

Cephalopod Cognition in an Evolutionary Context: Implications for Ethology

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Abstract What is the distribution of cognitive ability within the animal kingdom? It would be egalitarian to assume that variation in intelligence is everywhere clinal, but examining trends among major phylogenetic groups, it becomes easy to distinguish high-performing ‘generalists’ – whose behavior exhibits domain-flexibility – from ‘specialists’ whose range of behavior is limited and ecologically specific. These generalists include mammals, birds, and, intriguingly, cephalopods. The apparent intelligence of coleoid cephalopods (squids, octopuses, and cuttlefish) is surprising – and philosophically relevant – because of our independent evolutionary lineages: the most recent common ancestor between vertebrates and cephalopods would have been a small wormlike organism, without any major organizational structure to its nervous system. By identifying the cognitive similarities between these organisms and vertebrates, we can begin to derive some general principles of intelligence as a biological phenomenon. Here, I discuss trends in cephalopod behavior and surrounding theory, and suggest their significance for our understanding of domain-general cognition and its evolution.

Keywords Cephalopods · Cognitive evolution · Ethology · Comparative psychology

Introduction

It is sometimes suggested that Darwin did for biology what Copernicus did for astronomy. In demonstrating that the earth orbited the sun, and not vice versa, Copernicus removed humans from our privileged spot at the center of the universe. Similarly, one supposes, Darwin demonstrated how there could exist design with no designer, and so disillusioned us from fallacious misconceptions of humans as the

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‘chosen species’, sitting at the top of the divine *scala naturae* (Hodos and Campbell 1969).

In reality, anthropocentrism in biology lingered until the 1980s and 90s, when authors like Francisco Ayala and Stephen Jay Gould began to scrutinize the concept of evolutionary progress and the related view that humans are the ‘pinnacle’ or endpoint of evolution (Ayala 1988; Gould 1988; Ruse 1997). Natural selection, these authors pointed out, is not a directional process that aims to increase organismal complexity. Indeed, many species are so comfortably adapted to their ecological niche that they have persisted largely unchanged for millions of years (e.g., ‘living fossils’ such as the nautilus). Thus, natural selection is not proactive, but reactive: it enables organisms to adapt to the pressures they encounter in their environment. For different species this means different things; domain-general or humanlike intelligence is just one evolutionary strategy among many.

Ecological Egalitarianism and Comparative Cognition

This trend in evolutionary thought is perhaps nowhere so apparent as in ethology, the study of animal behavior and cognition (Galef 1987; Campbell and Hodos 1991). Researchers have abandoned the perspective that behavioral patterns can be cast into an ordered hierarchy, increasing in sophistication from protozoan stimulus–response to the human language faculty, in favor of a more egalitarian paradigm. This approach focuses on the notion of ecological, rather than absolute, intelligence. As Shettleworth (1998, p. 570) puts it, this means that “all species still extant are equally intelligent in their own ways, and the question become what different species’ intelligence consists of.”

Materially, this means that researchers in cognitive evolution focus on the identification and description of modules (‘mental organs’). A module is an independent and self-contained information processor within the brain (Barrett and Kurzban 2006). Each module has a specialized function, and is domain-specific – that is, it only accepts a certain kind of input. The modular paradigm in comparative psychology means that researchers look for the ecological problems a given species has had to solve, and identify the psychological mechanisms that provide the solution. By examining the distribution of these mechanisms, researchers can determine which are shared and which are unique, and begin to piece together a putative history of cognitive evolution (Fitch et al. 2010).

For the most part, the trend towards modularity is a step in the right direction. It is true that looking at animal cognition in absolute terms, or by implicit comparison to human cognition, is misleading, and that each organism must be understood in its own ecological and evolutionary context. There is, however, a possibility of carrying this line of thought too far. While we do not want to impose the framework of a strict linear hierarchy onto animal behavior, neither do we want to adopt the assumption a priori that cognitive variation is everywhere clinal. There may be real, non-gradualistic differences among cognitive faculties of different taxa, and these differences can inform our understanding of intelligence and its natural origins. In other words, to ensure an accurate and holistic understanding of cognitive evolution, it is necessary to keep the ‘comparative’ in comparative cognition.

