Central Target was also similar during the Center Easy and Center Difficult conditions. From Dukas and Kamil [2000].

eral equally cryptic and equally rewarding prey types, it should choose the most frequent type [Dukas and Ellner, 1993]. Such behavior might provide the less frequent types with a fitness advantage due to lower predation rates. This phenomenon is a case of ‘inverse frequency dependent selection’ [Clark, 1962; Endler, 1988; Futuyama, 1998]. If rare phenotypes have a selective advantage, there may be a general trend of increased phenotypic diversity within and among species [Clark, 1962]. What is the evidence for these two plausible phenomena?

Recently, a long term controlled laboratory study has evaluated the effect of prey-type abundance and similarity on the frequency of their detection by blue jays and on the consequent phenotypic variation of the prey [Bond

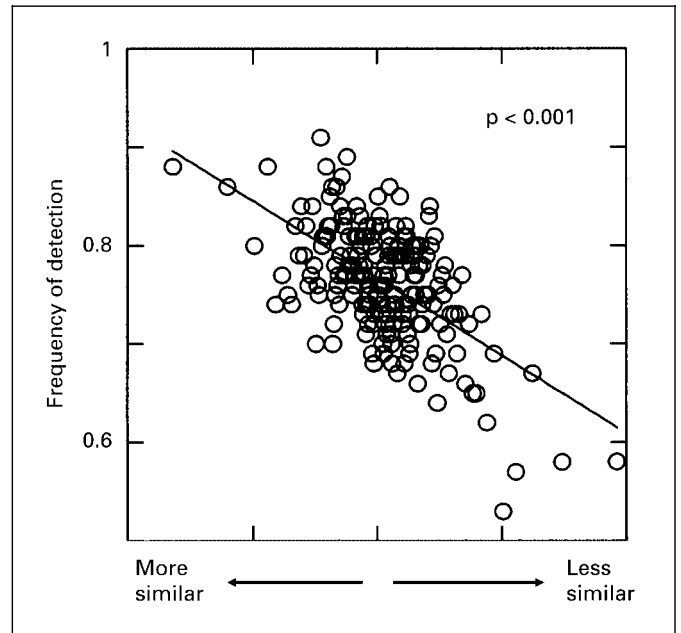


Fig. 7. Jays’ frequency of detecting cryptic digital moths was positively correlated with the moths’ similarity to the most recently detected moth ($r^2 = 0.35$, $p < 0.0001$). Modified from Bond and Kamil [2002].

and Kamil, 2002]. The jays ‘hunted’ for digital moths, which had virtual genes that determined their wing patterns. Two of the key treatments in this simulated-evolution study were the jay-selected lines and the frequency independent selection line. In the jay-selected lines, the moths that were not detected by the jays had a higher mating probability than the moths that were detected each ‘generation’ (day). The frequency independent selection treatment involved a simulation in which more cryptic moths had a higher mating probability. The explicit predictions were that: (1) in the jay-selected lines, moths more similar to recently detected moths would incur a higher detection probability; and (2) phenotypic variation would be higher in the jay-selected lines than under frequency independent selection.

For all the experimental trials, Bond and Kamil [2002] calculated an index of phenotypic similarity between each moth and the most recent previously detected moth. On average, a moth more similar to the recently detected moth was detected at a higher frequency than a moth less similar to the recently detected moth (fig. 7). This result suggests that the jays narrowed their focus of attention to specific features of the prey type they had recently detected. This behavior provided a selective disadvantage

