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Evolution of Learning and Cognition

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Introduction

How did we evolve our enhanced cognitive abilities compared to the rest of the animal kingdom? Is this even a proper topic for scientific analysis? Richard Lewontin, the Harvard population geneticist, famously wrote that "It might be interesting to know how cognition (whatever that is) arose and spread and changed, but we cannot know. Tough luck" (Lewontin, 1998, p. 130). Are things as dire as Lewontin suggested almost 20 years ago?

Although comparative psychologists do not have the analytical tools of other sciences, that does not mean that we cannot attempt to reconstruct the evolution of the processes underlying animal and human behavior (van Horik & Emery, 2011). We have a greater understanding of learning and cognition in a wider variety of species than ever before (Pearce, 2009; Shettleworth, 2010), and of processes that weren't studied at the time of Lewontin's article. Sophisticated phylogentic techniques have been developed to reconstruct the evolution of cognition (MacLean et al., 2012), however they are dependent on accumulation of sufficient amounts of usable data. Tasks with high ecological validity have been designed to support comparisons of distantly and closely related species, focusing on their natural abilities, such as food competition to investigate social cognition in chimpanzees (Hare, Call & Tomasello, 2001) and food-caching to investigate episodic-like memory, future planning and social cognition in corvids (Clayton, Dally & Emery, 2007). An appreciation of evolutionary forces aside from homology, such as convergence, has been applied to distantly related groups that appear to share common environmental pressures (Marino, 2002; Emery & Clayton, 2004).

In this chapter, I focus on the issue of whether the evolution of traits that do not fossilize, such as learning and cognition, can be reconstructed, and the methods that have been employed to do this, such as extrapolating function from brain size (extant and extinct creatures), empirical tests of learning and cognition on extant animals, and comparative techniques using large datasets and detailed phylogenies. I complete the chapter by addressing the question of what cognition may have evolved for, discussing recent studies attempting to correlate performance on cognitive tasks with reproductive success in wild animals.

Fossilized minds

A major issue in cognitive evolution is the fact that mental traits do not fossilize, unlike morphological ones. We can make extrapolations about the behavior of extinct creatures from the location of fossils, the remains of nests and eggs, the remains of any prey or the contents of stomachs at the time of death and even inferences based on the skeleton, such methods of locomotion or feeding. However, some of the best clues we have to an extinct animal's ability to understand its world are inferences based on the abilities of extant creatures. Unfortunately, this is fraught with problems because the relatives of extinct creatures may be separated by millions of years of evolutionary divergence. For example, the last common ancestor of chimpanzees and humans lived around 7 MYA (so 14 million years of separate evolution), which gave these two species plenty of time to develop into vastly different species. By reconstructing the evolution of a trait across a wide range of animals (see later), it is now possible to make stronger inferences that take into account similarities and differences in other pertinent variables that will have influenced cognitive evolution, such as diet, habitat or sociality (van Horik & Emery, 2011).

Darwin and the evolution of mind

Although Darwin was not the first scientist to be interested in the evolution of cognition, his theory of evolution by natural selection set the stage for the development of comparative psychology as a field of serious study. Darwin's famous statement that "the difference in mind between man and the higher animals, great as it is, certainly is one of degree not of kind" (Darwin, 1879/2004, p. 151) suggests, not only that cognition has evolved alongside other more tangible morphological traits, but that we can also evaluate the extent to which an animal's cognition is similar or different to that of our own. Basically, do animals do what humans do? This has been termed the ***anthropocentric approach***, where animals are given tests of human cognition (which are not faced in their natural lives), and their performance compared with humans. This approach creates lots of headlines and is useful in developing animal models of disorders of human cognition, but it has little ecological validity. The anthropocentric approach is dependent on an outdated view of evolution – ***scala naturae*** - in which animals progress along a hypothetical ladder from the simplest forms at the base to the most complex forms at the top (Hodos & Campbell, 1969). In terms of complex cognition, humans are assumed to be at the top and invertebrates at the bottom. Cognitive ability is ranked from poor to excellent (on whatever measure) and human cognition is used as the standard against which other species are compared.

The anthropocentric approach focuses on a limited number of species, as is not interested in the evolution of cognition per se, only whether processes are universal and can applied across a range of species. Studies using this approach have traditionally focused on either ends of a scale of proposed complexity; associative learning at one end (using rats and pigeons as model species) and human intelligence (theory of mind, language, analogical reasoning using great apes and dolphins as model species) at the other end. By concentrating on the use of a sterile testing environment (such as a Skinner box) and reducing the influence of contextual variables (such as biologically significant stimuli), tests based on the anthropocentric approach eliminated any effects of a creature's natural behavior from the tests and so eliminated any ecological validity.

The alternative is the ***ecological approach***, which focuses on how (and why) do animals do what they do? Animals are given cognitive tests based on problems faced in the wild. This would appear to be a more representative approach to discovering something about the cognitive capabilities of animals, as a species is given the opportunity to demonstrate how cognition influences their normal behavior. However, there are issues with this approach. By focusing on natural behaviors, it is more difficult to determine responses to novel problems, more difficult to eliminate extraneous variables not related to learning and cognition, and more difficult to compare species living in vastly different habitats and using different processes.

Recently, a combined approach utilizing both anthropocentric and ecological approaches has provided a means for testing some supposedly unique aspects of human cognition (Emery, 2006), namely theory of mind and mental time travel (see Chapters X and XX). By adapting tasks for specific animals based on how they may use these abilities in their natural lives; foraging and competing over food or hiding food for later consumption; task ecological validity is increased and is more representative of how specific skills may have evolved.

Some notes on evolutionary processes

There are two outcomes of evolutionary change, divergence (differences) or convergence (similarities; Papini, 2002). Species diverge from a common ancestor because of changes in ecological pressure, for example diet. Finches on the Galapagos Islands are a classic case in point. Descendants of an ancestral finch from the South American mainland moved into new habitats with new opportunities for foraging. As such, finches evolved new shaped beaks (through random genetic mutations) that could exploit these new resources and were more likely to survive and produce viable offspring that would also survive and produce their own offspring (***reproductive fitness***) than those individuals that did not adapt. Some species became specialized for eating seeds, other for eating cactus flowers, eating buds or insects. Another species has adapted a beak that enables them to make and use tools (Figure 1).

Insert Figure 1 About Here

When we think of modern evolutionary biology, we tend to think of ***homology***, namely when a common ancestor diverges into two or more new species. Traits shared between the two descendent species will have been retained from the common ancestor, but there will also be new traits that are not shared, which are the result of mutations occurring in descendants of the ancestor resulted in the new species.

However, this isn't the only process by which comparisons can be made across different species. Many species that are distantly related may also share common traits. For example, despite being distantly related, sharks and dolphins have evolved a body plan that is highly efficient for swimming and maneuvering in water at great speed. Other ancestors of these two groups do not share these anatomical features, so the most parsimonious explanation for their appearance is ***homoplasy***. This is an evolutionary process by which features are influenced by the same selection pressures – in this case, having to swim quickly through water. Streamlined swimming is achieved by the coordinated movements of a dorsal fin, two side ventral fins, and specific actions of the tail (dorsoventral for dolphins and lateral for sharks). This form of evolution is called ***convergence*** (as two or more distantly related species converge onto the same solution). We will discuss the application of convergence to the evolution of cognition later. There are two other forms of homoplasy; ***parallelism***, in which two or more closely related lineages independently evolve similar traits, such as food-caching in parids, nuthatches and corvids, and ***reversal***, where features are recovered from a remote ancestor that have been previously been lost in a more recent ancestor, such as leglessness in legless lizards and snakes.