Cognitive Trends in the Animal Kingdom: Generalists and Specialists

Surveying the animal kingdom from a coarse-grained perspective, a few trends become apparent. We see cognitive adaptation, to be sure: animals specialize in the skills that their ecological niche requires, such as the honeybee use of a symbolic ‘dance’ to communicate the location of a food source to hive-mates. Most species could accurately be described as cognitive ‘specialists’ in this way.

Beyond the specialists, however, we also see a few ‘generalist’ taxa. For these generalists, what may have started as adaptive, ecologically stereotyped and modular cognition has become flexible and domain-general. Consequently, their behavioral repertoires tend to be more diverse, and include some of the more oft-celebrated instances of animal intelligence (such as problem-solving without trial-and-error, tool use, etc.). In recent years, this notion of cognitive flexibility has earned a reputation as the best behavioral proxy for the vague term, ‘intelligence’ (Byrne 1995; Gibson 2002; Gould 2003).

If there is a real distinction to be made between these two groups – the specialists and the generalists – we would expect this to be reflected in their comparative neuroanatomy. Indeed, this appears to be the case when we examine encephalization – brain mass relative to body size (Jerison and Barlow 1985; Fig. 1 below). Plotting vertebrate organisms on a scatterplot with body mass on the X-axis and brain mass on the Y-axis, two distinct and roughly linear clusters emerge. This dual grouping reflects a tendency of certain organisms to have a larger brain mass for the same body mass. The lower mass includes fishes, amphibians and reptiles, while the higher mass includes mammals and birds – the generalists.

The domain-general intelligence of mammals comes as no surprise, given that this group comprises humans and our closest evolutionary cousins. Even outdated notions of cognitive evolution as a progressive phenomenon – in which the reptilian brain (homologous to the human basal ganglia or ‘inner brain’) grew outwards to reach mammalian and then primate status – corroborate the notion that mammals are among

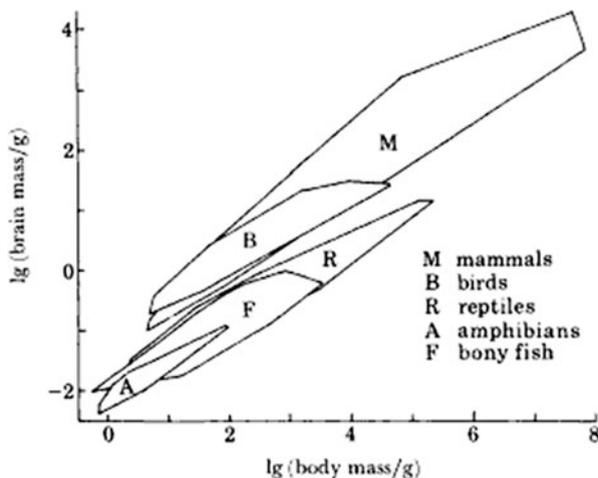


Fig. 1 Plotting the ratio of brain weight to body weight of various species yields two distinct clusters between ‘higher’ and ‘lower’ vertebrates. From Jerison, 1973

the smartest animals (MacLean 1990). Avian intelligence came as a larger surprise, given that their most recent common ancestor with mammals would have been a reptile, and reptiles are classic underperformers on the most commonly used cognitive tests (Burghardt 1977; Suboski 1992).

Nevertheless, the impressive cognitive capacities and flexible behavioral repertoires of birds, especially corvids such as crows and jays, have been well-documented, and the case for convergent cognitive evolution between birds and mammals has been closely examined (e.g., Emery and Clayton 2004; Emery 2006). These authors propose several common denominators between these taxa that may have driven or enabled the evolution of domain-general intelligence: omnivorous diets, variable habitat, long developmental periods, extended longevity, and pervasive social interactivity (*ibid.*). The last of these has a long – and controversial – history in the literature, and is often referred to as the ‘social intelligence hypothesis’: the idea that selective pressures favoring advanced social cognition drove the evolution of intelligence in humans and other organisms (e.g., Humphrey 1976).

An Unexpected Specialist

Intriguingly, there is one major group of invertebrates – the coleoid cephalopods (hereafter: cephalopods) – that deserves to be grouped with the generalists, both in terms of their behavioral repertoire (Hanlon and Messenger 1998) and their relativized brain size (Packard 1972). This group, which comprises octopuses, squids, and cuttlefishes, has garnered a great deal of attention from researchers in recent years for their surprisingly vertebrate-like cognition. [Nautilus, the aforementioned ‘living fossils,’ are the non-coleoid cephalopods, and are often taken to represent the organisms from which the coleoids evolved.]

