Cognitive Ecology II

Author: Gould, Kristy L.

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BOOK REVIEWS

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Cognitive Ecology II—edited by Reuven Dukas and John M. Ratcliffe. 2009. University of Chicago Press, Chicago. 372 pp. ISBN-13978-0-226-16936-1. $40.00 (paperback).

I have been immersed in the integrative approach to cognitive ecology research throughout my career. This field has grown tremendously since I first entered graduate school in 1992, and this growth is further demonstrated by how much has changed within the field since the publication of the first *Cognitive Ecology* in 1998. I was eager to read this second edition to see how others have been continuing this integrative approach in their research and what lies ahead in this field.

In the introduction, Reuven Dukas and John Ratcliffe clearly lay out the goal of this edition, which is to highlight the perspective that cognitive traits are products of natural selection and therefore can influence the fitness of individual organisms. In order to study cognitive traits, we need to take an integrative approach if we are to understand their evolution fully. This approach includes integrating mechanistic and functional analyses with the methods of psychology, ecology, and evolution. The cognitive traits that are the main focus of this book are learning, memory, and decision making.

The book is organized into four main parts. The focus of the two chapters of Part I is on the ultimate and proximate mechanisms of learning. In Chapter 2, Dukas tackles the question of why learning is important and empirically investigates this by using learning in fruit flies as an example. The fact that fruit flies, with an average life span of several days, are able to demonstrate learning in the same four areas as higher organisms (foraging, avoiding predators, aggression, and sexual behavior) provides evidence that the mechanistic aspects of basic learning must be highly conserved across the animal kingdom. Work with simple organisms can thus inform us of the importance of learning in all organisms and how this learning translates into consequences for fitness.

Chapter 3 discusses integrative research on foraging behavior in the honeybee (*Apis mellifera*). Fahrbach and Dobrin start the chapter with a wonderful analogy between the foraging honeybee and a human example of complex navigation, the London taxi driver. Taxi drivers demonstrate neural plasticity in a structure of the brain important for spatial navigation, the hippocampus. The volume of the hippocampus is positively correlated with the length of time a taxi driver has been on the job. This area of the brain has also been shown to be important in spatial navigation in other mammals and birds. In insects, the analogous neural structures are called the mushroom bodies, and in the honeybee the size of these structures is also positively correlated with foraging experience. The authors argue that understanding the neural aspects of learning in any organism will aid in designing better methods of research on learning and that experience-based brain plasticity is probably more common in animals than we think. One aspect they believe is missing is an understanding how individual differences in behavior, like foraging, may be linked to individual differences in neural structure. They believe this topic could be explored using methods already established in field experiments on foraging honeybees.

Part II emphasizes avian cognition in a number of forms and is most likely to interest readers of the *Condor*. These forms include memory, song, and innovation in birds. Chapter 4 focuses on the cognitive aspects of song communication and song learning in the Song Sparrow (*Melospiza melodia*). Beecher and Burt argue that flexibility in song learning is important and that the role of cognition, in general, has been largely ignored in studies of bird song communication. They summarize their research since publication of the first *Cognitive Ecology*, which has shown that young male Song Sparrows learn the songs of their adult male neighbors, thereby demonstrating the importance of context in learning song. This learning allows neighboring males to recognize a neighbor through song and thus perceive it as less of a threat. Therefore territory disputes can be resolved with minimal cost. Beecher and Burt are also beginning to test the "social eavesdropping hypothesis," which suggests that young males decide which songs to learn through listening to the social interactions among males that yield information such as dominance.

Chapter 5 integrates work on sexual signaling via song in songbirds and developmental issues in the avian brain. Searcy and Nowicki investigate the developmental-stress hypothesis as it relates to the specialized neural system for song in the bird brain. Early stresses in development, including poor nutrition and parasitism, are predicted to negatively affect the development of the song system because other areas of the brain are less costly to develop. The authors provide a good background on the song system, specifically the pathways for song production and song learning, although inclusion of a neuroanatomical diagram of the two systems would have been useful. They also provide useful background information on what is known about females' preference for song. Then they go on to describe experimental manipulations to induce developmental stress in various species and their effects on males' song and neural structure. It appears that a reduced diet during development affects the brain and males' song negatively in many species of birds. The authors suggest that future studies should examine the effects of developmental stress on other aspects of the male that could be important in females' choice: social dominance, function of the immune system, and cognitive abilities.