Learning and cognition

When discussing mechanisms of behavior, many researchers still fall back on an old, but misplaced dichotomy between learning and cognition. However, learning and cognition should not be seen as opposing forces, but rather part of a suite of mechanisms (psychological and biological) that contribute to an animal's survival and reproductive fitness. Apart from learning and cognition, we may include genes, hormones and species-specific (innate) behaviors into the mix. Supposed behavioral complexity does not necessarily have to relate to the underlying process. There are complex forms of learning that are akin to cognitive processes, especially those that are goal-directed (Dickinson & Balleine, 2000; Zentall, 2002).

How an individual interacts with its socio-ecological environment will subsequently influence the balance of psychological processes underlying their behavior. Let's try and address this issue with a hypothetical case of rabbits and foxes (Figure 2). Each species lives out its life according to the design of its brain and the information its brain has to process. Rabbits, for example, are herbivorous, gregarious, prey species. The food they eat is massively abundant and they have very little to do (cognitively) in order to find and process it – most of the hard work is undertaken by their gut digesting the tough cellulose. They live in large groups, but there is little evidence for any complex interactions between group members (foregoing *Watership Down*!). They breed (like rabbits) producing lots of little rabbits, most likely because their mortality rate is high from the threat of predation. Their learning and cognition will probably have evolved slowly, as they face few challenges that require a flexible solution. Food is abundant, so no need for advanced foraging cognition. Social interactions are likely driven by emotional and motivational states, so no need for advanced social cognition. Evading predators initially requires a predator detector, but ultimately the speed of getting away will be more relevant to staying alive than a computational brain (which is probably slower in initiating an evasion response compared to a lower level brain mechanism not dependent on cognition). Rabbit brains follow a basic mammalian plan, in that sensory information enters the sense organs (in particular the olfactory bulb), which in turn is processed by the cortex, is effected by the endocrine system and an appropriate motor plan is initiated (e.g. eat food, mate with female, nurture offspring, run from fox, etc.).

Insert Figure 2 About Here

By contrast, foxes are largely solitary (although they do live in small families around the breeding season), omnivorous (or at least since that they began to exploit urban environments) and predatory (feeding on rabbits, chickens, etc.). This existence requires a vastly different array of cognitive skills from rabbits. As foxes move between a solitary and a family existence, they need to be flexible in their social interactions. By adopting an omnivorous diet, they need to discriminate a wide variety of foods, and assess their potential as a new food, possibly using social learning to determine whether the food is edible or poisonous. As a predator, the fox needs to apply a variety of cognitive skills allowing them to assess the best (easiest) target and predict their next moves. Their brain also follows a basic mammalian plan, but they have a larger cortex, with extensive gyrification (cortical folding) and supposedly their behavior is more dependent on the cortex than rabbits. As such, rabbits could be said to have evolved a simple behavioral system based on general learning and a specialized cognitive adaption for predator avoidance, but with little evidence for flexible cognition. Foxes could be said to have evolved a more complex and plastic system, based on a core of general learning, but with an additional suite of flexibly deployed cognitive adaptations related to feeding, sociality and predation.

Adaptive specializations versus general processes

Most of forms of learning can be found across the animal kingdom (Macphail, 1982; Moore, 2004). This has developed into the ***general process view*** (Papini, 2002; Pearce, 2009). Thorndike (1911) originally proposed the idea of a universal Law of Effect after comparing the performance of a wide range of animals on a series of puzzle boxes in which the subject was assessed on the length of time it took them to learn how to get out of a locked box. Thorndike found little qualitative differences between the species (cats, dogs, monkeys, chicken and fish), only quantitative differences in speed of learning that were probably based on their attention, motivation and natural behaviors. Cats quickly learned to get out of the box as they inadvertently released the latch locking the box through their scratching, and subsequently learned the contingencies of how to get out of the box through trial-and-error learning.

By comparing distantly related species, such as bees and humans, we see commonalities in basic learning mechanisms, such as habituation, sensitization, classical and instrumental conditioning. It has been contested that as tests for these learning processes are frequently made in sterile lab environments (such as the Skinner box), they do not take into account differences in species' biology (Kamil, 1987). However, what these studies do proclaim is that in terms of learning, all species are equal and there is no evidence of a *scala naturae* ranking. Some scholars have gone further to suggest no species differences in cognition that cannot be explained by differences in perception, motivation, motor performance and environmental adaptability (perhaps with the exclusion of human language; Macphail & Bolhuis, 2001); although the evidence to date does not support this view (Shettleworth, 2010).

Basic learning processes may underlie other more complex aspects of cognition (indeed, the cognitive basis of learning has been relegated to the sidelines of comparative psychology based on a misplaced notion of dichotomy in which a process controlling a behavior may be either learning or cognition (not degrees of both). Indeed, some aspects of learning are highly cognitive (Dickinson & Balleine, 2000) and may be used in a flexible manner. If associative learning is viewed as a precursor to cognition or even a vital component of many cognitive operations, not as an alternative to it, then the idea of general processes shared across a wide range of species does not seem at odds with an ***adaptive specialization view*** of learning and cognition.

In the classic case of adaptive specializations of cognition, most corvids cache food to be retrieved some time later when food is scarce (long-term caching) or when thieves have left the scene (short-term caching; reviewed in Vander Wall, 1990). Whether birds cache lots of food and in lots of different places depends on a number of environmental factors, such as the elevation at which the species lives, competition from members of the same (or other) species (size of the social group), reliance on cached food over other food sources, etc. In turn, these biological factors appear to correlate with artificial measures of spatial memory and the size of the hippocampus; the brain region supporting space, navigation and memory (Smulders, Gould & Leaver, 2010). So, birds such as Clark's nutcrackers (*Nucifraga columbiana*), which live at high elevations, cache up to 30,000 pine seeds in specific locations and retain spatial information for up to 9 months later, retrieve those seeds with an 80% accuracy. By comparison, western scrub-jays (*Aphelocoma californica*) live at a lower elevation (down to sea level), cache far fewer pine seeds (6,000 per year) and are less accurate in retrieving them after a shorter retention interval. In lab tests, scrub-jay memory for cache sites is less efficient than Clark's nutcrackers. The nutcracker hippocampus is relatively larger than the western scrub-jay hippocampus (Roth, Brodin, Smulders, LaDage & Pravosudov, 2010; however see below). Together we see a clear relationship between caching proficiency, habitat, spatial memory in the lab and the size of the hippocampus Smulders et al, 2010).

However, the picture is not that straightforward. In reviewing studies linking spatial memory, hippocampus and caching in birds, Macphail and Bolhuis (2001) found many cases that did not fit this overall picture, i.e. some species were highly accurate at locating caches, but demonstrated a reduced performance on lab spatial memory tasks. If caching and spatial memory had co-evolved, then birds that cache a lot should be better at all spatial memory tasks. There are other problems with this story. Western scrub-jays do not just eat and cache pine seeds. They also live in a harsh environment, but not because it is extremely cold, but because it can get extremely hot (living in California, Nevada and Arizona), with little water. This causes other problems, but a significant issue for a bird that caches invertebrates and berries is that they perish quickly in the heat, and become inedible (so the time between fresh and decayed food can vary depending on the weather conditions). Scrub-jays live in family groups (compared to territorial Clark's nutcrackers), and protect their caches from potential thieves. Challenges facing western scrub-jays are different from those facing Clark's nutcrackers, but no less difficult. As such, they may rely on different brain regions, perhaps circuits processing information related to timing and social context as well as spatial memory. A reassessment of the western scrub-jay hippocampus found it was larger than in Clark's nutcrackers and all other corvids (Pravosudov & de Kort, 2006). Scrub-jays may cache as many *total* food items as Clark's nutcrackers, but of different types requiring different forms of processing related to perishability. Therefore, the classic case of adaptive specializations for ecology, brain and cognition in food-caching corvids is not as clear as has been presented in the past, and requires a more subtle appreciation of ecological, psychological and neural variables.