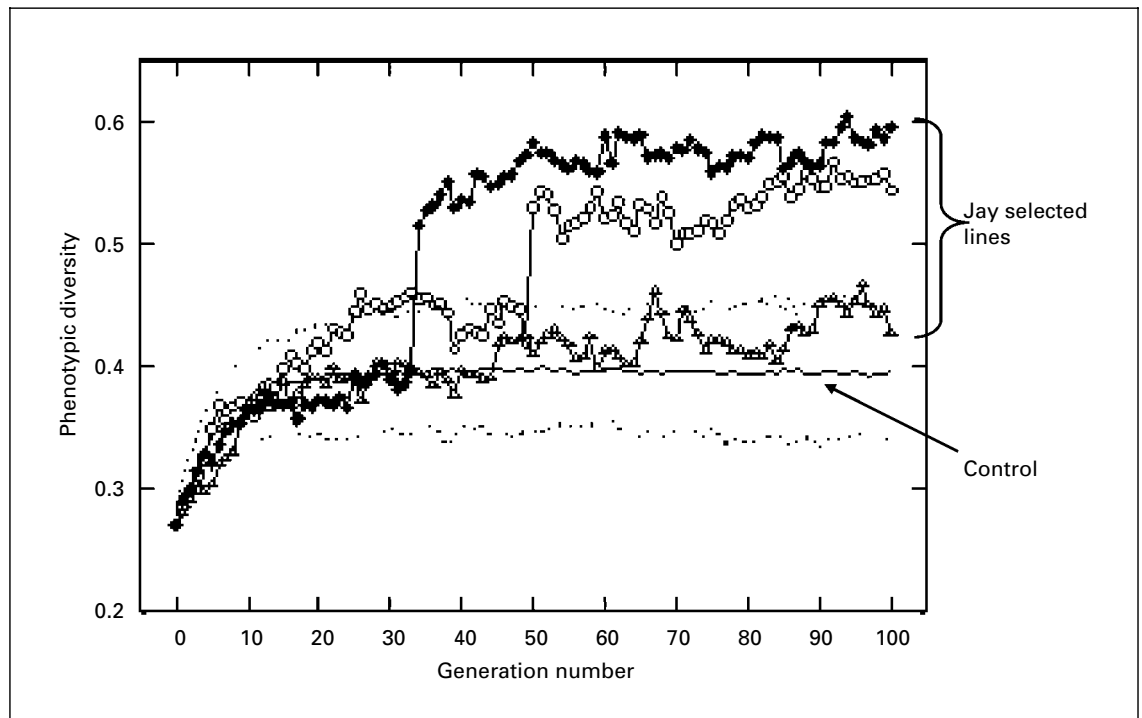


Fig. 8. The phenotypic variation of moths in the jay-selected lines was significantly higher than moth variation in the simulated frequency-independent control by the end of the experiment ($p < 0.0001$). Modified from Bond and Kamil [2002].

for prey items similar to that type and a selective advantage for distinct prey.

How did this selective hunting by the jays affect moth phenotypic evolution? After 100 moth generations, the three jay-selected lines showed significantly higher phenotypic variation than the frequency independent control. Two out of the three jay-selected lines showed an abrupt shift to a higher level of phenotypic diversity, which was produced by an explosive spread of mutant regulatory ‘genes’ affecting global levels of brightness or contrast (fig. 8).

Why Is Attention Limited? An Ecological Analysis

Limited attention hinders foragers’ probability of detecting cryptic food items (fig. 3). Perhaps even worse, a forager may be less likely to notice an approaching predator while engaged in an attention-demanding task (fig. 6). The data indicating potential fitness costs of limited attention [Dukas and Kamil, 2000, 2001] raise the question, why is attention limited? Clark and Dukas [2003]

examined this issue with a model of foraging under the risk of predation.

We envisioned a forager that, upon entering a patch, first pauses to scan its surroundings for predators and only then commences searching for food. The forager focuses attention on some portion of the visual field at any given time and successively moves its focus of attention until covering the whole visual field. The forager’s probability of detecting a concealed predator depends on its attentional capacity and its focus of attention, defined as the visual angle attended to at any given time.

We first asked what would be the optimal focus of attention for a given attentional capacity. If attention is divided over a wide angle, no minute details can be detected. Hence the detection probability is always higher for the minimal attentional focus (see above section on search rate). For a certain attentional focus, a larger attentional capacity would allow higher detection (fig. 9). The reason is that a larger volume of neural machinery devoted to processing information at any given time would allow more refined perception.

