

# EVOLUTIONARY BIOLOGY OF ANIMAL COGNITION

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■ **Abstract** This review focuses on five key evolutionary issues pertaining to animal cognition, defined as the neuronal processes concerned with the acquisition, retention, and use of information. Whereas the use of information, or decision making, has been relatively well examined by students of behavior, evolutionary aspects of other cognitive traits that affect behavior, including perception, learning, memory, and attention, are less well understood. First, there is ample evidence for genetically based individual variation in cognitive traits, although much of the information for some traits comes from humans. Second, several studies documented positive association between cognitive abilities and performance measures linked to fitness. Third, information on the evolution of cognitive traits is available primarily for color vision and decision making. Fourth, much of the data on plasticity of cognitive traits appears to reflect nonadaptive phenotypic plasticity, perhaps because few evolutionary analyses of cognitive plasticity have been carried out. Nonetheless, several studies suggest that cognitive traits show adaptive plasticity, and at least one study documented genetically based individual variation in plasticity. Fifth, whereas assertions that cognition has played a central role in animal evolution are not supported by currently available data, theoretical considerations indicate that cognition may either increase or decrease the rate of evolutionary change.

## INTRODUCTION

Cognition can be defined as the neuronal processes concerned with the acquisition, retention, and use of information. Cognition determines behavioral traits that affect animal ecology and evolution. Examples include habitat selection, choice of food and diet breadth, predator avoidance, mate choice, social behavior, and behavioral shifts that lead to adaptive radiations (Mayr 1963, Dukas 1998a). The major cognitive traits include (a) perception, defined as the translation of environmental signals into neuronal representations; (b) learning, which is the acquisition of neuronal representations of new information, such as a new association between a stimulus and an environmental state, a new association between a stimulus and behavioral pattern, or a new motor pattern; (c) long-term memory, which consists

of passive representations of information already learned; (*d*) working memory, consisting of a small set of neuronal representations active over some short duration; (*e*) attention, referring to the neuronal representations activated at any given time; and, finally, (*f*) decision making, involving the determination of action given the known states of relevant environmental features and experience (Dukas 1998a, Dukas 2002, Platt 2002).

Historical and social factors delayed extensive research on the evolutionary biology of animal cognition for much of the twentieth century. The major contributor to this delay was slow acceptance of the evidence that cognitive traits, like any other animal feature, are determined by a mixture of genetic and environmental factors (Richards 1987, Plomin et al. 2001). The old barriers are rapidly fading owing to increased knowledge about, and integrative research on, the genetics, neurobiology, and evolutionary biology of cognition (Dukas 1998a, Shettleworth 1998). A remaining impediment, however, is the sheer complexity of brains and other neural centers. Compared with some morphological and anatomical traits that have been subjected to intense evolutionary research (Futuyma 1998), cognitive traits are more difficult to quantify, they are typically labile, and the neurobiology underlying them is only partially understood. Thus, an evolutionary biologist tackling cognition must also be well acquainted with the relevant neurobiology and proper behavioral techniques used to quantify cognitive traits.

Modern evolutionary research has greatly benefited from thorough research programs that documented large heritable variation for various phenotypic traits, the effects of such traits on fitness, and the evolution of phenotypic traits in the wild. A mature evolutionary discipline of animal cognition can also gain from similar research that evaluates to what degree (*a*) there is genetically based individual variation in cognitive traits, (*b*) cognitive traits affect animal fitness, and (*c*) cognitive traits evolve. Below I review some of the most convincing evidence for the above requirements. Then I discuss two related topics, environmental effects on cognition and the effect of cognition on evolution. Space limitations prevent me from citing all relevant studies.

## GENETIC VARIATION IN COGNITIVE TRAITS

A cognitive trait can evolve only if there is genetically based variation in this trait among individuals. Genetic variation is known for all cognitive traits, but the quantity and quality of information varies widely, with much of the nonhuman data restricted to learning, memory, and decision making.

### Genetic Variation in Perception

**COLOR VISION** There is substantial genetically based individual variation in human color vision. Some of this variation is caused by single amino acid substitutions that cause minor shifts in color perception (Gegenfurtner & Sharpe 1999). Humans with normal color vision possess three opsin photopigments with peak

sensitivities in the blue, green, and red regions. The genes for green and red opsins reside on the X chromosome. Hence, all males with recessive mutations in these genes but only females homozygous for such mutations show deficiencies in color perceptions, varying from dysfunctions to minor anomalies. For example, males lacking either a functional red opsin or a functional green opsin perceive color in two rather than the normal three dimensions; this condition is typically referred to as color blindness. Among European males, about 1% and 1.3% of individuals possess dysfunctional red and green opsins, respectively, and approximately 1% and 4.5% possess anomalous red and green opsins, respectively. There is a considerable variation in color-vision deficiency among human populations. Although approximately 7.4% of males of European descent show color-vision deficiency, only fewer than 2% of aboriginal males in Australia, Brazil, the South Pacific Islands, and North America have such deficiencies (Sharpe et al. 1999). Minor anomalies in color vision are common. For example, approximately 56% of European males have a point mutation substituting Serine for Alanine at codon 180 of the red opsin, which causes a slight red shift in color perception (Sharpe et al. 1999).

There has been extensive research on color vision in many animals (Gegenfurtner & Sharpe 1999, Briscoe & Chittka 2001), but little information exists on genetically based variation among individuals in color perception in animals other than primates. Two noted exceptions involve fish. First, Endler et al. (2001) selected for increased spectral sensitivities to either red or blue light in four lines of guppies (*Poecilia reticulata*). All four lines showed significant responses to selection and significant heritabilities for spectral sensitivity. Second, Fuller and colleagues (Fuller et al. 2004; R.C. Fuller, personal communication) documented heritable variation in retinal cone distribution in bluefin killifish (*Lucania goodie*). Fish inhabiting clear spring water had relatively higher expressions of ultra violet (UV) and violet opsins. In contrast, fish from a murky swamp had relatively higher expressions of yellow and red opsins.

**TASTE** The best-studied taste polymorphism involves human sensitivity to bitter substances containing the chemical group  $\text{N-C}=\text{S}$  (Fox 1932). Although much of the empirical work involved synthetic phenylthiocarbamide (PTC),  $\text{N-C}=\text{S}$  occurs naturally in various wild plants, including turnip and cabbage. Among people of European descent, approximately 65% identify PTC as bitter, whereas the rest perceive it as tasteless. In contrast, close to 100% of aboriginal Africans and North Americans identify PTC as bitter (Kalmus 1971, Prutkin et al. 2000). A somewhat similar polymorphism occurs in wild mice, which show individual variation in sensitivity to the bitter sucrose octaacetate (SOA) (Warren & Lewis 1970). Both the human and mouse polymorphisms are attributed to recessive tasteless genes inherited in a simple Mendelian fashion (Warren & Lewis 1970, Kalmus 1971).