When considering adaptive specializations, we tend to use broad categories to dictate what we mean by environmental challenges faced by a species, however evolution does not work with such sweeping brush strokes. When we say that an animals' cognition is influenced by the size of their social group, is this measure subtle enough to investigate any relationships between these factors? Group size correlates with neocortex size in primates (Dunbar 1992), but what is it about group size that requires a larger neural processor? Does increasing the size of the group require a greater ability to keep track of individuals and their (third-party) relationships with others? What cognitive processes aid such an ability; transitive inference, social memory or tracking relationships across space and time? As cichlids (*Astatotilapia burtoni*) and cleaner wrasse (*Labroides dimidiatus*) use all or some of these abilities with their comparatively tiny brains (Grosenick, Clement & Fernald, 2007; Salwiczek & Bshary, 2011; Salwiczek et al., 2012), why do primates need much larger brains to achieve the same aim? Do primates have to process information about a larger social group? I may have a large network of acquaintances, but I don't know what they get up to at any one time. The resultant flood of information would be overwhelming and largely redundant. I need, by comparison, a system that doesn't retain lots of information about relationships over time, rather one that updates when things change. This would be akin to not watching a TV soap opera for years, but learning about all the new characters and their relationships (which will have inevitably have changed in the time since I last saw the show) after a short period of watching again.

Does cognition evolve?

How do we determine whether cognition evolves? Behavior does not fossilize, so we are largely restricted to comparing proxies for cognition in extant and extinct species, and the results of cognitive tests across extant species. The only biological trait left behind once a species becomes extinct, and which relates to that species' cognition is an imprint of their brain on the inside of the skull. This imprint can be used to create an endocast of the brain, which in turn can be used to estimate brain size, and supposedly intelligence. Brain size has also been calculated for a large number of extant birds and mammals (Roth, 2013), and is perhaps the only measure currently available that represents cognition across a wide range of species. But, which measure of brain size to use? Although overall or absolute brain size has been criticized as a useful measure of cognition because there is a strong correlation between body size and brain size, and the brain itself is involved in many more functions aside from cognition, in some comparative analyses, absolute brain size is the best predictor of intelligence (at least across primates; Deaner, Isler, Burkart & van Schaik, 2007). This may because, ultimately, number of neurons restricts the brain's ability to make calculations.

Jerison (1973) proposed a measure for comparing species based on brain size, but controlling for body size, called the ***Encephalization Quotient*** (EQ). EQ is the size of the brain over that expected for an average sized species in the same class (i.e. for mammals, a cat with an EQ of 1.0 has a brain the exact size expected for its body). An EQ larger than 1 describes a species with a brain that is larger than expected, and an EQ less than 1, a species with a brain smaller than expected. Rabbits have an EQ of 0.4, whereas foxes have an EQ of 1.6. This compares to the EQ of elephants (1.3), chimpanzees (2.5), dolphins (5.3) and *Homo sapiens* (7.8), which makes broad sense based on what we know about their cognitive abilities.

Another calculation that has been used to compare species is brain weight as a percentage of total body weight (Roth, 2013). Using this measure, smaller animals, such as mice have proportionally larger brains than larger animals, such as whales. Mice have a brain that is around 12% of total body weight, compared to blue whales with a brain less than 0.01% of total body weight. As the smallest animals are not necessarily the smartest on cognitive tests, this measure needs further investigation across other vertebrate and invertebrate classes.

What is clear is that total brain size is not the best proxy for cognition (intelligence). We have very good evidence in mammals that the cortex is the seat of cognition, and pallial regions in birds, such as the nidopallium and mesopallium, play a similar role (Emery, 2006). Other regions play supporting roles in other aspects of cognition, such as the basal ganglia, cerebellum, hippocampus and amygdala, but the extent of their contribution differs across species, and the size of these different regions fluctuates depending on the needs of the specific animal. It is important to understand something not only about the size of the whole structure, and the size of individual parts, but also how these structures work together. This has been termed ***mosaic evolution***, and explains the function of mammalian (Barton & Harvey, 2000) and avian brains (Iwaniuk, Dean & Nelson, 2004).

We have already discussed how one region of the avian brain, the hippocampus, responds to a certain class of stimuli – spatial information – and that hippocampal volume appears to be related to a species' reliance on spatial memory. Unfortunately, this is not as simple as presented, as updates to the hippocampal database have had substantive effects on this particular brain-behavior relationship (Roth et al., 2010). Roth, Brodin, Smulders, LaDage and Pravosudov (2010) go as far as to suggest that volume is a poor measure of hippocampus, and that more relevant features for spatial memory are number and size of neurons, variations in connectivity patterns and number of synapses. A similar focus on these subtle measures (as well as cell density, and degree of gyrification in mammals) would be appropriate for other brain regions (see also Healy & Rowe, 2007).

Methods for comparing species

Contextual variables and systematic variation

Whilst brain size provides a simple proxy for cognition that can be used across a wide range of species to investigate the evolution of cognition, it does not replace experiments to evaluate cognitive performance. A difficult issue is how to compare species on a level playing field. A recent cartoon highlights this issue nicely. A scientist compares problem solving in a cat and a squid. The squid happily sorts through different objects in their tank, whereas the cat has floated to the surface of their water-filled tank dead. The caption reads, "Professor Zapinsky proved that the squid is more intelligent than the housecat when posed with puzzles under similar conditions". Bitterman (1965) addressed this issue by describing the role of ***contextual variables*** on learning and cognition. He suggested species differ in the capacity to learn due to differences in perceptual, motivational and motor processes. A task, such as the Wisconsin General Testing Apparatus (WGTA), was originally designed for a visual primate that can perceive color, and requires the ability to manipulate objects (Harlow, 1949). It is therefore unsuitable for a goldfish, pigeon or honeybee without appropriate modifications. Bitterman (1965) named this attempt at control ***systematic variation***. He advocated changing subtle parameters during each experiment until a positive result was found or a consistent negative result was concluded. However, as Kamil (1987) pointed out, this is an impossible situation. It is impossible under these conditions, to discover whether a species difference in learning or cognition exists between two species that is not due to contextual variables.

Some contextual variables may be necessary to demonstrate intelligence. For example, Povinelli (2000) ran a long study to determine whether chimpanzees have a 'theory of mind'. He concluded, after some initial successes, that chimpanzees do not need a theory of mind, as reading subtle behavioral cues is sufficient for their day-to-day social interactions. However, another chimpanzee research lab (Tomasello and colleagues) found the opposite, which they interpreted as providing positive evidence for chimpanzee theory of mind (Hare et al., 2001). One difference between labs was the way their chimps were tested. Povinelli's studies depended on their chimps using an unnatural begging gesture to indicate their understanding (i.e. beg to the human who can see you or who has seen something in the past), whereas Tomasello's studies used an ecologically valid food competition paradigm where subordinate chimps had to assess another's visual access based on their perspective. In both cases, the contextual variables were quite different, and may easily have lead to differences in the performance of their chimpanzees. We may speculate that the more natural contextual variables of Tomasello and colleagues' experiments lead to their positive results and the less natural contextual variables of Povinelli's experiments lead to their negative results (although this doesn't necessarily say anything about the underlying cognitive processes).