Cephalopods are ready learners, apt to explore new environments and to acclimate to novel objects by playing with them (Kuba et al. 2003; Mather and Anderson 1999). They outperform the specialist vertebrates at basic associative learning tasks with arbitrary stimuli; current research focuses on higher-order cognitive tasks (Vitti 2010). Hvorecny et al. (2007), for instance, found evidence of conditional discrimination, an ability common to birds and mammals and rare elsewhere. In this experiment, octopuses and cuttlefish were trained to find their way out of two near-identical mazes with different escape routes. After training was complete, the subjects were put in either maze in randomized order. Using visual information, they were able to recall which maze was which, and approach the correct exit directly rather than by trial and error.

There are also reports of tool use. Mather (2009) suggested the modification of homes by rearranging rocks and debris as a potential instance; and some octopuses have been documented carrying coconut shells with them as they skim the ocean floor and withdrawing into the shell for protection (Finn et al., 2009). Additionally, Fiorito and Scotto (2005) report a case of observational learning, which, if confirmed, would be remarkable – most mammals fail at such tasks. Most critically, patterns of behavior are domain-general and can be adopted in a range of circumstances, as in the use of propulsive water jets to build shelters, repel fish, or manipulate objects (Mather 2008).

While the breadth of the cephalopod behavioral repertoire is remarkable in its own right, it becomes all the more so when examined in an evolutionary context (Fig. 2).

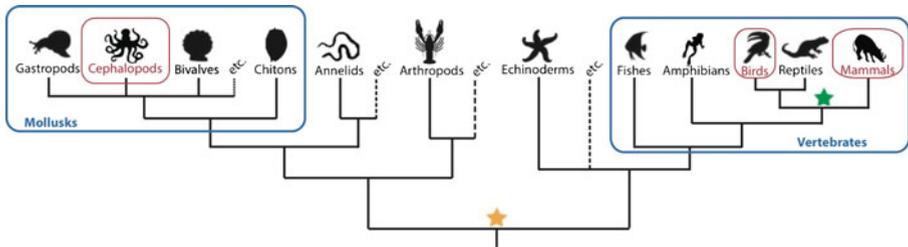


Fig. 2 Phylogenetic tree indicating the evolutionary relationship between cephalopods, birds and mammals. Stars indicate the location of the most recent common ancestor (MRC) between cephalopods and vertebrates (yellow, ~600 million years ago) and between birds and mammals (green, ~300 million years ago)

Cephalopods are molluscs, like snails and oysters, and are more closely related to these organisms (obvious ‘specialists’) than to vertebrates. By comparison, the convergent evolution of domain-general cognition in birds and mammals is not altogether surprising – the most recent common ancestor between these taxa would have been a reptile, with the basic global organization of vertebrate neuroanatomy already in place. By contrast, the most recent common ancestor between a cephalopod and any vertebrate would have been microscopic, with minimal holistic organization to its rudimentary nervous system (Knoll and Carroll 1999; Hejnol and Martindale 2008).

Consequently, the cephalopod nervous system looks completely alien in comparison to our own: their brains are shaped like donuts surrounding the esophagus (leading to instances of sudden brain death when a cephalopod eats a bony animal that is too large for its throat), and two-thirds of the nerves are distributed throughout the arms, each of which is controlled by its own ganglion (leading some researchers to opine that each arm has its own ‘brain’, although this characterization is disputable) (Budelmann 1995). Cephalopods pose a mystery because these major neuroanatomical differences – which reflect their independent evolutionary trajectory over the past 600 million years – are, from a cognitive standpoint, superficial: cephalopods are capable of much the same behavior witnessed in generalist vertebrate species.

Such a dramatic case of convergent evolution calls for explanation, on two fronts. First, we want to know the selective pressure or pressures that drove cognitive evolution in cephalopods to rival that of birds and mammals. Second, we want to understand the solution that these groups are converging on – what does domain-flexible intelligence consist in, and what are the specific capabilities it furnishes?