There are, however, costs associated with both a narrow attentional focus and a larger attentional capacity. A

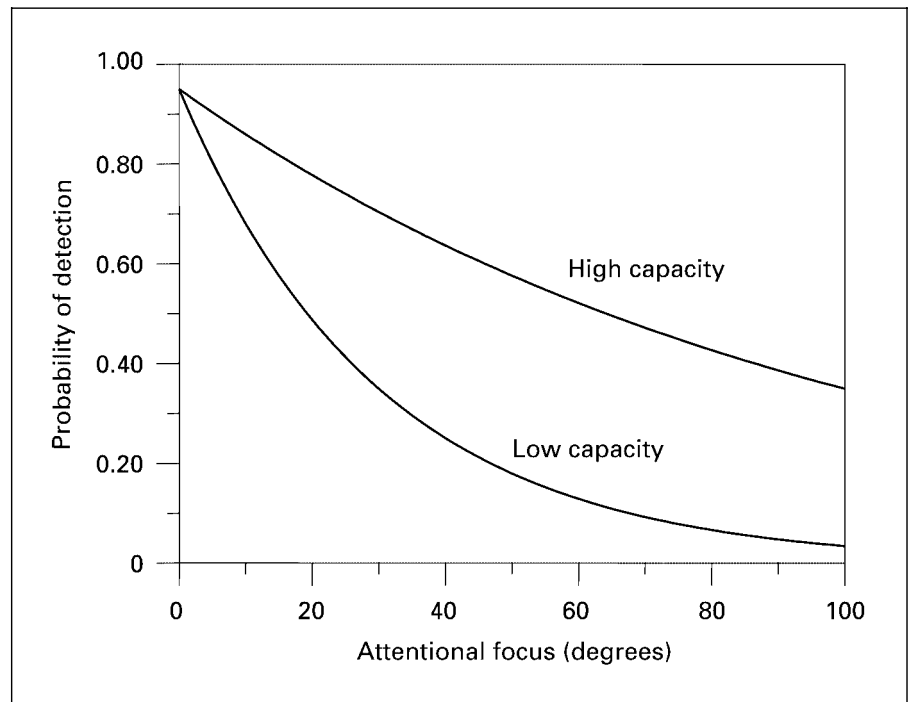


Fig. 9. The probability of detecting a hidden predator is positively correlated with attentional capacity and negatively correlated with the focus of attention. Modified from Clark and Dukas [2003].

narrow attentional focus implies that it would take a longer time to scan the whole visual field, leaving less time to forage. A larger attentional capacity requires a larger neuronal tissue devoted to visual detection and this means larger metabolic expenditures. Overall, this set of conflicting functions can be evaluated with a model. For any magnitude of attentional capacity, the forager's decision depends on its energy reserves, with the optimal attentional focus being highest with low reserves. The reason for this is that, with low reserves, the forager can minimize the time spent scanning for predators by employing a wide attentional focus and thus maximize the feeding time, which is required for increasing its dangerously low reserves. This strategy, however, would result in a higher predation probability. With high reserve levels, the forager can afford to spend a larger proportion of its time successively attending to narrow angles of the visual field before initiating feeding (fig. 10a). This strategy enables the forager to gain sufficient energy while incurring a low probability of predation.

The optimal attentional focus is lower with low than high attentional capacity. There are two reasons for this result. First, with low attentional capacity, only a relatively narrow attentional focus would allow sufficiently high probability of predator detection (fig. 9). Second, a higher attentional capacity is associated with larger metabolic

expenditures and, therefore, more time devoted to feeding and less time available for predator scanning, the latter requiring a broader attentional focus.

The analysis of the optimal attentional focus led to our next question, which was, what is the optimal attentional capacity? To calculate the optimal attentional capacity, we had to use an explicit function relating attentional capacity to metabolic costs. Unfortunately, we currently know little about the contribution of brain tissue to metabolic rate in general and attentional capacity in particular. We thus made two assumptions based on the available information. First, the overall metabolic cost of the brain amounted to approximately 15% of the total metabolic cost. Second, there was an accelerating increase in cost with capacity, reflecting the fact that a linear increase in brain volume is associated with a decelerating increase in computational power [Deacon, 1990; Allman, 1999; Zhang and Sejnowski, 2000]. Furthermore, we considered two parameter values in the cost equation, amounting to relatively low and high metabolic costs of attentional capacity. With these realistic assumptions, the optimal attentional capacity turns out to be 40° for low cost and 24° for high cost (fig. 10b). This is much lower than the maximal attentional capacity of 180° allowed in the model.