Comparative tests of learning

Throughout the history of comparative psychology, a number of tests have been devised to compare species on learning and cognition. These tests were based on measuring a parameter to reasonably sort species based on performance, so they can be ranked (not entirely different from human IQ tests). Unfortunately, this tends to result in forming a performance scale from lowest to highest, which does not always correlate with a species' natural talents (although do frequently correlate with measures of brain size, such as EQ). Whether the test used actually measures anything to do with intelligence remains controversial. For example, one of the first measures used was speed of learning, as it was assumed the smartest species learned the fastest. This assumption has not proved correct. Skard (1950) compared rats (*Rattus norvegicus*) and humans (*Homo sapiens*) on how quickly they solved a complex maze, but there was no difference in the number of trials taken before their performance was error free. Similarly, Warren (1965) compared goldfish (*Carassius auratus*), chickens (*Gallus gallus*), cats (*Felis catus*), horses (*Equus ferus caballus*) and rhesus monkeys (*Macaca mulatta*) on their speed to learn discriminations (approach one of two stimuli to gain a reward), and found no difference. Angermeier (1984) tested a large number of species (honey bees [*Apis mellifera*], queen triggerfish [*Balistes vetula*], koi [*Cyprinus carpio*], silverbarb [*Barbonymus gonionotus*], quail [*Coturnix coturnix*], chickens, pigeons [*Columba livia*], rats, raccoons [*Procyon lotor*], rabbits [*Oryctolagus cuniculus*] and human infants) on their speed to perform a simple action to gain food, such as press a lever, peck a disc or push a rod (as appropriate for the specific animal). The number of rewards delivered before the subjects reached a criterion level of responding at a constant rate was used as the measure of performance. Surprisingly, the bees took the fewest number of trials, and the human infants the greatest number of trials (i.e. the slowest to learn), with the species ranked on a reverse *scala naturae*. As this result is completely counterintuitive from what we know about learning and cognition, it was deemed that speed of learning was not an appropriate measure of intelligence.

A better test, as it relates to a more palpable aspect of intelligence (flexible rule learning) is serial reversal learning. In this task - based on the ability to discriminate two stimuli - the subject is trained that one stimulus, A, leads to reward (S+), whereas the alternative stimulus, B, leads to non-reward (S-). Once the animal has learned these relationships, then the contingencies are reversed. Now choosing B is rewarded and choosing A is not rewarded. Once this has been learned, the reward contingencies are reversed again. If the animal has learned a 'win-stay, lose-shift' rule that if the previous reward is no longer given, that they should switch to the previously non-rewarded stimulus on the next trial, we should expect to see the number of errors on trial 2 become reduced across successive reversals. This method has been used to compare species within the same animal group (birds, Gossette, Gossette & Riddell, 1966; primates, Rumbaugh, 1970), and across different groups (birds and mammals, Gossette & Gossette, 1967), but similar issues related to contextual variables have cast doubt on the utility of this method (Macpahil, 1982).

A similar paradigm to reversal learning is the learning set, which is also based on the ability to discriminate two stimuli (shape, color, space, brightness, sound, smell, etc.) and learn reward contingencies associated with each stimulus. In the original studies, Harlow (1949) used the WGTA to test a monkey whilst pairs of colorful objects were presented in front of them, and allow them to choose one. Once the monkey had made a choice, the experimenter could drop a barrier preventing an additional choice, and re-bait for the next trial. In a typical trial, the monkey was presented with a red ball and a yellow pyramid. If the subject chose the ball, they received a treat; if they chose the pyramid, they weren't rewarded. The subject was presented with this same pair of objects until they reached a correct response criterion. On the first trial, the monkey had a 50% chance of making the correct choice, but their choices should have become more accurate the greater the amount of trials they received. After passing the criterion for the first object pair, the monkeys were then presented with two novel objects, and they had to learn the reward contingencies for these objects. This continued for a series of 8 object discriminations, with the monkeys given 6 trials to learn each new set. Harlow's monkeys performed around 75% correct by the 6th trial of the 8th set of objects, suggesting they had learned a 'win-stay, lose shift' rule. To measure performance, the monkeys' responses during the 2nd trial with a new set of stimuli were recorded. The monkeys only discover the reward contingencies on the first trial, so if they had learned a rule, they could transfer this rule to all novel stimulus sets. Therefore, on the 2nd trial they should respond correctly (as the rule can be universally applied, unless the contingencies change, as in reversal learning).

Learning sets are said to reflect the ability of 'learning to learn' and so should be applicable across species, as long as contextual variables are considered (see below). Learning sets have typically been used to compare species, such as across various lab animals (rhesus monkey, squirrel monkey, marmoset, cat, rat and squirrel; Warren, 1965), species that vary in an ecological variable, such as diet (carnivores; Doty, Jones & Doty, 1967) or between species of birds (Wilson, Macintosh & Boakes 1985).

The use of learning sets as a guide to an animal's intelligence have been questioned due to different performances across different tests. One striking case was that of dolphins (*Tursiops truncates*). When tested on a visually-based learning set discriminating different shapes, a dolphin demonstrated very little evidence for learning (Herman, Beach, Pepper & Stalling, 1969), whereas on a learning set using auditory discrimination, a different dolphin displayed >85% success on the 2nd trial (Herman & Arbeit, 1973). Although it is difficult to form solid conclusions from studies of only one subject, these results do suggest that contextual variables have to be considered. Rats do poorly in learning sets that are visually based (Warren, 1965), but achieve significantly better results when the discrimination is spatial (Zeldin & Olton, 1986) and even better when the discrimination is olfactory (Eichenbaum, Fagan & Cohen, 1986).

Ecological differences in learning and cognition

An additional problem with the aforementioned tests is there is little theory behind why the species should differ, aside from differences in general intelligence. Unfortunately, the *scala naturae* tends to rear its ugly head. Recent comparative tests have shifted focus from general intelligence to adaptive specializations. They question whether closely related species (that we might expect to have evolved homologous cognitive abilities) that differ in the type of ecological information they need to process (diet, sociality, etc.), also differ in a proposed underlying psychological process. For example, transitive inference has been proposed as essential for recognizing the position of members of a social hierarchy and the relationships between them. As such, species living in more complex social groups should better form inferences about the relative position of two separated items in an ordinal scale than species that form less complex social groups. Social pinyon jays (*Gymnorhinus cyanocephalus*) and less social western scrub-jays were given tests for transitive inference using color or spatial information (Bond, Kamil & Balda, 2003). In both cases, the pinyon jays learned faster than the scrub-jays, and acted as though they had formed a linear hierarchy of the list items, however both species performed well when given novel transfer pairs. Although we have to be cautious about making any claims from speed of learning (see earlier), this result does suggest a subtle difference in a non-social form of learning that may relate to a social application of that learning. In a similar study using serial reversal tasks, pinyon jays outperformed both Clark's nutcrackers and western scrub-jays on both color and spatial reversals, producing a fewer amount of errors (Bond, Kamil & Balda, 2007). In this case, the authors suggested that serial reversal is related to ecological complexity. Pinyon jays are more social than scrub-jays, who in turn are more social than Clark's nutcrackers, but in terms of feeding, Clark's nutcrackers and pinyon jays both eat and cache a larger amount of seeds and live at a higher elevation than scrub-jays (although remember our earlier caveat). As the performance of nutcrackers and scrub-jays was equivalent, does this mean that performance on serial reversal is also a good proxy for social, not ecological complexity?

Comparisons between primates on a series of five interrelated tests of inhibitory (or self) control (Amici, Aureli & Call, 2008), as another proxy for flexibility, found that those species who displayed the least number of errors lived in fission-fusion societies (in which individuals need to be flexible, as they move between groups and have to form new relationships and learn other's relationships anew). This study is interesting, as the species tested were not necessarily closely related (capuchin [*Cebus apella*], spider monkey [*Ateles geoffroyi*], long-tailed macaque [*Macaca fascicularis*], orangutan [*Pongo pygmaeus*], gorilla [*Gorilla gorilla*], chimpanzee [*Pan troglodytes*] and bonobo [*Pan paniscus*]), five tests of the same process were employed, and the species were compared on a measure related to a different form of social complexity.

A final study comparing two closely related New World monkey species, cotton-top tamarins (*Saguinus oedipus*) and common marmosets (*Callithrix jacchus*), investigated differences in the performance of a discounting task that could be related to differences in foraging ecology. In the first task, the monkeys were given a temporal discounting task (Stevens, Hallnan & Hauser, 2005), in which they had to wait a delay period before gaining food. In the second task, the monkeys were given a spatial discounting task, in which they had to travel a certain distance before receiving a reward (Stevens, Rosati, Ross & Hauser, 2005). In the temporal task, the marmosets waited longer before receiving food than the tamarins, whereas in the spatial task, the tamarins travelled further to receive food than the marmosets. Stevens and colleagues (2005a, b) interpreted these species differences as due to differences in species' diet. Marmosets are gumivorous, having to wait for tree sap to exude before eating. By contrast, tamarins are insectivorous, and have to catch flying insects, so have to move around before being able to eat.