**SMELL** A few studies have documented significant genetically based individual variation in response to various odors in fruit flies (Fuyama 1978, Alcorta &

Rubio 1988, Mackay et al. 1996). Becker (1970) conducted two artificial selection experiments, which yielded flies insensitive to insect repellents. These fly studies, however, did not provide direct evidence that the variation was in the perception of, rather than response to, odors. In humans, more than 89 cases of insensitivity to specific odors have been described with frequencies varying from 0.1% to 47% among specific odors and human populations (Amoore 1971, Griff & Reed 1995). At least one of these cases, insensitivity to the musk pentadecalactone, which occurred in about 7% of people tested, was attributed to a recessive allele affecting specific odor perception (Whissell-Buechy & Amoore 1973).

**HEARING** Perhaps the only known naturally occurring, genetically based individual variation in hearing pertains to musical pitch recognition in humans. Drayna et al. (2001) used a test involving distorted tunes to quantify pitch recognition in monozygotic and dizygotic twins. Subjects showed wide variation in test scores, with approximately 25% having a perfect score and 40% performing poorly. These results were not correlated with peripheral hearing, suggesting that pitch recognition involved nonperipheral components of the auditory system. The estimated heritability in this study was 71%, although this figure may be an overestimate. Other human studies have also documented a genetic component underlying perfect pitch. Although various species have been used as model systems for studying hearing impairment (Steel & Kros 2001), there is apparently no data about genetically based individual variation in sound perception in nonhuman species.

**CROSS-MODALITY VARIATION** In addition to individual differences within a single perceptual mode, one would expect to find variation between modes among individuals inhabiting different perceptual environments. Culver et al. (1995) documented large genetically based variation in sensory organs between adjacent populations of the amphipod *Gammarus minus*. Individuals from surface springs, which are exposed to natural light, have relatively short antennae and large eyes each consisting of about 40 ommatidia. In contrast, neighboring individuals occupying underground caves, which live in constant darkness, have relatively long antennae and tiny eyes each containing approximately five ommatidia. The external differences in morphology extend to the brain, with surface individuals having an optic lobe twice as large and olfactory lobe 25% smaller than cave individuals (Culver et al. 1995).

## Genetic Variation in Learning and Memory

The best evidence for naturally occurring, genetically based individual variation in learning and memory comes from artificial selection experiments. Tolman (1924), Heron (1935), and Tryon (1940) initiated the artificial selection studies on learning. They used rats assessed for their spatial learning ability in mazes and then bred the rats to produce divergent lines of good and bad performers within a few generations. There was no evidence, however, that these early lines of “maze bright”

and “maze dull” rats indeed reflected selection on spatial learning ability. Rather, apparently much of the differences could be attributed to traits such as motivation and fearfulness. In a later study, Thompson selected for rat lines of good and bad spatial learners while controlling for emotional and motivational variables (Fuller & Thompson 1978).

Further artificial selection experiments on learning used blowflies (*Formia regina*) (McGuire & Hirsch 1977) and fruit flies (*Drosophila melanogaster*) (Lofdahl et al. 1992). Both studies employed protocols consisting of individual flies learning to respond to stimuli associated with sugar solution, and they documented rapid and widely divergent changes in learning ability. For example, in the fruit fly study, the proportion of flies showing good learning increased from 19% to 77% in the “bright” line and decreased to approximately 2% in the “dull” line over 25 generations (Lofdahl et al. 1992).

Mery & Kawecki (2002) also documented rapid increase in learning ability in fruit flies (*D. melanogaster*) under strong artificial selection. Their protocol involved a training trial in which one of two types of fruit juice substrates was associated with quinine, which is strongly aversive to flies. During the successive test trial, neither substrate contained quinine, but the experimenters collected eggs for the next generation only from the substrate that had not contained quinine in the training trial. That is, only the flies that remembered to seek the substrate that had been quinine-free during training had positive fitness. Subsequent experiments indicated that, compared with the control line, flies from the “bright” line showed higher learning rates and lower rates of memory decay (Mery & Kawecki 2002).

It is unknown which genes determined the changes in learning and memory in the fly lines under artificial selection. However, research on the molecular biology of learning has established that major genes can readily alter learning and memory parameters. To date, 60 genes involved in learning and memory have been identified in fruit flies (Dubnau et al. 2003), and it is estimated that between 500 to 1000 genes are part of the fly networks of learning and memory (T. Tully, personal communication).

In humans, at least three naturally occurring genetic variants have been linked to memory ability. First, the apolipoprotein E (APOE) gene has three alleles, resulting from single nucleotide substitutions. Among Western Europeans and North Americans, the frequencies of these alleles, labeled  $\epsilon 2$ ,  $\epsilon 3$ , and  $\epsilon 4$ , are 8%, 78.5%, and 13.5%, respectively. In some populations in Scandinavia and Africa, however, the frequency of  $\epsilon 4$  is 20% or higher. There is a well-established association between the  $\epsilon 4$  allele and susceptibility to late onset Alzheimer’s disease (Raber et al. 2000, Smith 2000). In addition, nondemented, middle-aged carriers of  $\epsilon 4$  perform significantly worse on learning and memory tests compared with people carrying only the  $\epsilon 2$  and  $\epsilon 3$  alleles (Flory et al. 2000, Parasuraman et al. 2002).

Another polymorphism linked to memory involves a G to A substitution in the catechol-O-methyltransferase (COMT) gene. This substitution results in a Valine (Val) to Methionine (Met) substitution at position 108/158 of the COMT enzyme, which catabolizes released dopamine. The Val and Met alleles are codominant,

with Met homozygotes having  $\frac{1}{4}$  of COMT activity of Val homozygotes. In a healthy population of 55 people, 82% had at least one Val allele. A standard test of working memory revealed highly significant effects of the COMT genotype, with the Val/Val scoring lowest and Met/Met scoring highest (Egan et al. 2001).

Finally, the Met allele of the brain-derived neurotrophic factor (BDNF) results in a single amino acid substitution from Val to Met at position 66 of the BDNF protein. In a control sample of 133 people, 32% carried at least one Met allele. People carrying the Met allele showed significantly poorer memory about details in short stories (episodic memory). Furthermore, two types of brain imaging revealed that the Met carriers had abnormal functioning of neurons in the hippocampus, the brain region involved in episodic memory (Egan et al. 2003).