Theories of Cephalopod Evolution

The most long-standing theory regarding the evolution of cephalopod cognition, sometimes referred to as the ‘Packard scenario’, holds that competition with bony fishes was the primary selective force driving their development (Packard 1972; Aronson 1991; Grasso and Basil 2009). This theory is based on the fossil record, which shows that these groups proliferated in the same place at the same time (roughly 65 million years ago). Bony fishes were particularly formidable competitors because they were agile, visual predators - owing to the development of larger and more efficient eyes, as well as the swim bladder, which facilitates buoyancy control (Helfman et al. 2009). Cephalopods extant at

the time adopted one of two strategies to respond to this pressure: nautiloids avoided their competitors by migrating deeper, while coleoids grew in size and complexity to compete alongside the vertebrates.

Another contributing factor to the development of cephalopod cognition may have been the loss or internalization of the nautiloid shell (Mather 2011). The immediate predecessors to coleoid cephalopods could rely on their shell not only for protection but also for buoyancy and movement. Thus, the loss of this structure introduced pressure on cephalopods to develop acute environmental awareness and cunning, as well as efficient locomotion and agility.

It would be surprising, however, if competition with bony fishes and the loss of the shell provided sufficient selective pressure to yield such behaviors as tool use and observational learning. It is more likely that such vertebrate-like behaviors were enabled by the compounding of nervous system complexity that came with the development of other, more basic, cognitive capabilities, such as those involved in sensory perception. Coleoid cephalopods all have very effective vision, in contrast to nautiluses, which are primarily olfactory animals (Grasso and Basil 2009). In another remarkable instance of convergent evolution, coleoid cephalopods evolved a camera eye that functions almost identically to analogous vertebrate structure. The major difference between the two is that vertebrates, unlike cephalopods, have a small blind spot where the optic nerve passes through the optic disc of the retina (our brains compensate for this blind spot by integrating information from our two eyes). The cephalopod optic nerve approaches the photoreceptor cells of the optic disc from behind, rather than poking through it. The advent of robust vision is believed to contribute to cognitive evolution more generally because a sudden wealth of visual information would necessitate the sophistication of pathways to process and utilize that information. Besides vision, coleoid cephalopods also make use of deft locomotive capabilities (in spite of minimal body rigidity) and camouflage techniques, each of which requires a great deal of neural complexity and precision to function adequately.

While it is hard to say with certainty what role social interaction – whether inter- or intra-specific – may have played in the course of cephalopod evolution, it seems unlikely that it was a major driving force, given the inconsistency of sociality observed in modern coleoids, and given the complete absence of kin recognition (Boal 2006). While the paucity of relevant evidence – owing to the few species that have been studied, difficulties in experimental setup, lack of work focusing on sociality, and unhelpful fossil record – make conclusive statements difficult, cephalopods present a possible counterexample to the social intelligence hypothesis.

Similarly, of the ecological factors Emery (2006) proposes as driving forces of the convergent evolution of mammal and avian cognition, only one – variable habitat – also appears applicable to cephalopods. This is not to diminish the importance of sociality, omnivorous diets, long developmental periods, or extended longevity in the evolution of mammalian or avian intelligence, but rather to suggest that these factors are not themselves indispensable for domain-general cognition to evolve. The tentative conclusion, then, is that the primary driving force in the evolution of intelligence is a competitive, demanding, and unstable environment, as observed in the evolution of cephalopods, mammals, and birds.

Principles of Intelligence

Because of their phylogenetic distance from mammals and birds, cephalopods offer a unique point of comparison for domain-general intelligence, and allow us to determine a few common denominators that appear to be essential to this mode of cognition. Intriguingly, although social behavior does not appear necessary for the evolution of this cognition, as described above, an awareness of self and other does appear to be a byproduct of it, with reports of observational learning in octopuses, as well as numerous anecdotal claims of conscientious behavior from cephalopod trainers (Hanlon and Messenger 1998).

Advanced perceptual faculties do appear to be one important component of domain-flexible intelligence, which makes sense, given that cognitive processing is only useful inasmuch as it can operate on the external world. In the case of cephalopods, mammals, and birds, visual perception appears to be the dominant paradigm, but this does not necessarily entail that another sensory modality could not perform equally well.

Of course, for perception to be useful it must be focused. Accordingly, executive control of attention appears to be a major enabling factor for domain-general cognition, and cephalopods (like mammals and birds) appear to attend to relevant stimuli for sustained periods of time (prompting the anecdotal quip that these animals appear to be actively thinking about a problem before acting). Relatedly, memory (which is sometimes considered an extension of attention – Shettleworth 1998) is a facultative capacity that allows organisms to retain the information they attend to, and so process that information towards useful ends.