Reconstructing cognitive evolution

One problem with comparing species using cognitive tasks is that the number of species that can be tested is usually quite limited (without the possibility of collaboration) and contribute little to theories of evolutionary change. Those studies that have compared more than two species using the same task (e.g. Bond et al., 2007) have compared closely related species differing in some ecological variable (such as sociality or caching propensity). Another approach is to analyze published literature across a wider group of animals, such as primates, and use meta-analytic techniques to determine shared patterns of response and species differences (see Deaner, van Schaik & Johnson, 2006). However, the problem with this method is that the tests were not designed explicitly to compare species, so subtle methodological differences between the tests of different labs (or even different experiments by the same lab) will have affected any results.

Early attempts to reconstruct the evolution of cognition were restricted to comparing various socio-ecological, life history and morphological measures (EQ, relative brain size, neocortex ratio, etc.) as proxies for cognition (see van Horik & Emery, 2011 for brief review). For example, neocortex size was compared across primates and used to predict whether primates living in larger groups or with larger home ranges, had a larger neocortex (Dunbar 1992). Assumptions of these studies include 1) that the brain measure selected is the correct one (Healy & Rowe, 2007), 2) that the brain measure is a good proxy for cognition (Healy & Rowe, 2007) and 3) that the ecological variable to be compared represents complexity (i.e. that increased group size says something meaningful about social complexity; Holekamp, 2007).

Despite these past issues, the improvement in sophisticated phylogenetic techniques have meant that the comparative method can be used effectively to examine the evolution of cognitive traits across a wide range of species and make predictions about the abilities of species that have not been tested or cannot be tested because of logistical issues, or because the species has become extinct (MacLean et al., 2012). Let us say that we have been able to test 10 species of macaques for their ability to group faces into categories; sex, age, emotional expression, etc. We have been able to construct a macaque phylogeny using morphological and molecular data. We can then plug in our values for face categorization (e.g. number of trials to reach a criterion of 80% correct trials in a series of test sessions) for all those species that have been examined (Figure 3). We should not be too concerned about contextual variables across a relatively homogenous group as macaques. Then using sophisticated statistical techniques, we can work out the likelihood that those species that weren't tested will learn at the same rate (i.e. number of trials) as their closest relatives (and at different rates from their more distant relatives).

Insert Figure 3 About Here

Of course, this is a simplified version of a more complex story (see MacLean et al., 2012 for a review of the nuances involved in employing phylogenetics to cognition). In a simple analysis of the evolution of gaze following, Fitch, Huber and Bugnyar (2010) constructed a phylogeny of those reptiles, birds and mammals that have been assessed for their sensitivity to simple gaze cues, such as the presence of the eyes and their ability to follow another's gaze geometrically (i.e. around barriers). They found that the ability to perceive eyes is a trait that is found across all species tested, probably as an adaptation for detecting predators and is likely to have evolved in the common ancestor of reptiles, birds and mammals through homology (although it should be stressed that amphibians – the closest relatives of the stem amniote ancestor – have not been examined for gaze sensitivity). For geometrical gaze following, only a few species (corvids, apes) definitely display this ability, whereas most others do not or have yet to be tested. In evolutionary terms, it is likely that geometrical gaze following evolved independently in corvids and apes through convergence. What this brief study highlights is the lack of data on a wide range of species using the same experimental paradigm, geometric gaze following (compared to gaze sensitivity).

A more recent attempt to rectify this problem, brought together a large group of researchers at the beginning of the study to make sure that all species were tested using comparable methods (MacLean et al., 2014). The focus of the study was the evolution of self-control in 36 species of birds (n = 7) and mammals (n = 29), namely the ability to inhibit a counterintuitive behavior, such as reaching towards food when a clear barrier is in the way or searching for food in one location when it has clearly been moved to a different location. This skill has been suggested to be related to flexible thinking, allowing an animal to disengage from one activity, food, social partner, etc. and move onto another when the conditions have changed. MacLean and colleagues (2014) found that more closely related species had more similar scores on the two self-control tests used, and this score was predicted by the species' absolute brain size and related to dietary complexity. Although there are many problems with this study, especially its inevitable focus on primates and few other species, it is important for demonstrating that this sort of study is possible.

What are the reproductive advantages of being cognitive?

Why be cognitive? Many species are extremely successful, in terms of their reproductive fitness (i.e. viability and number of offspring produced), without having evolved large brains or complex cognitive repertoires. We are probably justified in saying that the most effective species are those that only have to find food, avoid being eaten and sexually reproduce. And yet, cognition has evolved or else we (as a species) would still be stuck at the bottom of the ocean filtering our food.

For a cognitive trait to evolve, it must confer some advantage to the individual that possesses the trait over one who does not. Traits evolve through natural or sexual selection. A trait that aids individual survival influences reproductive success by keeping the individual alive longer enough to produce viable offspring. For example, female baboons (*Papio anubis*; Silk, Alberts & Altmann, 2003) and feral horses (Cameron, Setsaas & Linklater, 2013) form strong social bonds (friendships) with others, requiring socio-cognitive skills. This extended social network helps raise the infants and protect them from danger and subsequently increase the infants' survival rates. A trait that aids sexual selection may make the individual more attractive to the opposite sex, so they mate and produce offspring who retain that trait (Boogert, Fawcett & Lefebvre, 2011). Cognition may be sexually selected, as different traits aid males and females differently. Males express traits attractive to females – visual displays, dancing, fighting ability, singing, ability to provide (cooperation) – whereas females discriminate between males, enabling them to choose the male with the best qualities to be passed down to their offspring. Problem solving has been suggested as a trait that may be naturally and/or sexually selected.

Bowerbirds create complex structures (bowers) that function to provide females with the means to choose between different males, and the quality of the bower reflects the genetic quality of its creator. Male satin bowerbirds (*Ptilonorhynchidae violaceus*) decorate their bowers with colorful objects, but are averse to red objects and will remove them from their bowers. This discrimination has probably evolved because females do not choose males who use red objects on their bowers. Males that discriminate red objects from objects of other colors and remove them are more likely to attract mates than those that do not. Keagy, Savard and Borgia (2009) presented male bowerbirds with problems that required them to either remove red objects (by first removing a transparent cover) or cover them up (as the objects were attached to the ground). They found that males that removed the barrier the quickest had the greatest mating success (number of matings in a season). There was no relationship between mating success and the amount of each red object covered over. In a subsequent study (Keagy, Savard & Borgia, 2011) using six cognitive tests (although all biologically relevant to bowerbirds [bower decoration, vocal mimicry and bower rebuilding]), there was no clear relationship with males' performance on the tasks and their mating success (see also Isden, Panayi, Dingle & Madden, 2013 for a similar result using more traditional psychological tests, such as reversal learning and spatial memory).

Great tits (*Parus major*) were also examined for any relationship between problem solving and reproductive success. In this case, the tests examined a trait more directly linked to survival rather than sexual selection. Birds had to remove a lever from an apparatus in order to receive a food reward, and so favored individuals with quicker trial-and-error learning and perceptual-motor feedback (Cole, Morand-Ferron, Hinks & Quinn, 2012). Female birds that solved the task (solvers) produce larger clutches of eggs than females who did not solve the task (non-solvers). These differences were not related to other variables, such as time of breeding or the quality of individual habitats. However, female solvers were also more likely to desert their nests (and their offspring) than non-solvers, so the probability that their offspring would successfully fledge was reduced for solvers. One reason for this could be that male and female solvers invested more in their future offspring at an earlier stage when offspring mortality was high than in the later food provisioning stage when offspring had a better chance to survive on their own. Another more likely reason is associated with disturbances at the nest (usually attributed to predator presence, but in this case trapping the parents). Leaving the nest early enough may allow the birds to produce another brood.