## Genetic Variation in Attention

Little information is available about genetic variation in attention, which has been studied only in humans. The  $\epsilon 4$  allele of the APOE, which was discussed in the section on learning and memory, has also been linked to small reductions in performance on visual attention tasks in nondemented older adults (Greenwood et al. 2000, Parasuraman et al. 2002). Attention deficit hyperactivity disorder (ADHD) is characterized by difficulty of sustaining attention on a task for more than a few minutes and by overall restlessness. In North America, ADHD has been diagnosed in about 3% of boys and 1% of girls, and twin studies indicate high heritability of ADHD (Plomin et al. 2001). A few polymorphic genes have been linked to ADHD. The most consistent finding is a positive small association between the 7-repeat allele of the dopamine  $D_4$  receptor gene (DRD4) and ADHD (Faraone et al. 2001).

## Genetic Variation in Decision Making

Traditional research on animal behavior has accumulated considerable data about heritable variation in behavior. Although much of that variation is probably attributed to decision making, many studies did not evaluate noncognitive alternatives. Hence this section focuses only on selected cases of probable variation in decision making within the three evolutionarily important categories of habitat choice, foraging, and mating behavior.

**HABITAT CHOICE** The two classes of studies reviewed here are taxis in fruit flies (*D. melanogaster*) and exploratory behavior in great tits (*Parus major*). Either behavior can affect the genetic makeup of populations, generate assortative mating, and lead to speciation.

Adult fruit flies (*D. melanogaster*) typically show negative geotaxis and positive phototaxis. Classic experiments in the 1960s, however, documented large individually based variation in tactic response: Experiments employing strong directional selection readily generated divergent lines of flies showing extremely negative and positive geotaxis and negative and positive phototaxis (Erlenmeyer-Kimling

et al. 1962, Hadler 1964). Similar results were also obtained with *D. pseudoobscura* (Dobzhansky & Spassky 1967). The four *D. pseudoobscura* lines selected for divergent tactic responses were tested for mating preference. All six possible combinations of pairings between the negative and positive geotactic and phototactic lines were tested, and all six tests revealed significant assortative mating after 5 and 11 generations of selection (Del Solar 1966). That is, several weeks of directional selection on tactic response were associated with a change in mating preference, which could lead to incipient speciation. Toma et al. (2002) recently identified specific genes involved in geotaxis by comparing mRNA expression from the heads of fly lines selected for negative and positive geotaxis. Toma and colleagues focused on three of the identified genes and verified through mutant analyses that these genes indeed affected geotaxis.

Individuals show large genetically based variation in their tendency to explore and to seek novel situations (McClearn 1959). Two related studies evaluated the heritability of novelty seeking in great tits (*Parus major*). One study involved bi-directional artificial selection over four generations in captivity. Hand-reared juveniles were tested for their latency (*a*) to visit four out of five artificial trees in a novel environment, and (*b*) to approach two distinct objects, a small battery and a pink rubber toy. Both up and down selection lines showed large changes each generation in mean score, and the heritability ( $h^2$ ) was approximately 0.5 (Drent et al. 2003). The other study consisted of successive captures, brief laboratory tests for novelty seeking, and releases of wild-caught great tits. The heritability estimates in this study, which were based on both parent-offspring and sibling analyses were between 0.2 to 0.4 (Dingemanse et al. 2002). Exploratory behavior is positively correlated with natal dispersal in great tits. Hence, variation in exploratory behavior may translate into variation in the genetic structure of great tit populations (Dingemanse et al. 2003).

**FORAGING** One of a few studies indicating genetic variation in feeding preference in vertebrates is Arnold's (1981a,b) work on garter snakes (*Thamnophis elegans*) in California. Much of that research focused on geographic variation in the slug-eating habit between snake populations in slug-rich and slug-poor areas. However, all the snake populations showed genetically based polymorphism for both chemoreceptive responses to slugs and the consequent behaviors of either slug feeding or slug avoidance. Populations sympatric with slugs consisted of approximately 76% slug-eating snakes. In contrast, the frequency of slug-eating individuals was only about 17% in slug-poor habitats. Genetic variation for host preference is also well known in a variety of herbivorous insects (Futuyma & Peterson 1985, Funk & Bernays 2001).

The *foraging* gene of *D. melanogaster* provides a rare example of a single locus underlying a major naturally occurring behavioral polymorphism. Fly larvae with the dominant rover allele, *for<sup>R</sup>*, exhibit significantly longer foraging movements on the food medium than do larvae homozygous for the sitter allele, *for<sup>S</sup>*. The two morphs, however, show no behavioral difference in the absence of food.

Density-dependent selection during the larval stage determines the frequency of the *for* alleles, with sitters having a selective advantage under low densities and rovers being more successful in crowded conditions (Sokolowski et al. 1997). Somewhat similar genetically based variation in behavior occurs in the nematode, *Caenorhabditis elegans*, in which the 215F isoform of the *npr-1* gene is associated with social feeding behavior, whereas the 215V isoform is linked to solitary behavior. Naturally occurring nematodes of the social morph move rapidly on bacterial food substrate and aggregate to feed together, whereas worms of the solitary morph move slowly and feed alone (De Bono & Bargmann 1998).

**MATING BEHAVIOR** Three major components of sexual behavior in fruit flies (*D. melanogaster*), courtship song, mating latency, and mating duration, show genetically based individual variation. The courtship song of male fruit flies, which is generated by wing vibration, has strong effects on mating success. Six generations of artificial bi-directional selection on the song's interpulse interval (IPI) were sufficient to generate a short line with an average IPI 10% shorter than that of the long IPI line. That is, there was sufficient genetic variation to generate rapid divergence in the song and to increase IPI beyond the normal range of the species (Ritchie & Kyriacou 1996). IPI is affected by the *per* gene. A few amino acid substitutions in that gene determine the 50% difference in IPI between the closely related *D. melanogaster* and *D. simulans* (Wheeler et al. 1991, Tauber & Eberl 2003).

Manning (1961) applied bi-directional selection on mating latency in *D. melanogaster* by isolating and breeding separately the 10 fastest and 10 slowest pairs to mate among 50 males and 50 females placed in culture bottles. Compared with a control line, the average mating latency was half as long in the two fast lines and eight times longer in the two slow lines. Experiments with selected males and unselected females indicated that males from the fast lines initiated courtship more quickly and licked females more frequently than males from the slow lines but that the fast males exhibited less nonsexual activity than the slow males (Manning 1961). Lines of flies with short and long mating latencies have also been selected in *D. simulans* (Manning 1968) and *D. pseudoobscura* (Kessler 1968).