Chapter 6, by Pravosudov, continues the focus on avian brain development but addresses the constraints of nutritional stress on spatial memory and development of the hippocampus. He discusses the "adaptive priorities in brain development hypothesis," which states that developmental stress may favor investment in traits that are important for individual survival at the cost of less

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important traits. He argues that, according to this hypothesis, spatial memory in scatter-hoarding birds is an important survival trait and therefore should be invested in even under developmental stress. However, his research with Western Scrub Jays (*Aphelocoma californica*) raised on a reduced diet suggests otherwise. These birds have a smaller hippocampus and do poorly on tasks entailing spatial memory. As discussed in the previous chapter, developmental stress is also linked to smaller neural structures in the song system, although song production and learning are not as important to individual survival. Pravosudov argues that the reason the hippocampus and song system may both be negatively affected by developmental stress is that these two areas of the avian brain develop at about the same time and both rely on the production of new neurons for their growth and maintenance through adulthood. Therefore, in both areas developmental stress could be impairing the stem cells from which new neurons are derived. The ideas in chapters 5 and 6 provide many ideas for further research on the development of the avian brain as it relates to cognitive traits such as song learning and spatial memory.

In Chapter 7, Sol addresses the "cognitive-buffer hypothesis" for the evolution of large brains. It takes more time in development to grow a disproportionately larger brain, which delays reproduction. One way of compensating in terms of individual fitness is to lengthen the time for reproduction. In other words, live longer. There appears to be a relationship between relative brain size and lifespan in many organisms. A bigger brain also affords an animal the ability to modify its behavior adaptively in the face of a changing or novel environment. Studies have shown a correlation between a larger brain and complex cognitive behavior, thus supporting the "cognitive-buffer hypothesis." Examples of behavioral flexibility in many organisms are provided in a table and include behaviors that depend on three main categories of cognition: innovation, learning, and decision making. While behavioral flexibility has been shown in both the field and laboratory, direct field evidence showing that behavioral flexibility in novel or changing environments does increase individual fitness is lacking. Sol mentions three situations in which we might be able to see such direct evidence, including invasion into new environments, exposure to habitat that has been altered through human activity, and seasonal habitats. He concludes with areas for future research, including the costs of extended parental care in young with delayed development and the idea that a longer life is more likely to expose an organism to more environmental changes, thus increasing the demand for behavioral flexibility.

Part III is about the cognitive aspects of decision making, specifically, mate choice and predator–prey interactions. The focus of Chapter 8, by Ryan, Akre, and Kirkpatrick, is on the cognitive aspects of mate choice. I was surprised to find out that there has been very little research on the role of learning and memory in mate choice. Therefore, this seems like an area ripe for investigation. The first part of the chapter, which could have been pared down, gives the reader a background about detection and perception of mating signals by females. Next, the authors discuss what is known about how females evaluate mating signals and make mate-choice decisions, which they point out has not been investigated with respect to the internal mechanisms involved. Most of their examples come from research on frogs using acoustic signals, but similar principles can be applied to other organisms that use mating signals as well. The authors demonstrate that mate-choice experiments should be designed to test for choice that is not based on generated preference functions. They also discuss areas for future research related to the role of memory in mate choice. These include situations where working memory should be important, such as those in which a female is assessing many mates at once and those in which the communicative mating signal is not continually present. The strategy that a female uses could also vary between being highly cognitive in nature or not, depending on the situation and context. Finally, females' adaptations for learning and memory could also bias the kinds of mating signals that evolve. All of these factors highlight the potentially fruitful work ahead in this area of research.