In another study relating problem solving to reproductive success in great tits, using a novel string-pulling task, nests containing more than one parent who solved the task had higher nestling survival to fledging than non-solvers (Cauchard, Boogert, Lefebvre, Dubois & Doligez, 2013). More studies are needed before a clearer picture between cognition and reproductive success can be established.

Convergent evolution of cognition

If we adopt an ecological view of cognitive evolution, then the idea that two very distantly related species have evolved similar cognitive abilities through convergence now makes sense. Emery and Clayton (2004) presented such a case for the convergent evolution of intelligence in corvids and apes. Corvids and apes are separated by around 300 million years of evolution, and have evolved rather different brains. Although avian and mammalian brains are very different at the macro-level, the way they are connected, especially with respect to the processing of sensory and motor information, is very similar (Clayton & Emery, 2015). The claim for convergent evolution is based on four shared factors; biology, socio-ecology, behavior and psychology (van Horik, Clayton & Emery, 2012). Corvids and apes are highly visual animals, processing detailed information about an object's form, color and motion using binocular vision. They have appendages that can make fine manipulative actions, resulting in complex food processing skills. Both have large brains relative to their body size (indeed, they are approximately equal; Emery & Clayton, 2004). Most corvids and apes live in complex social groups, with individuals forming long-term bonds. They have a complex diet, and some species are omnivorous. Species from each family have been recorded using and making tools, and those species not seen using tools in the wild are capable of doing so in captivity.

Of most relevance here is whether the convergences just described for biological, socio-ecological and behavioral traits have resulted in a convergence of cognitive traits? Emery and Clayton (2004) examined a number of studies in which corvids and apes were tested on comparable abilities and found significant convergences in memory (mental time travel), social and physical cognition. They suggested a suite of four cognitive tools at the heart of these shared abilities, namely imagination, causal reasoning, flexibility and prospection. In the years since the first proposal, researchers have discovered that the similarities of ape and corvid cognition run deep, and some experiments in physical cognition have revealed strikingly similar methods for processing information about tools and how tools work (Emery & Clayton, 2009).

van Horik, Clayton and Emery (2012) extended this idea to other species sharing many of the same biological, socio-ecological and behavioral traits, such as parrots, elephants, dolphins, killer whales, and possibly raccoons and hyenas (see also Emery, 2006). It remains to be seen whether other species should be added to such a list, how comparisons at the cognitive level can be made, and whether the mechanisms underlying these shared traits are the based on similar principles.

Conclusions

Have we made any progress since Lewontin's (1998) disparaging analysis of the evolution of cognition? I believe that we have made great progress, but still have a long way to go and a lot more data to collect. We now possess many tools that were unavailable 20 years ago, especially sophisticated phylogenetic techniques that can make sense of large data sets. We have learned a lot more about a wider range of subjects than ever before, and as is seen in the flourish of studies described in this book, psychology is now a truly comparative science. We have started to appreciate that evolution is not just constrained to homologous processes, and analogy based on shared selection pressures in vastly distant species can be just as, if not as, important. We have designed tasks that can be used to test distantly related species on a level playing field. Finally, we are starting to take cognition out of the lab and examine, in the field, what cognition is for and what advantages it provides an animal in both it's own survival and that of subsequent generations. It will be exciting to see what we will know in 20 years time.

References

Amici, F., Aureli, F., & Call, J. (2008). Fission-fusion dynamics, behavioral flexibility and inhibitory control in primates. *Current Biology, 18*, 1415-1419.

Angermeier, W. F. (1984). *The evolution of operant learning and memory*. Basel: Karger.

Barton, R. A., & Harvey, P. H. (2000). Mosaic evolution of brain structure in mammals. *Nature, 405*, 1055-1058.

Bitterman, M. E. (1975). Comparative analysis of learning—are laws of learning the same in all animals? *Science, 188*, 699–709.

Bond, A. B., Kamil, A. C., & Balda, R. P. (2003). Social complexity and transitive inference in corvids. *Animal Behaviour, 65*, 479-487.

Bond, A. B., Kamil, A. C., & Balda, R. P. (2007). Serial reversal learning and the evolution of behavioral flexibility in three species of North American corvids (*Gymnorhinus cyanocephalus, Nucifraga columbiana, Aphelocoma californica*). *Journal of Comparative Psychology, 121*, 372-379.

Boogert, N. J., Fawcett, T. W., & Lefebvre, L. (2011). Mate choice for cognitive traits: a review of the evidence in nonhuman vertebrates. *Behavioural Ecology, 22*, 447-459.

Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences, 106*, 13850-13853.

Cauchard, L., Boogert, N. J., Lefebvre, L., Dubois, F., & Doligez, B. (2013). Problem-solving performance is correlated with reproductive success in a wild bird population. *Animal Behaviour, 85*, 19-26.

Clayton, N. S., & Emery, N. J. (2015). Avian models for human cognitive neuroscience: A proposal. *Neuron*, 86, 1330-1342.

Clayton, N. S., Dally, J. M., & Emery, N. J. (2007). Social cognition by food-caching corvids. The western scrub-jay as a natural psychologist. *Philosophical Transactions of the Royal Society B., 362*, 507-522.

Cole, E. F., Morand-Ferron, J., Hinks, A. E., & Quinn, J. L. (2012). Cognitive ability influences reproductive life history variation in the wild. *Current Biology, 22*, 1808-1812.

Darwin, C. (1879/2004). *The descent of man, and selection in relation to sex*. London: Penguin.

Deaner, R. O., van Schaik, C. P., & Johnson, V. E. (2006). Do some taxa have better domain-general cognition than others? A meta-analysis of nonhuman primates studies. *Evolutionary Psychology, 4*, 149-196.

Deaner, R. O., Isler, K., Burkart, J., & van Schaik, C. (2007). Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain, Behavior & Evolution, 70*, 115-124.

Dickinson, A. & Balleine, B. W. (2000). Causal cognition and goal-directed action. In C. Heyes, & L. Huber (Eds.), *The evolution of cognition* (pp. 185-204). Cambridge, MA: MIT Press.

Doty, B. A., Jones, C. N., & Doty, L. A. (1967). Learning set formation by mink, ferrets, skunks and cats. *Science, 155*, 1579-1580.

Dunbar, R. I. M. (1992). Neocortex size as a constraint on group size in primates. *Journal of Human Evolution, 22*, 469-493.

Eichenbaum, H., Fagan, A., & Cohen, N. J. (1986). Normal olfactory discrimination learning set formation and facilitation of reversal learning after medial-temporal damage in rats: Implications for an account of preserved learning abilities in amnesia. *Journal of Neuroscience, 6*, 1876-1884.

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*,1903–1907.

Emery, N. J., & Clayton, N. S. (2009). Tool use and physical cognition in birds and mammals. *Current Opinion in Neurobiology, 19*, 27-33.

Fitch, W. T., Huber, L., & Bugnyar, T. (2010). Social cognition and the evolution of language: Constructing cognitive phylogenies. *Neuron, 65*, 795-814.

Gossette, R. L., & Gossette, M. F. (1967). Examination of the reversal index (RI) across fifteen different mammalian and avian species. *Perceptual & Motor Skills, 24*, 987-990.

Gossette, R. L., Gossette, M. F., & Riddell, W. (1966). Comparison of successive discrimination reversal performances among closely and remotely related avian species. *Animal Behaviour, 14*, 560-564.

Grosenick, L., Clement, T. S., & Fernald, R. D. (2007). Fish can infer social rank by observation alone. *Nature, 445*, 429-432.

Hare, B., Call, J., & Tomasello, M. Do chimpanzees know what conspecifics know? *Animal Behaviour, 61*, 139-151.

Harlow, H. F. (1949). The formation of learning sets. *Psychological Review, 56*, 51-65.