Copulation in *D. melanogaster* lasts an average of 20 minutes. Analyses of natural populations and bi-directional selection indicated low but significant heritabilities of mating duration, with the genetic variation attributed mostly to males. Twenty generations of divergent selection caused little increase but about 50% decrease in mating duration (MacBean & Parsons 1967).

## FITNESS CONSEQUENCES OF COGNITIVE TRAITS

The other fundamental condition for the evolution of a certain cognitive trait is that the genetically based individual variation in this trait is associated with variation in fitness. Currently, a relatively small body of literature links cognitive traits to



survival and reproductive success. In addition to reviewing that literature here, I also discuss key studies relating cognition to performance measures such as foraging success and growth rate, which may be positively correlated with fitness. I focus on three major categories for which data exist: perception, learning, and decision making.

## Perception and Fitness

Cave and surface-spring populations of the amphipod *Gammarus minus* exhibit genetically based individual variation in eye and antenna sizes (see the subsection Cross-Modality Variation). Jones et al. (1992) computed selection gradients on the basis of individual mating success and fecundity in *Gammarus* and found significant directional selection for smaller eyes in caves and larger eyes in springs. Both populations, however, showed significant directional selection for longer antennae corrected for body size, suggesting that perhaps differential survival, which was not measured, acted against longer antennae in spring populations (Jones et al. 1992).

The genetics and evolution of color vision have been studied extensively (see sections above and below). Only recently, however, have a few studies examined the benefits of trichromatic over dichromatic vision. Most new world monkeys (platyrrhine) show polymorphism in color vision. In these species, a single polymorphic X-linked locus encodes a middle- to long-wave opsin. Together with the autosomally encoded short-wave opsin, the polymorphic locus generates dichromatic vision in all males and homozygous females and trichromatic vision in heterozygous females (Jacobs 1998). An elegant experiment in marmosets (*Callithrix geoffroyi*) took advantage of that polymorphism and documented a higher detection rate of orange food items by trichromatic than dichromatic individuals. The trichromatics, however, showed no higher detection rate of green food items compared with the dichromatics (Caine & Mundy 2000). Theoretical calculations also indicate that trichromatic vision could increase fruit detection against leaf background (Osorio & Vorobyev 1996, Regan et al. 2001). Two studies, however (Dominy & Lucas 2001, Lucas et al. 2003), indicated that trichromatic vision is crucial for detecting preferred leaves but not fruits in several primate species.

## Learning and Fitness

The intuition that learning has positive effect on fitness has rarely been tested in the field. A notable exception involves the optimal timing of egg laying in great and blue tits (*Parus major* and *P. caeruleus*). Matching the timing of nestling feeding with the local peak in food abundance is positively associated with fitness (Thomas et al. 2001). Peak food abundance varies among habitats, and birds must predict the peak a few weeks in advance to time their egg laying properly. The timing of egg laying depends partially on innate population-specific responses to photoperiod (Lambrechts et al. 1997). Field evidence suggested, however, that experience in the first breeding season influenced successive timing of egg laying in great tits

(*Parus major*) (Nager & van Noordwijk 1995). A later experiment (Grieco et al. 2002) involving manipulation of food availability during nestling feeding in blue tits (*P. caeruleus*) indeed indicated that females with higher food supplies during nestling feeding laid eggs later than control females in the following year. Further experiments may critically examine the role of learning in altering the timing of egg laying.

A critical laboratory test linking learning to fitness involved grasshoppers (*Schistocera americana*) that had to choose between nutritionally balanced and nutritionally deficient food types. Grasshoppers in the learning treatment could learn to associate the balanced food with reliable taste, color, and spatial cues. In contrast, the random treatment had these cues varying randomly over time, hence preventing learning. The learning grasshoppers had significantly higher growth rates than the random grasshoppers (Dukas & Bernays 2000). Other laboratory studies indicating positive effects of learning on fitness involved (a) higher mating success in wild-type than learning-deficient male fruit flies (*D. melanogaster*) (Gailley et al. 1985); (b) increased reproductive success in parasitoid wasps (*Biosteres arizanus*) that were allowed to rely on learning for host choice (Dukas & Duan 2000); and (c) higher survival and reproduction of herbivorous mites (*Tetranychus urticae*) that learned to prefer one host plant species over another (Egas & Sabelis 2001).

Learning also allows individuals to anticipate and adjust a priori to events with major physiological impacts (Hollis 1997). For example, heroin-induced mortality in heroin-experienced rats was lower when the drug was injected in the environment previously associated with the drug than when it was injected in a familiar place not linked to the drug before. This difference in survival was attributed to physiological changes occurring prior to heroin injection in the predictable environment (Siegel et al. 1982). In natural settings, physiological preadjustment mediated by learning can increase (a) tolerance of extreme temperatures (Kissinger & Riccio 1995), (b) probability of winning a fight, (c) male reproductive success, and (d) the likelihood of predator avoidance (Hollis 1997).

## Decision Making and Fitness

Numerous studies suggest that animal decisions influence fitness, but empirical research linking most types of decisions to fitness is scarce. This section focuses on three central categories of decisions determining fitness: foraging, antipredator behavior, and mate choice.

**FORAGING** A rare field study linking foraging decisions to lifetime fitness involved crab spiders (*Misumena vatia*), which are semelparous, sit-and-wait predators that hunt for insect prey on flowers. Adult females vary in their success of choosing the best hunting sites and prey types. Spiders that chose sites with higher prey densities had higher growth rates and greater lifetime egg production (Morse & Stephens 1996). A long-term study in four treatment populations of zebra finches (*Taeniopygia guttata*) manipulated the birds' rate of food intake by varying

handling time while allowing for similar daily total food intake. Fecundity, survival, and the consequent population growth rate were all highly positively correlated with feeding rate (Lemon 1991).

**ANTIPREDATOR BEHAVIOR** The northwest garter snake (*Thamnophis ordinoides*) shows continuous variation in color pattern (stripedness) from three complete bright stripes, to spots, to no markings at all. Survival of juvenile garter snakes in the field was higher in individuals with opposite combinations of stripedness and the behavioral tendency to perform reversal evasive movements during escape from predators. That is, survival was highest in striped snakes showing little reversal and in unstriped snakes with high reversal scores. This association between color pattern and behavior probably reflects visual predators' difficulty in judging the speed of moving striped snakes, as well as the advantage of a broken, cryptic pattern for evasive snakes (Brodie 1992).