Chapter 9 examines an integrative approach to understanding monogamy in male prairie voles (*Microtus ochrogaster*). Phelps and Ophir provide a very nice synthesis of field ecology, behavior and cognition, neuroscience, and genetics in understanding the evolution of monogamy as a reproductive strategy. The majority of male prairie voles adopt the resident strategy of monogamy, guarding a female on their home territory from other males. A minority of males, however, adopt the wandering strategy, which entails an enlarged home range with the potential for encountering a large number of females for extra-pair copulations. They summarize research that shows the importance of the peptide vasopressin in triggering the aggression needed to be a resident male and contributing to male paternal care found in this monogamous system. While the key areas of the brain related to pair-bonding receive vasopressin at specific receptor sites, there is no difference in receptor expression between resident and wandering males. However, two other areas of the brain that project to the hippocampus do differ in their expression of vasopressin receptors and are related to the differences in space-use patterns between the two mating strategies. Wandering males have lower expression of vasopressin receptors in these two brain areas, whereas resident males have higher expression, suggesting that vasopressin mediates the ability in spatial navigation needed for each mating strategy. The authors also summarize recent work on genetic variation related to vasopressin-receptor abundance in certain areas of the brain, providing hypotheses for further research related to mating strategies.

Chapter 10 discusses an interesting aspect of cognition related to predation that most cognitive ecologists do not think about: cognition in the embryo. Warkentin and Caldwell give a background on detection theory and how it applies to assessment of predation risk. The ability to discriminate among cues so as to reduce errors, such as missed cues or false alarms, is crucial for any organism that is potential prey. Integration of multiple forms of information from the environment can aid in such a task but requires a more complex neural processing system. Embryos in eggs are subject to predation, especially in situations where the eggs are not defended by a parent, as in the case of the species discussed in this chapter, the red-eyed tree frog (*Agalychnis callidryas*). The embryos of this frog can engage in escape hatching in the presence of predatory snakes. This choice, however, is a trade-off. Hatching early avoids potential mortality, but it gives up the relative safety of the egg by exposing the hatchling to aquatic predators. It appears, through clever experiments, that embryos of the red-eyed tree frog can use vibrational cues to determine if the threat of physical disturbance of the egg cluster is severe enough to warrant premature hatching. Specifically, they have to discriminate between the vibrations of rain (not a threat) and the vibrations created when the eggs are being preyed on, usually by snakes (threat). Embryos appear to sample for a period of time before making the behavioral decision to hatch, suggesting that this discrimination is complex because of the trade-offs mentioned earlier and is fairly flexible. The idea of a flexible learning strategy in a frog embryo is something that many of us interested in studying animal cognition have probably never even considered. This work suggests that we have underestimated certain abilities of embryos and provides ideas for further research.

Ratcliffe rounds out this section in Chapter 11 by discussing the predator–prey interactions of bats and moths and how cognition in both groups of organisms can be important. For the reader not familiar with this area of research, the detailed background information, for both bats as predators and moths as prey, was informative but could have been condensed further. Eared moths appear to have evolved ears to detect bats' echolocation calls that then allow them to respond with evasion. The behavioral responses that eared moths make to evade being captured by bats are energetically costly, so their choice is a trade-off between engaging in evasive behaviors and finding a mate. Ratcliffe suggests ways of testing the hypothesis that certain moth species evolved ears to detect bat echolocation, summarizes neuroethological research on the auditory system of eared moths, and gives more examples of the choices that eared moths make. With respect to bats, some species show behavioral flexibility in the foraging strategies they use when searching for moths. They can either engage in hawking (catching moths while flying) or gleaning (catching moths as they rest on substrate). Many other species of bats specialize in one strategy or the other. Bat species with a behaviorally flexible foraging strategy tend to have larger brains. Ratcliffe gives other examples of behavioral flexibility in foraging bats with larger brains which provide ideas for further research on the cognitive abilities of these bats.