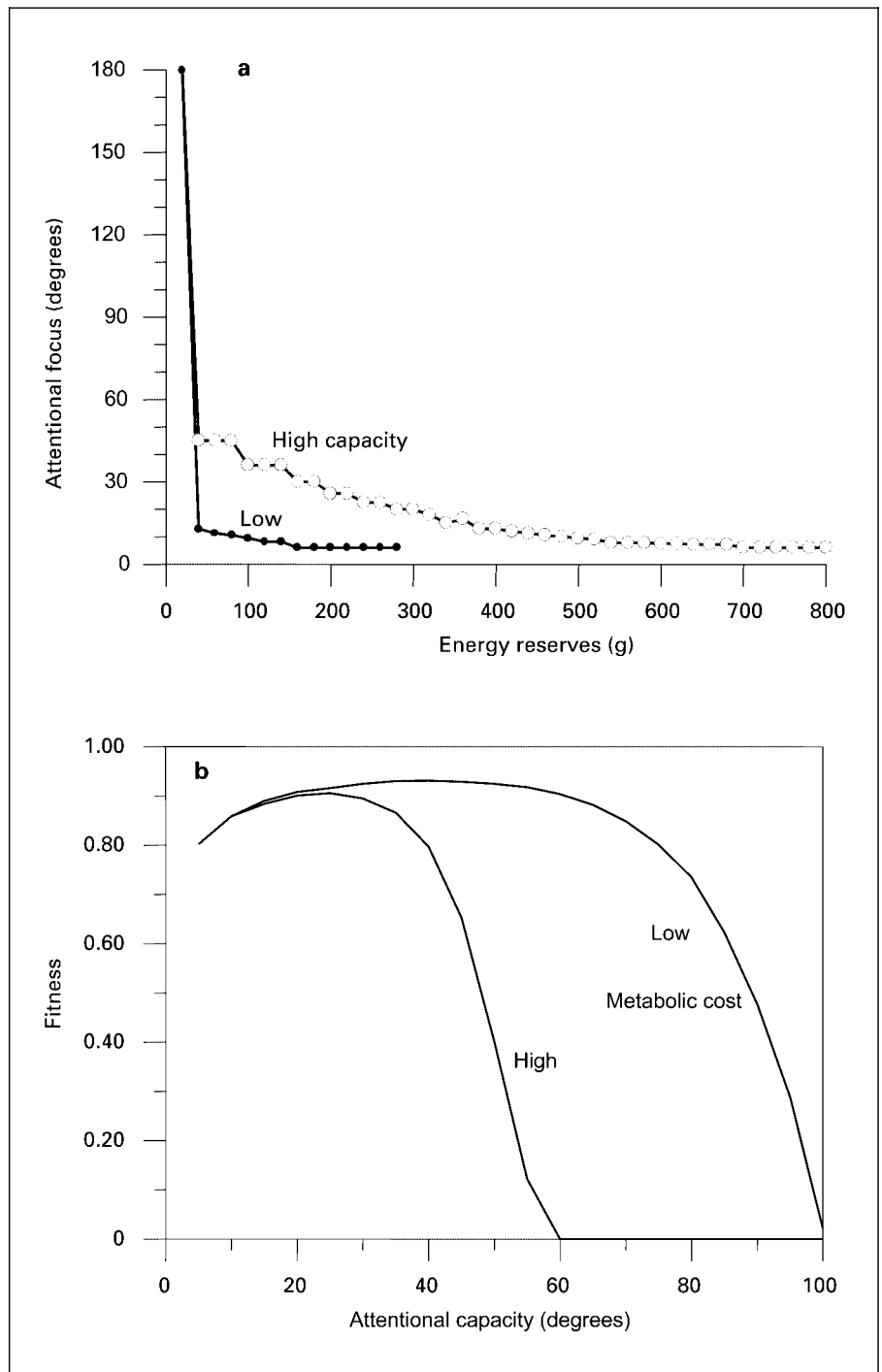


Fig. 10. a The optimal focus of attention is a negative function of both the level of reserves and attentional capacity. **b** Fitness as a function of attentional capacity for two values of metabolic cost. Modified from Clark and Dukas [2003].