Many animals rely on indirect cues associated with predators for antipredatory behavior (Kats & Dill 1998). Wolf spiders (*Pardosa milvina*) exposed to silk and excreta from their spider predator (*Hogna hellus*) showed a shift in space use involving vertical climbing on container walls, a behavior that was linked to higher survival when exposed to the predator. Overall, survival of wolf spiders exposed to predator silk and excreta cues and predators was higher than that of wolf spiders placed with predators but not exposed to the cues (Persons et al. 2002).

**MATE CHOICE** Compared with other categories of decisions, a much larger body of literature from a wide variety of taxa indicates that mate choice decisions in both females and males have positive effects on fitness. Documented benefits of mate choice include (a) avoiding inviable offspring through interspecific mating; (b) better fertilization ability or fecundity; (c) better partner or offspring care; (d) superior territory; (e) lower risk of predation, disease, or injury; and (f) producing offspring of higher heritable quality (Andersson 1994, Moller & Alatalo 1999, Moller & Jennions 2001). A recent example relating female mate choice to fitness is work on the cricket, *Gryllus lineaticeps*, in which females reared on a low-nutrition diet had higher survivorship and more fertilized eggs when mated to males with preferred song than to other males (Wagner & Harper 2003). A recent example of a fitness effect of male mate choice is a study indicating that male house mice (*Mus domesticus*) from a feral source population fathered more offspring that had greater survivorship when they mated with their preferred female rather than with other females (Gowaty et al. 2003).

## THE EVOLUTION OF COGNITIVE TRAITS

The best available information about evolution of cognitive traits is for color vision and decision making, most likely because they are easier to quantify than other traits. Other examples examined in this section mostly represent highly suggestive cases requiring further research.

## Perception

**COLOR VISION** Compared with other senses, color vision is more accessible to genetic and molecular analyses, which, combined with phylogenetic techniques, has allowed researchers to reconstruct key events in the evolution of color vision. Color perception is highly variable among vertebrates. The common ancestor of terrestrial vertebrates had four types of photopigments, which have been preserved in many birds and reptiles and some mammals. Most placental mammals (Eutheria), however, are dichromatic: They have only a short-wavelength sensitive photopigment (S) encoded by an autosomal gene and a long-wavelength sensitive photopigment (L) encoded by a gene on the X chromosome. Color vision is poor at low light intensities, and this fact can explain the evolutionary loss of tetra-chromatic vision in early mammals, which were presumably nocturnal. Improved color vision, however, evolved in anthropoid primates. In old world anthropoids, duplication followed by divergence of the L gene created distinct L photopigment and middle-range photopigment (M). Similar, though independent, duplication and divergence of the L gene took place in new world howler monkeys (*Alouatta* spp.). In other new world anthropoids, no duplication of the L gene has occurred. Rather, the L gene is polymorphic and encodes distinct L and M photopigments, creating trichromatic vision in heterozygous females but dichromatic vision in all other individuals (Jacobs 1998, Nathans 1999, Surridge et al. 2003). It is assumed that diurnal activity selected for trichromatic vision in anthropoid primates. Evidence indicating advantages of trichromatic over dichromatic vision in food finding is presented in Perception and Fitness, above. Excellent, though less-detailed, information pertaining to adaptive evolution of color vision in various ecological settings exists for other taxa, including fish (Yokoyama & Yokoyama 1996, Sugawara et al. 2002), birds (Hart 2001), and insects (Briscoe & Chittka 2001).

**OLFACTION** The evolution of trichromatic vision in old world anthropoid primates just discussed paralleled evolutionary degradation of the vomeronasal system in these species (Zhang & Webb 2003). Many terrestrial vertebrates perceive pheromones primarily through the vomeronasal organ. Genes encoding the TRP2 ion channel and V1R pheromone receptors, which are unique to the vomeronasal pheromone transduction pathway, were impaired in a common ancestor of old world anthropoid primates (Catarrhines) approximately 23 million years ago. Further inactivation of pheromone receptor genes has been an ongoing process in these species. In contrast, TRP2 genes are functional in new world monkeys (Platyrrhines) (Zhang & Webb 2003).

## Learning and Memory

The best evolutionary research on learning and memory consists of extensive work on spatial memory in birds that cache a large number of food items in scattered locations. This research program has not yet evaluated the genetic basis of spatial

memory, however. Research on spatial memory has documented two major findings. First, bird species that rely more heavily on retrieval of cached food show better spatial memory than closely related noncaching species (Balda & Kamil 1989, Pravosudov & Clayton 2002). Many, though not all, the experiments documented the predicted positive association between reliance on spatial memory and performance on spatial memory tasks (reviewed in Shettleworth 2003). Overall, the positive evidence is highly compelling because it comes from several laboratories and distinct bird taxa.

The second finding from research on spatial memory was based on extensive research that indicated that the hippocampus is involved in spatial memory (Sherry & Vaccarino 1989). Analyses controlling for phylogeny indicated that in both European and North American birds, relative hippocampus volumes are larger in species that store food than in nonstoring species (Krebs et al. 1989, Sherry et al. 1989). Similar results were obtained in a within-species comparison: Individual black capped chickadees (*Poecile atricapilla*) from Alaska, which rely more heavily on stored food than intraspecific individuals from Colorado, had larger hippocampus volumes and showed better spatial memory than the Colorado birds (Pravosudov & Clayton 2002).

As already mentioned, the genetic basis of spatial memory is unknown. Work on mice has recently identified two quantitative trait loci, *Hipp1a* and *Hipp5a*, which explain 25% of the heritable variation in hippocampus size (Peirce et al. 2003). Furthermore, artificial divergent selection in mice for high and low open field activity resulted in structural hippocampal changes (Hausheer-Zarmakupi et al. 1996). Although these studies indicate genetic effects on hippocampus structure, they do not link such effects to spatial memory. In contrast, environmental effects, especially tasks requiring spatial memory, influence hippocampus size (Clayton 2001).

In sum, bird species and populations that cache food have larger hippocampus volumes, which allow them to depict better spatial memory compared with noncaching species. Some of the documented difference in hippocampus volume and spatial memory likely reflects an evolved cognitive change, but the evolutionary scenario must be augmented with relevant genetic information.