Healy, S. D. & Rowe, C. (2007). A critique of comparative studies of brain size. *Proceedings of the Royal Society B.*, 274, 453-464.

Herman, L. M., & Arbeit, W. R. (1973). Stimulus control and auditory discrimination learning sets in the bottlenosed dolphin. *Journal of the Experimental Analysis of Behavior, 19,* 379-394.

Herman, L. M., Beach, F. A., Pepper, R. L., & Stalling, R. B. (1969). Learning-set formation in the bottlenose dolphin. *Psychonomic Science, 14*, 98-99.

Hodos, W., & Campbell, C. B. G. (1969). Scala naturae: Why there is no theory in comparative psychology. *Psychological Review, 76*, 337-350.

Holekamp, K. E. (2007). Questioning the social intelligence hypothesis. *Trends in Cognitive Sciences, 11*, 65-69.

Isden, J., Panayi, C., Dingle, C., & Madden, J. (2013). Performance in cognitive and problem-solving tasks in male spotted bowerbirds does not correlate with mating success. *Animal Behaviour, 86*, 829-838.

Iwaniuk, A. N., Dean, K. M., & Nelson, J. E. (2004). A mosaic pattern characterizes the evolution of the avian brain. *Proceedings of the Royal Society B., 271*, S148-S151.

Jerison, H. J. (1973). *Evolution of the brain and intelligence.* Amsterdam: Academic Press.

Kamil, A. C. (1987). A synthetic approach to the study of animal intelligence. In D. W. Leger (Ed.) *Nebraska symposium on motivation, 1987: Comparative perspectives in modern psychology* (pp. 257-308). Lincoln, NE: University of Nebraska Press.

Keagy, J., Savard, J.-F., & Borgia, G. (2009). Male satin bowerbird problem-solving ability predicts mating success. *Animal Behaviour, 78*, 809-817.

Keagy, J., Savard, J.-F., & Borgia, G. (2011). Complex relationship between multiple measures of cognitive ability and male mating success in satin bowerbirds, *Ptilonorhynchus violaceus*. *Animal Behaviour, 81*, 1063-1070.

Lewontin, R. C. (1998) The evolution of cognition: Questions we will never answer. In D. Scarborough & S. Sternberg (Eds.), *An invitation to cognitive science, Volume 4: Methods,* *models, and conceptual issues.* MIT Press: Cambridge, MA.

MacLean, E. L., et al. (2012). How does cognition evolve? Phylogenetic comparative psychology. *Animal Cognition, 15*, 223-238.

MacLean, E. L., et al (2014). The evolution of self-control. *Proceedings of the National Academy of Sciences, 111*, E2140-E2148.

Macphail, E. M. (1982). *Brain and intelligence in vertebrates*. Oxford: Clarendon Press.

Macphail, E. M., & Bolhuis, J. J. (2001). The evolution of intelligence: adaptive specializations versus general process. *Biological Review, 76*, 341-364.

Marino, L. (2002). Convergence of complex cognitive abilities in cetaceans and primates. *Brain, Behavior & Evolution, 59*, 21-32.

Moore, B. R. (2004). The evolution of learning. *Biological Review, 79*, 301-335.

Papini, M. R. (2002). Pattern and process in the evolution of learning. *Psychological Review, 109*, 186–201.

Pearce, J. M. (2009). *Animal learning & cognition* (3rd edition). Hove, UK: Psychology Press.

Povinelli, D. J. (2000). *Folk physics for apes*. New York: Oxford University Press.

Pravosudov, V. V., & de Kort, S. R. (2006). Is the western scrub-jay (*Aphelocoma californica*) really an underdog among food-caching corvids when it comes to hippocampal volume and food caching propensity? *Brain, Behavior & Evolution, 67*, 1-9.

Roth, G. (2013). *The long evolution of brains and minds.* Dordrecht, Germany: Springer.

Roth, T. C., Brodin, A., Smulders, T. V., LaDage, L. D., & Pravosudov, V. V. (2010). Is bigger always better? A critical appraisal of the use of volumetric analysis in the study of the hippocampus. *Philosophical Transactions of the Royal Society B.*, 365, 915-931.

Rumbaugh, D. M. (1970). Learning skills of anthropoids. In L. A. Rosenblum (Ed.) *Primate behavior: Developments in field and laboratory research* (pp. 1-70). New York: Academic Press.

Salwiczek, L. H., & Bshary, R. (2011). Cleaner wrasses keep track of the “when” and “what” in a foraging task. *Ethology, 117*, 939-948.

Salwiczek, L. H., Pretot, L., Demarta, L., Proctor, D., Essler, J., Pinto, A. I., Wismer, S., Stoinski, T., Brosnan, S. F., & Bshary, R. (2012). Adult cleaner wrasse outperform capuchin monkeys, chimpanzees and orang-utans in a complex foraging taks derived from cleaner-client reef fish cooperation. *PLoS ONE, 7*, e49068.

Shettleworth, S. J. (2010). *Cognition, evolution & behavior*. New York: Oxford University Press.

Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science, 302*, 1331-1334.

Skard, O. (1950). A comparison of human and animal learning in the Stone multiple T-maze. *Acta Psychologia, 7*, 89-109.

Smulders, T. V., Gould, K. L., & Leaver, L. A. (2010). Using ecology to guide the study of cognitive and neural mechanisms of different aspects of spatial memory in food-hoarding animals. *Philosophical Transactions of the Royal Society B.*, 365, 883-900.

Stevens, J. R., Hallnan, E. V., & Hauser, M. D. (2005a). The ecology and evolution of patience in two New World primates. *Biology Letters, 1*, 223-226.

Stevens, J. R., Rosati, A. G., Ross, K. R., & Hauser, M. D. (2005b). Will travel for food: spatial discounting and reward magnitude in two New World monkeys. *Current Biology, 15*, 1855-1860.

Thorndike, E. (1911). *Animal intelligence*. New York: Macmillan.

van Horik, J., & Emery, N. J. (2011). Evolution of cognition. *Wiley Interdisciplinary Reviews: Cognitive Science, 2*, 621-633.

van Horik, J., Clayton, N. S., & Emery, N. J. (2012). Convergent evolution of cognition in corvids, apes and other animals. In T. Shackleford, & J. Vonk (Eds.) *The Oxford handbook of comparative evolutionary psychology* (pp. 80-101). New York: Oxford University Press.

Vander Wall, S. B. (1990). *Food hoarding in animals*. Chicago: University of Chicago Press.

Warren, J. M. (1965). Primate learning in comparative perspective. In A. M. Schrier, H. J. & F. Stollnitz (Eds.) *Behavior of nonhuman primates: Modern research trends* (pp. 249-281). New York: Academic Press.

Wilson, B., Mackintosh, N. J., & Boakes, R. A. (1985). Transfer of relational rules in matching and oddity learning by pigeons and corvids. *Quarterly Journal of Experimental Psychology B., 37*, 313-332.

Zentall, T. R. (2002). A cognitive behaviorist approach to the study of animal behavior. *Journal of General Psychology, 129*, 328-363.

Zeldin, R. K., & Olton, D. S. (1986). Rats acquire spatial learning sets. *Journal of Experimental Psychology: Animal Behavior Processes, 12*, 412-419.

Figure 1: Phylogenetic tree of Darwin's finches found on the Galapagos Islands. Each finch species evolved from a common finch ancestor that travelled from the South American mainland to the Galapagos, and then diversified as each species exploited different habitats on the islands. The main target of diversification was the beak used to feed on different foods (seeds, cactus flowers, buds and insects). A similar process of diversification could also account for differences in cognitive abilities in both closely and distantly related species.