Another important commonality among these taxa is the primacy of associative learning. Researchers have often commented that this capacity is foundational for higher-order cognitive processes, and indeed, the ability of mammals, birds and cephalopods to perform conditional discrimination, for example, appears to necessitate first being able to form primary associations among stimuli. Critically, however, these higher-order processes necessitate a certain degree of flexibility of association: while many specialist species can perform associative tasks, they are often limited to ecologically familiar stimuli (e.g., Suboski 1992). Thus, associative learning appears to be necessary but not sufficient for the development of higher-order cognition.

Conclusion

Cephalopod behavior is a philosophically significant phenomenon because it provides an example of how phylogenetically disparate species can converge on the same cognitive solution to ecological instability – and so allows us to understand the evolution of intelligence. It suggests that the most critical factor in selection for domain-general intelligence is variability and hostility in the environment, with other selective pressures (such as the development of cognitive architecture to support advanced perceptual systems) playing a secondary role. Mammals, birds and cephalopods all appear to have responded to the broad ecological pressures presented by their highly variable and competitive habitats through the development and sophistication of flexible, rather than modular, modes of cognitive processing.

Moreover, the similarities between domain-general intelligence in vertebrates and invertebrates allow us to understand which faculties are most conducive to the development of advanced, flexible cognition. Among these are attention-directing mechanisms, memory, and robust associative learning capabilities. Most intriguingly, although mental phenomena necessitating a ‘theory of mind’ (such as self-consciousness and awareness of others) do not appear to be essential to the evolution of domain-general intelligence, they appear to be common byproducts of such cognition. Clarifying the ways that cephalopods and other organisms employ theories of mind will shed further light on the way these forms of cognition relate to intelligence, as well as the way that these organisms are similar to or dissimilar from humans.

While purely anthropocentric modes of comparison are outdated – and, more critically, often obscure the complexity and intricacy of animal cognition – it can nonetheless be informative to employ comparative strategies when studying ethology and cognitive evolution. In the particular case of cephalopod cognition, drawing a comparison with birds and mammals helps us to understand domain-flexible intelligence and its evolution as a natural phenomenon that may have occurred multiple times along multiple clades in the animal kingdom.

References

- Aronson, R. B. (1991). Ecology, paleobiology, and evolutionary constraint in the octopus. *Bulletin of Marine Science*, 49, 245–255.
- Ayala, F. J. (1988). Can ‘progress’ be defined as a biological concept? In M. Nitecki (Ed.), *Evolutionary progress* (pp. 75–96). Chicago: University of Chicago Press.
- Barrett, H. C., & Kurzban, R. (2006). Modularity in cognition: framing the debate. *Psychological Review*, 113, 628–647.
- Boal, J. G. (2006). Social recognition: a top down view of cephalopod behavior. *Life & Environment*, 56(2), 69–79.
- Budelmann, B. U. (1995). The cephalopod nervous system: What evolution has made of the molluscan design. In O. Breidbach & W. Kutsch (Eds.), *The nervous system of invertebrates: An evolutionary and comparative approach*. Berlin: Birkhauser Verlag.
- Burghardt, G. M. (1977). Learning processes in reptiles. In C. Gans & D. Tinkle (Eds.), *Biology of the Reptilia: Ecology and behavior*. New York: Academic.
- Byrne, R. (1995). *The thinking ape: Evolutionary origins of intelligence*. Oxford: Oxford University Press.
- Campbell, C. B., & Hodos, W. (1991). The scala naturae revisited: evolutionary scales and anagenesis in comparative psychology. *Journal of Comparative Psychology*, 105(3), 211–221.
- Emery, N. J. (2006). Cognitive ornithology: the evolution of avian intelligence. *Philosophical Transactions of the Royal Society B*, 361, 23–43.
- Emery, N. J., & Clayton, N. S. (2004). The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science*, 306(5703), 1903–1907.
- Fiorito, G., & Scotto, P. (2005). Observational learning in *Octopus vulgaris*. *Science*, 256(5056), 545–547.
- Finn, J. K., Tregenza, T., & Norman, M. D. (2009). Defensive tool use in a coconut-carrying octopus. *Current Biology*, 19(23), R1069–R1070.
- Fitch, W. T., Huber, L., & Bugnyar, T. (2010). Social cognition and the evolution of language: constructive cognitive phylogenies. *Neuron*, 65(6), 795–814.
- Galef, B. G. (1987). Comparative psychology is dead! Long live comparative psychology. *Journal of Comparative Psychology*, 101(3), 259–261.
- Gibson, K. R. (2002). Evolution of human intelligence: the roles of brain size and mental construction. *Brain, Behavior and Evolution*, 59, 10–20.