Research on song learning in oscine song birds (suborder oscines) provides another example for possible adaptive evolution of specific learning ability. In most oscines, young males learn aspects of their song from older adults. Song-repertoire size is positively associated with males' mating success (reviewed in DeVoogd 1998) and with volumes of the song control nucleus high vocal center (HVC) (DeVoogd et al. 1993, Szkeley et al. 1996). In zebra finches (*Taeniopygia guttata castanotis*), there is genetically based individual variation in HVC volume (Airey et al. 2000), which is positively associated with song-learning ability (Ward et al. 1998, Airey & DeVoogd 2000). This finding suggests that selection on larger song repertoire led to the evolution of enhanced song-learning ability and larger HVC.

Wright and colleagues (Wright et al. 1996, Marinesco et al. 2003) have taken a novel approach to examining the evolution of learning. They compared neuronal correlates of learning in the mollusc *Aplysia californica* and five related species.

*Aplysia* has been a prime model species for research on the neurobiology of learning (Kandel 2001). In *Aplysia*, learning has been linked to serotonin-induced increased spike duration and excitability in mechanosensory neurons of the tail-withdrawal reflex. Applications of serotonin in the five related species caused (a) only increased spike excitability in the two ancestral species, (b) both increased spike duration and excitability in two closely related species, and (c) neither increased duration nor increased excitability in another closely related species. These results led Wright et al. (1996) to suggest that increased spike duration in response to serotonin arose more recently in the evolution of the *Aplysia* group and that a learning-related mechanism was lost in one species. Further work with the *Aplysia* species group could evaluate the adaptive significance of the documented learning-related differences (Wright et al. 1996).

## Volume of Brain Parts

In addition to research just discussed on spatial memory and song repertoire, several studies employing phylogenetic analyses have documented positive correlations between presumed enhancement of a certain cognitive ability and the volume of brain parts devoted to that trait. Examples include (a) presumed visual resolution as indicated by eye size and optic-lobe mass in birds (Brooke et al. 1999), (b) probable increased reliance on olfaction associated with nocturnal activity and enlarged olfactory bulb in birds and mammals (Healy & Guilford 1990, Barton et al. 1995), (c) frequency of feeding innovations (novel or unusual feeding behaviors) and the volumes of hyperstriatum ventrale and neostriatum in birds and neocortex and striatum in primates (Reader & Laland 2002, Lefebvre et al. 2004), and (d) larger brain size in mammals with more challenging feeding behaviors: fruit- versus insect-feeding bats (Eisenberg & Wilson 1978) and nonherbivorous versus herbivorous rodents and primates (Clutton-Brock & Harvey 1980, Mace et al. 1981). Finally, another noteworthy finding is that animal domestication was associated with large decreases in volumes of certain brain parts (Kruska 1988). All the examples above require further detailed investigations on the mechanisms generating the associations between brain and ecology and their genetic foundations.

## Decision Making

The best available data on evolution of decision making exists for feeding and antipredatory behavior.

**DIET IN PHYTOPHAGOUS INSECTS** Many insects that feed on plant material specialize on a single host species, which typically also serves as the mating ground. Hence, host choice is a crucial decision because host shift may lead to reproductive isolation and incipient speciation (Mayr 1963, Funk et al. 2002). A well-recorded recent host shift involved adoption of introduced apples (*Malus pomila*) by apple maggot flies (*Rhagoletis pomonella*) that originally exploited native hawthorn (*Crataegus* spp.) in North America approximately 150 years ago.

Currently, the apple and hawthorn races are genetically distinct, and there is little migration of individuals between the two hosts (Feder et al. 1994). Recently, host preferences of flies reared from larvae on an artificial diet were tested using synthetic blends of apple and hawthorn volatiles. In all populations examined, flies showed strong affinities to their natal host. Moreover, flies of the hawthorn race, which were raised on apple in the laboratory for two generations, also showed a strong preference for hawthorn over apple. These results indicate that the apple race of *R. pomonella* has altered its response to fruit volatiles over the past 150 years, increasing its preference for apples and reducing its response to hawthorn (Linn et al. 2003). The evolution of host choice in phytophagous insects has been well studied in a variety of other systems as well (Funk et al. 2002).

**ANTIPREDATORY BEHAVIOR** One of the best documented cases of evolution in the wild involves populations of guppies (*Poecilia reticulata*) occurring in distinct high- and low-predation pools in Trinidad. The principle guppy predators in that system are pike cichlids (*Crenicichla alta*). In addition to the natural variation among pools, there were a few experimental introductions of fish about 25 years ago. Fish from distinct predation regimes differ in various traits, including color, life history, mating, foraging, and antipredatory behaviors (reviewed in Endler 1995, Magurran et al. 1995). A laboratory study evaluated divergent evolution of antipredatory behavior in Trinidad guppies by transferring wild-caught fish to predator-free aquaria and testing a second generation of laboratory-born offspring. Offspring from both natural and introduced high-predation populations were significantly more likely to escape predation by pike cichlids than were offspring from natural and introduced low-predation populations. In the case of the guppies from pools with introduced predators, the results indicate evolutionary change in antipredatory behavior within approximately 30 generations (O'Steen et al. 2002). The exact cognitive mechanisms underlying that change have not yet been quantified.

In eastern North America, larvae of damselfly species in the genus *Enallagma* that grow in lakes with fish predators show distinct antipredatory behaviors compared with larval *Enallagma* spp. occupying fishless lakes in which dragonfly larvae are the top predators. Phylogenetic analysis suggested that fish lakes were the ancestral habitat of these damselflies, from which at least two independent lineages of dragonfly-lake species arose recently (Brown et al. 2000). The transition to dragonfly-lakes was associated with (a) increased activity in the absence of predators; (b) loss of antipredatory response to fish; and (c) adoption of an escape response to approaching predators, a tactic that reduces dragonfly but not fish predation (McPeck 1990, Stoks et al. 2003). Preliminary evidence suggests that much of the behavioral differences have a genetic basis, and research in progress is critically examining this issue (M. McPeck, personal communication). Dragonfly-lake damselflies (*E. boreale*), however, did learn to show antipredatory response to a fish predator (northern pike, *Esox lucius*) after simultaneous exposure to stimuli from the predator and injured conspecific damselflies (Wisenden et al. 1997).

## ENVIRONMENTAL EFFECTS ON COGNITIVE TRAITS

In the sections above, I focused on genetic variation and did not explicitly discuss phenotypic plasticity. Most phenotypic traits, however, are determined by an interplay between an individual's genes and numerous internal and external factors, including nutrition, temperature, social environment, and interactions with other species. Consequently, a single genotype can have a whole set of phenotypes, termed norm of reaction, under different combinations of environmental conditions (reviewed in Futuyma 1998, Pigliucci 2001). In many anatomical and morphological characteristics, environmental effects are restricted to early developmental stages. A simple example for such irreversible plasticity is the positive association between adult body size and nutritional quality during development in many insects. Other traits can show reversible plasticity throughout ontogeny. For example, initiating a few weeks of weight lifting by a human adult would result in increased volumes of a few muscles. Quitting that exercise regime, however, would be associated with rapid atrophy of the same muscles.