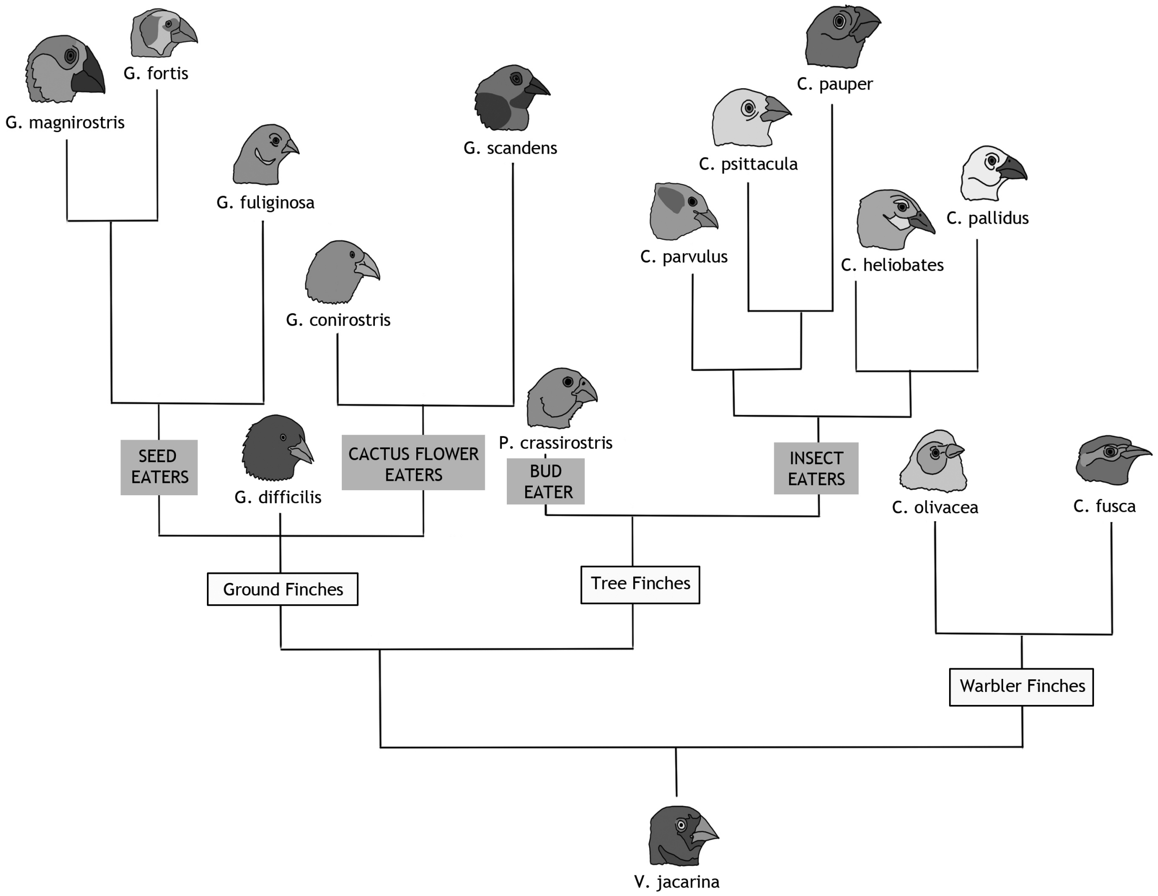

Figure 2: Animals will differ in the application of their learning and cognition because of differences in the structure of their brains and the ecological functions to which they have been put to use. In presenting a hypothetical example of foxes and rabbits, we can see that foxes need to apply their abilities to a suite of functions that need a degree of flexibility, whereas rabbits utilize their abilities in a rather rigid form. Their brains appear to reflect these differences in learning and cognition.

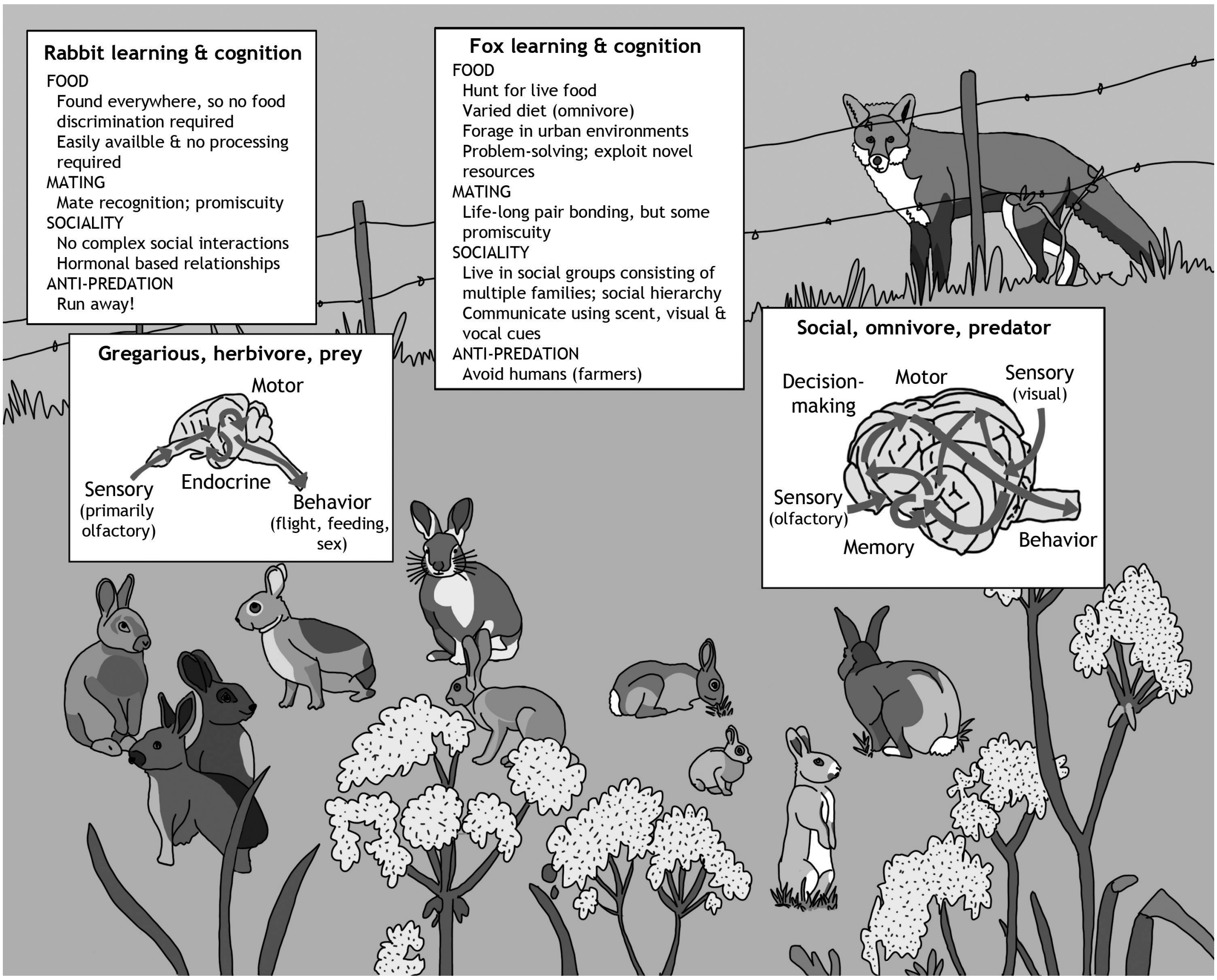

Figure 3: A hypothetical phylogenetic tree of macaques (species 1-10) that could be used to reconstruct the evolution of a cognitive trait, such as facial categorization. Black dots represent species tested on the cognitive task, whereas white dots represent species that have not been tested (or are unavailable for testing). Gray boxes represent the common ancestor of two species. Species to the right are 'more evolved' and share more common ancestors than species to the left. If there is a beneficial progression in performance as we move to the right of the tree, we predict (with the greatest parsimony) that species' performance should get better as they become more related to species 10 (for which we possess performance data – this species learns discriminations very quickly and can transfer to novel stimuli).