Part IV includes three chapters representing different aspects of social cognition. Chapter 12, by Manser, focuses on functionally referential alarm calls. Her main examples come from the meerkat (*Suricata suricatta*), but examples from other animals shown to have referential aspects to their calls are also discussed, including birds such as the Black-capped Chickadee (*Poecile atricapillus*) and Siberian Jay (*Perisoreus infaustus*). One question that has not been addressed is to what functionally referential alarm calls actually refer. They could be labeling certain aspects of a predator, giving instructions on appropriate responses that others should make, or they could refer to the escape behavior of the caller. Manser tests this question with meerkats and concludes that they are most likely referring to what kind of predator is approaching (a denotative signal). She then goes on to discuss other forms of information that can be conveyed in the meerkat's alarm calls, such as how far away the predator is, whether it is moving or stationary, and the urgency of the situation. She also mentions that a meerkat's behavioral response to an alarm call is a trade-off between the risk of predation and foraging. Therefore, denotative alarm calls allow each individual to make its own decision when informed of the kind of predator approaching. She concludes that a focus on this process of decision making in respect to functionally referential alarm calls should be interesting for future research, as well as neurobiological studies to determine if differences in alarm-call information are correlated with activity in different areas of the brain.

In Chapter 13, Kendal, Coolen and Laland discuss the tradeoffs in the use of social and personal information as sources of learning. In most of their examples they focus on learning about foraging. Social information can be useful in reducing search time and predation risk during foraging, but it may be less accurate. Personal learning may increase search time and predation risk, but, on the basis of the current situation, it is likely to be more accurate. Two questions related to the decision to use social information are addressed. First, when should it be used, and, second, from whom is the social information gained? When discussing the strategies used to address these questions, the authors provide theoretical background for each topic, as well as empirical evidence that is tied to the theory. They give evidence from diverse animals, including fish, rats, primates, and humans. From research about when social information should be used, they conclude that the strategy "copy when using personal information is costly" has strong theoretical and empirical support. "Copy when uncertain," because of lack of information, unreliable information, or outdated information has also been empirically demonstrated, depending on the context of the situation. From both a theoretical and an empirical perspective, how an animal identifies sources of social information needs to be explored further, as well as how different strategies for the use of social information are implemented.

The last chapter in this section uses the overall theme of the book, how an integrative approach to studying cognitive ecology can be beneficial, and applies it to understanding the use of social information in birds. In Chapter 14, Federspiel, Clayton, and Emery specifically focus on integrating what they call the three E's—ecology, ethology, and evolutionary history—in understanding comparative cognition. They give a very useful background on social learning, including defining the various types and addressing why social information can be beneficial. They also give some general examples of how sociality can influence cognition by reviewing work on transitive inference in the highly social Pinyon Jay (*Gymnorhinus cyanocephalus*) and how this could be investigated further in terms of how these birds might use social information as they cache and recover seeds. The main part of the chapter presents case studies from four families of birds, the Corvidae, Psittacidae, Anatidae, and Tetraonidae. The authors discuss what is known about representatives of each family in terms of their social structure, how the three E's may influence their use of social information, and empirical research that has successfully been used to draw conclusions about certain behaviors and cognition through this integrative approach. They also provide many examples of avenues for future integrative research on the use of social information in birds and reiterate the importance of good communication between researchers in various disciplines.

Overall, the various chapters in the book do a good job of providing diverse representation, in terms of both the organisms discussed and the questions addressed. They also successfully highlight the common thread throughout, namely, the importance of studying cognitive traits in ecologically relevant systems from an integrative perspective. The chapters each provide specific examples of this integration including understanding the role of the brain, genetics, and ecology in the evolution of cognitive traits such as learning, memory, and decision making. The chapters also drove home the message that there needs to be more communication among the various disciplines studying animal behavior and cognition. This communication can be enhanced by purposefully immersing future researchers in integrative perspectives or through collaborations among different individuals with specific expertise. Either way, it is through this integration that future cognitive ecology research will continue to provide an exciting and productive view of the nature of cognitive traits in ecologically relevant systems. I recommend this book to anyone interested in cognitive ecology and anyone who does research in one of the many disciplines that are integrated within this field.—KRISTY L. GOULD, Department of Psychology, Luther College, Decorah, IA 52101. E-mail: goulkr01@luther.edu.