The norm of reaction may be either nonadaptive, as in the case of body size and nutrition just mentioned, or adaptive, as in the change in muscle volume in response to power requirements. Most importantly, different genotypes may have distinct reaction norms. Such genetically based individual variation in the norm of reaction, or gene by environment interaction, implies that the norm of reaction can evolve. Note that evolutionary biology employs a statistical definition of "interaction": the terms "phenotypic plasticity" and "reaction norm" only imply environmental effects on the genotype. The term "gene by environment interaction" is restricted to cases where the environment has different effects on different genotypes (reviewed in Futuyma 1998, Pigliucci 2001). Most phenotypic plasticity studies have dealt with morphological characteristics. Cognition, however, can also be analyzed within the phenotypic-plasticity framework (Dukas 1998b).

Two key questions about phenotypic plasticity of cognitive traits are pertinent: (a) Is there evidence for adaptive phenotypic plasticity of cognitive traits in ecologically relevant settings? (b) Is there genetic variation for reaction norms of cognitive traits?

### Adaptive Phenotypic Plasticity of Cognitive Traits in Ecologically Relevant Settings

Before discussing adaptive plasticity, I must review the extensive literature on apparently nonadaptive brain plasticity. Note, however, that little evolutionary research on cognitive plasticity has been carried out. Hence, adaptive patterns may underlie at least some cases of apparently nonadaptive cognitive plasticity. Many parts of the brain require feedback from the environment for proper development. For example, in kittens with one eye covered for two months after birth, most neurons in the striate cortex depicted normal receptive fields corresponding to the normal eye, but only a few neurons were influenced by the deprived eye. Monocular



visual deprivation had a smaller negative effect in older kittens and no effect in adults (Wiesel & Hubel 1963). In natural settings, all developing individuals are typically exposed to visual feedback in both eyes. Hence, such external effects on vision can probably be regarded as nonadaptive plasticity.

Another well-studied example of apparently nonadaptive plasticity involves environmental enrichment, defined as laboratory housing conditions typically consisting of large space, exercise, various inanimate objects, and social stimulation (van Praag et al. 2000). Compared with mammals grown in the typically highly deprived laboratory setting, mammals under environmental enrichment exhibit better learning and memory and increased brain size, neuron size, dendritic branching, and synapses per neuron, as well as different expression of genes linked to neuronal structure, synaptic plasticity, and transmission (Rampon et al. 2000, van Praag et al. 2000). Similar effects of environmental enrichment on brain and behavior have been documented for fruit flies (*D. melanogaster*) (Technau 1984, Heisenberg et al. 1995, Dukas & Mooers 2003). Because the actual comparison in environmental-enrichment studies is between highly deprived and less-deprived laboratory settings, the documented plasticity probably reflects a need for proper environmental feedback for brain development and maintenance. The sections below discuss some of the available evidence for adaptive phenotypic plasticity of cognitive traits in ecologically relevant settings.

**PERCEPTION** Sustained experiences that demand specific use of a narrow range of a sensory modality result in a magnified neuronal representation of that range in the cortex (Kaas 1991, Nudo et al. 1996). For example, tactile discrimination performed with a single finger in adult monkeys resulted in an enlarged neuronal map for that finger, accompanied by enhanced discrimination ability on the tactile task (Recanzone et al. 1992). Such reversible plasticity implies allocation of metabolically expensive neuronal tissue on the basis of current behavioral needs, but no research has evaluated the adaptive value of that brain plasticity.

**LEARNING AND MEMORY** Learning is an example of phenotypic plasticity (Dukas 1998b), and evidence for adaptive learning was reviewed above in the section on learning and fitness. Nonetheless, a relevant question is whether there are known cases of adaptive norms of reaction for learning and memory abilities. Recent research on neurogenesis suggests such adaptive plasticity. The hippocampus and song nucleus in song birds generate new neurons throughout life. In black capped chickadees (*P. atricapillus*), hippocampal neurogenesis peaks in the fall, coinciding with high demands for spatial memory during peak caching activity. In adult male canaries (*Serinus canaria*), as well as in a few other species, peak neurogenesis in the HVC occurs during the breeding season (Barnea & Nottebohm 1994, Smulders et al. 2000, Tramontin & Brenowitz 2000, Nottebohm 2002). Similarly, neurogenesis occurs in the hippocampus of adult mammals. Several studies documented either increased neurogenesis or increased survival of new neurons in subjects under either exercise regimes or intense learning activities (Gould et al.

1999, van Praag et al. 2000). However, no direct evidence links neurogenesis to learning and memory, and some data appear to disagree with such a link. For example, neurogenesis also occurs in the HVC of adult male zebra finches and adult male song sparrows (*Melospiza melodia*) even though they learn their songs before sexual maturity (Tramontin & Brenowitz 1999, Nottebohm 2002).

In sum, there is strong evidence for both seasonal and activity-dependent plasticity in the rate of either generation or survival of new neurons. Such brain plasticity appears adaptive because it correlates with activities such as navigation, food caching, and singing. To date, however, no empirical data have either directly linked brain plasticity to learning and memory or demonstrated the adaptive significance of such plasticity.

**DECISION MAKING** By definition, all decisions amount to phenotypic plasticity: individuals decide to perform activity  $x$  in one environmental state, perform activity  $y$  in response to another environmental state, or remain inactive given yet another environmental state. Evidence for adaptive decision making was discussed in the section Decision Making and Fitness, above. Here, I briefly review data on adaptive norms of reaction for decision making. Most animals exhibit apparently adaptive antipredator behavior in response to indirect and direct information about the presence of predators (Kats & Dill 1998, Lima 1998). Relyea (2003) compared age-specific responses of gray-treefrog tadpoles (*Hyla versicolor*) to odors of their dragonfly-larvae predators (*Anax longipes*). In addition to constant presence and constant absence of predatory cues, Relyea also either introduced or removed predatory cues during three stages of the 18-day experiment. Only young tadpoles responded to predation risk by hiding. By day 10, there was no difference in hiding between the predation and nonpredation treatments. Activity level under predation risk was lower than under nonpredation conditions throughout most of the tadpole ontogeny but similar at the end of the experiment. Overall, late in ontogeny, the tadpoles reduced employment of antipredatory behavior and relied mostly on morphologically plastic antipredatory responses, including greater body mass, shorter bodies, and longer tails. That is, the tadpoles exhibited an age-specific reaction norm for antipredatory behavior. The reduced use of antipredatory behaviors probably reflected their high cost in terms of reduced feeding and growth rate and perhaps the increased effectiveness of the antipredatory morphology (Relyea 2003). Other well-studied cases of apparently adaptive norms of reactions in decision include the effect of body reserves on feeding and antipredatory behavior (Cuthill & Houston 1997) and effects of experience on aggression (Yeh et al. 1996) and sexual behavior (Crews 2003).