In sum, our model indicates that a relatively low attentional capacity, which requires successive allocation of focused attention, constitutes an optimal strategy that balances the need to process high rates of information flow with the cost of building and maintaining brain tissue.

Although it is legitimate to consider limited attentional capacity as a given constraint and study its effects on behavior, we can go beyond and examine the neurobiological, ecological and evolutionary factors that determine attentional capacity.

Conclusions and Testable Predictions

The extensive body of literature on the neurobiology and behavioral aspects of attention in humans and monkeys [Kastner and Ungerleider, 2000; Pashler et al., 2001; Treue, 2001] indicates that limited attention has strong effects on performance in these species. The available data for other species, though limited, suggest that limited attention constrains animals' food search and the ability to balance simultaneous search for food and predators. Although these two effects of limited attention are likely to decrease animal fitness, no direct evidence exists in support of this proposition. The notion that selective search by predators influences the evolution of prey visual appearance through inverse frequency dependent selection [Clark, 1962] precedes experimental cognitive research on attention [Moran and Desimone, 1985; Spitzer et al., 1988]. However, experimental evidence in support of this hypothesis exists only from a simulated evolutionary study done on computers [Bond and Kamil, 2002]. Finally, an ecological model of attention illustrates why attention may be limited [Clark and Dukas 2003] but it is based on crucial untested assumptions about cognitive costs.

In sum, limited attention appears to influence animal ecology and evolution but there is currently little experimental evidence to substantiate this statement. Hence, I will conclude this review with a set of testable predictions and provide a brief background for each.

Attention in Nature: Limited Attention Constrains Food Search by Drift-Feeding Fish

Most animals move in search of food and this makes them hard to follow with the level of detail necessary for testing hypotheses about limited attention. One exception is drift feeding fish, which stay sedentary at one spot in the moving stream and wait for food items to come to them. This means that the experimenter can readily observe and videotape individuals in natural or semi-natural stream settings to investigate the effects of variables such as water velocity and prey conspicuousness on the focus of search by a drift feeding fish. Earlier experimental work [O'Brian and Showalter, 1993] and a recent model [Hughes and Dukas, unpublished data] suggest that limited attention strongly affects the search strategy and capture success of drift feeding fish. For example, when prey is cryptic due to increased debris in the stream, the fish should focus their search on a narrower angle than when prey is conspicuous.

Selective Attention by a Single Predator Causes Divergent Selection in the Visual Appearance of Sympatric Prey Species

Theory [Endler, 1988; Abrams, 2000] and laboratory experiments [Bond and Kamil, 2002] indicate that selective attention can result in inverse frequency dependent selection and, consequently, divergence in the visual appearance of prey. Indeed such mechanism has been proposed for a few systems including leaf-shape variation among *Passiflora* species attacked by *Heliconius* butterflies [Gilbert, 1975], the dissimilarity in visual appearance of coexisting cryptic moth species subjected to bird predation [Ricklefs and O'Rourke, 1975] and polymorphism in various species such as *Cepaea* land snails [Clark, 1968], and happy face spiders, *Theridion grallator* [Gillespie and Oxford, 1998]. However, there is no evidence that selective attention by a single predator species has been responsible for patterns of divergent appearance in any taxon. Feasible alternatives for the apparent divergence include chance and the activity of a few predators with distinct perceptual abilities. Therefore, the prediction about divergence due to inverse frequency dependent selection requires a critical test. A few feasible natural systems for such research are: (1) *Passiflora* and its *Heliconius* butterflies just mentioned [Gilbert, 1975]; (2) the two sympatric *Aristolochia* species in east Texas, which have distinct leaf shapes, and their herbivore, the pipevine swallowtail butterfly, *Battus philenor* [Rausher, 1978; Papaj, 1986]; and (3) some aquatic crustacean with color polymorphism and its fish predator [see Popham, 1942].