- Gould, S. J. (1988). Trends as changes in variance: a new slant on progress and directionality in evolution. *Journal of Paleontology*, 62(2), 319–329.
- Gould, J. L. (2003). Animal cognition. *Current Biology*, 14, 372–375.
- Grasso, F. W., & Basil, J. A. (2009). The evolution of flexible behavioral repertoires in cephalopod molluscs. *Brain, Behavior and Evolution*, 74, 231–245.
- Hanlon, R. T., & Messenger, J. B. (1998). *Cephalopod behavior*. Cambridge: Cambridge University Press.
- Hejnol, A., & Martindale, M. Q. (2008). Acoel development supports a simple planula-like urbilaterian. *Philosophical Transactions of the Royal Society B*, 363(1496), 1493–1501.
- Helfman, G., Collette, B. B., Facey, D. H., & Bowen, B. W. (2009). *The diversity of fishes: Biology evolution and ecology*. New York: Wiley Blackwell.
- Hodos, W., & Campbell, C. B. (1969). Scala naturae: Why there is no theory in comparative psychology. *Psychological Review*, 76, 337–350.
- Humphrey, N. K. (1976). The social function of intellect. In P. P. G. Bateson & R. A. Hinde (Eds.), *Growing points in ethology* (pp. 303–317). Cambridge: Cambridge University Press.
- Hvorecny, L. M., Grudowski, J. L., Blakeslee, C. J., Simmons, T. L., Roy, P. R., Brooks, J. A., et al. (2007). Octopuses (*Octopus bimaculoides*) and cuttlefishes (*Sepia pharaonis*, *S. officinalis*) can conditionally discriminate. *Animal Cognition*, 10(4), 449–459.
- Jerison, H. J. (1973). *Evolution of the brain and intelligence*. New York: Academic.
- Jerison, H. J., & Barlow, H. B. (1985). Animal intelligence as encephalization (and discussion). *Philosophical Transactions of the Royal Society of London B*, 308(1135), 21–35.
- Knoll, A. H., & Carroll, S. B. (1999). Early animal evolution: emerging views from comparative biology and geology. *Science*, 284, 2129–2137.
- Kuba, M., Meisel, D. V., Byrne, R. A., Griebel, U., & Mather, J. A. (2003). Looking at play in *Octopus vulgaris*. *Berliner Paläontologische Abhandlungen*, 3, 163–169.
- MacLean, P. D. (1990). *The triune brain in evolution: Role in paleocerebral functions*. New York: Plenum Press.
- Mather, J. A. (2008). To boldly go where no mollusc has gone before: personality, play, thinking and consciousness in cephalopods. *American Malacological Bulletin*, 24, 51–58.
- Mather, J. A. (2009). Home choice and modification by juvenile *Octopus vulgaris*: specialized intelligence and tool use? *Journal of Zoology*, 233(3), 359–368.
- Mather, J. A. (2011). Consciousness in cephalopods? *Journal of Cosmology*, 14.
- Mather, J. A., & Anderson, R. C. (1999). Exploration, play, and habituation in octopuses. *Journal of Comparative Psychology*, 113, 333–338.
- Packard, A. (1972). Cephalopods and fish: the limits of convergence. *Biological Reviews*, 47(2), 241–307.
- Ruse, M. (1997). *Monad to man: The concept of progress in evolutionary biology*. Cambridge: Harvard University Press.
- Shettleworth, S. J. (1998). *Cognition, evolution, and behavior*. New York: Oxford University Press.
- Suboski, M. D. (1992). Releaser-induced recognition learning by amphibians and reptiles. *Animal Learning and Behavior*, 20(1), 63–82.
- Vitti, J. (2010). The evolution and distribution of animal consciousness. *Collections of the Harvard University Archives: Theses*. Cambridge: Harvard University Press.