## Genetic Variation for Reaction Norms of Cognitive Traits

There is probably no data pertaining to genetic variation in cognitive plasticity except for that involving decision making. However, the lack of information probably indicates that little research on this topic has been carried out.

Many zooplankton species exhibit diurnal vertical migration, with individuals found in deeper water during the day than at night. This behavior reduces predation by visual predators such as fish (Ringelberg 1999). Clones of *Daphnia magna* show large genetic variation in their preferred water depth in daylight. Furthermore, different daphnia clones vary in their responses to the presence of fish odor in the water, with clones from habitats with high fish predation responding more strongly and moving to deeper water than clones from habitats with no fish predation (De Meester 1993, De Meester 1996). Research at a Belgian pond revealed that the large genetic variation in plasticity allowed rapid evolution of daphnia responses to temporal variation in fish predation over 30 years (Cousyn et al. 2001).

## EFFECTS OF COGNITIVE TRAITS ON EVOLUTION

Learning and decision making can expose individuals to, and enhance survival in, new niches and adaptive zones. This fact suggests that cognitive traits play an important role in evolutionary change and speciation (Baldwin 1896, West-Eberhard 2003). Three recent independent analyses, however, have reached the similar conclusion that phenotypic plasticity may speed up, slow down, or have no net effect on evolutionary change (Robinson & Dukas 1999, Huey et al. 2003, Price et al. 2003). On the one hand, although an environmental change might cause extinction of a nonplastic population, plasticity could enable population persistence, allowing evolutionary change in the new environment. On the other hand, if plasticity is sufficient for maximizing fitness in the new environment, the existing genetic variation would remain hidden from natural selection. Hence, no evolutionary change would occur, and a return to the old environment would result in complete reversal to the ancestral type (Robinson & Dukas 1999, Huey et al. 2003, Price et al. 2003).

Elegant experiments by Waddington (1953, 1959) clearly illustrate that plasticity can indeed enhance evolutionary change. However, the overall effect of phenotypic plasticity in general and cognitive traits in particular on evolutionary change is still unknown. On the negative side, there is no evidence that enhanced cognitive abilities increased the rate of morphological evolution in either great apes or hominoids (Lynch & Arnold 1988). On the positive side, a few studies in birds documented positive correlations between relative brain size and (a) the number of species per taxon (Nicolakakis et al. 2003), (b) the number of subspecies per species (D. Sol, G. Stirling, N. Nicolakakis, and L. Lefebvre, unpublished manuscript), and (c) invasion success (Sol et al. 2002). In birds, brain size is highly positively correlated with the size of the hyperstriatum ventrale (HV), the part of the telencephalon most closely involved in multimodal sensory integration and learning. HV size is positively correlated with behavioral flexibility in birds (Lefebvre et al. 2004). Hence, at least in birds, some cognitive abilities are positively correlated with measures of evolutionary change.

## CONCLUSIONS AND PROSPECTS

Relatively little research on the evolutionary biology of animal cognition has been carried out. Nevertheless, data compiled from several disciplines indicate that (a) there is genetically based individual variation in cognitive traits, (b) cognitive traits affect animal fitness, and (c) cognitive traits evolve. That is, cognitive traits can be subjected to evolutionary research like any other animal feature following established techniques employed in numerous studies mentioned in this review. Compared with working on morphological traits, however, studying cognitive traits involves two additional difficulties. First, cognitive traits are typically quantified through whole-animal behavioral tests. Second, many cognitive traits are more labile than morphological characteristics. Both issues can be addressed with properly controlled experimental protocols that can reliably quantify a given cognitive feature through behavior.

Cognitive phenotypes, like morphological and physiological phenotypes, are determined by genes and environment. Hence, employing tools developed for studying phenotypic plasticity mostly in the morphological domain could enhance research on the genetics and evolution of cognitive plasticity. Learning, memory, and decision making are types of phenotypic plasticity, and some information is available about their genetics, adaptive value, and evolution. We know little, however, about adaptive phenotypic plasticity of perceptual traits, including vision, hearing, and olfaction. Another important issue requiring future research involves adaptive environmental effects on cognitive traits. For example, compared with flies grown at low density, are the brains of flies developed under crowded conditions better adapted for migrating in search of new food sources (Heisenberg et al. 1995)? Finally, in spite of extensive research on brain plasticity, we know little about genetic variation in reaction norms of cognitive traits. For example, is there genetically based variation in the effect of food caching experience on hippocampal neurogenesis? And does this variation translate into future differences in memory?

The last section of this review suggests that assertions of a unique role for cognition in enhancing evolutionary change are currently not supported by sufficient critical data. Although theory indicates that cognition could either increase or decrease the rate of evolution (Robinson & Dukas 1999), further empirical work on that topic is highly desirable.

In various places throughout this review, I mention what further information is necessary to advance research on the evolutionary biology of animal cognition. In addition, a few major issues that warrant close examination are listed below. A fair amount of data exists on genetic variation in cognitive traits. How does such natural genetic variation affect behavior and fitness, and what factors help maintain this variation? There are probably no observational data on the evolution of cognitive traits in the wild, although such research is highly feasible. For example, the amphipod system studied by Culver et al. (1995) seems ideal for further investigation of the evolution of perceptual traits and their correlated brain

regions. Until recently, evolutionary studies on cognition have mostly focused on benefits while ignoring costs. Various costs, however, including energy to maintain neuronal machinery and process information, and time to process complex information, can affect the fitness consequences of cognitive traits (Dukas 1999, Bernays 2001, Laughlin 2001, Mery & Kawecki 2003). Further information on this topic is needed.

In sum, this review indicates that animal cognition can readily be placed within an evolutionary framework. The evolutionary analysis highlights key issues requiring future research, which will help us understand animal cognition, its evolution, and the role of cognition in animal evolution.

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