Attentional Requirements Are Reduced with Experience, Allowing Enhanced Dual-Task Performance

The experimental evidence indicates that limited attention constrains animals' ability to focus on more than one difficult task at any given time. In humans, however, 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, new drivers typically fully focus on operating an automobile, negotiating traffic and navigating, whereas experienced drivers may rely on 'automatic pilot' for these tasks while devoting most attention to a conversation with a passenger [LaBerge and Samuels, 1974; Pashler et al., 2001].

Although the changes in attentional requirements with skill acquisition have been studied only in humans, they most likely exist in other species as well. This suggests, for

example, that an animal devoting five minutes to handling a novel food might be less likely to notice an approaching predator than an animal spending the same time handling a familiar food. Consequently, young, inexperienced animals may incur a much higher predation risk due to limited attention. The effect of experience on the residual ability to perform a secondary task may be tested with a protocol modified from Dukas and Kamil [2000], which involves subjects that are either experienced or inexperienced with a primary task.

Courtship Displays Are Designed to Attract and Sustain Female Attention

Courtship settings sometimes involve females engaged in non-mating tasks and males that must attract the females' attention. This can be done, for example, by using abrupt movements. Typically, animals would direct their eyes towards moving objects, which may be a prey or predators, in order to inspect it closely. 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].

In addition to initially attracting a female's attention, courtship displays might have been selected to keep the female's focus on the male. It is possible that the continuous movement and constantly changing visual stimulation typical of many courtship displays serves to sustain female attention [see Endler, 1992]. One way of testing these ideas is by modifying the protocol employed by Lang and colleagues [2000], who created edited video clips in order to test for the effect of camera changes in the same visual scene on viewers' attention and memory which were measured behaviorally and physiologically through measurements of head and eye movement and heart rate.

A Larger Relative Brain Size Is Associated with Increased Daily Metabolic Expenditure

To understand cognitive abilities and constraints we must quantify not only their behavioral, ecological and evolutionary effects, but also their cost [Dukas, 1999b]. One cost that is likely to limit a cognitive ability is the metabolic expenditure associated with brain tissue. Several studies indicate that a larger cognitive ability is associated with a larger volume of brain tissue devoted to that ability [e.g., Krebs et al., 1989; DeVoogd et al., 1993; Lefebvre et al., 1997; Brooke et al., 1999]. It is also known that brain tissue is among the more metabolically expensive tissues in animals [Hawkins, 1985; Hochachka and

Somero, 2002]. However, no study has tested whether increased relative brain tissue is associated with an increase in daily metabolic requirements. Alternatively, it is possible that increased brain tissue is compensated for by a reduced volume of some other metabolically expensive tissue such as liver, kidney, or muscle. An attractive model system for testing the effect of brain size on metabolic costs is *Drosophila*, in which brain size has been altered through behavioral and genetic manipulation [Barth and Heisenberg, 1997; Heisenberg, 1997].

Prospects

Limited attention has important behavioral consequences that probably affect animal ecology and evolution. Much of the ideas about limited attention remain to be tested as outlined above. The few ecological studies on the effect of limited attention focus on the prey-predator domain. Limited attention, however, might influence other behaviors such as courtship [Hebets, unpublished data]. The suggested mechanisms that determine limited attentional capacity [Clark and Dukas, 2003] should be quantified. Similar mechanisms may underlie other cognitive constraints not discussed here including limited learning rate, forgetting and the limited capacity of working memory. All of these constraints may have far reaching ecological and evolutionary consequences. A notable example is the highly restricted diet of many insect herbivores, which might be caused by neuronal limitation on the amount of information about distinct host plants an insect can process [Bernays and Funk, 1999; Bernays, 2001].

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