CHAPTER

5

Convergent Evolution of Cognition in Corvids, Apes and Other Animals

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Abstract

Over the past 30 years, a cognitive renaissance has produced startling revelations about how species perceive their physical and social worlds. Once considered mere automata by Descartes, recent research supports claims that many animals possess advanced cognitive capacities (Shettleworth, 2010). Moreover, advanced cognition appears to have arisen across numerous species, many of which are distantly related, but which share a number of traits, such as large relative brain size, complex sociality and behavioral flexibility. Is the evolution of advanced cognition the result of a series of adaptive specializations driven by the shared selection pressures that species face in their environments? With our expanding awareness of cognitive processes across species, attributes such as causal reasoning, mental time travel or mental attribution, once thought unique to humans, invite careful reconsideration of their evolutionary origins.

Key Words: behavioral flexibility, convergent evolution, relative brain size, sociality, tool use

Introduction

Our understanding of the convergent evolution of cognition hinges on comparative studies among phylogenetically distinct species. This is not to say that comparative cognition is solely restricted to studies of distantly related species; comparisons between closely related species, such as humans and other primates, especially chimpanzees, also reveal compelling insights into the divergent processes of cognitive evolution (e.g., Tomasello & Call, 1997). However, the defining criterion of convergent evolution is that it occurs across distantly related species. As a result, the convergent evolution of adaptive traits can be considered to arise independent of phylogeny shaped by common solutions to similar socio-ecological problems.

By considering cognition as an adaptive specialization—that is, a trait that is driven by environmental selection pressures—such selection pressures can be shared among distantly related species that face similar socio-ecological challenges. As a result, analogous adaptations may evolve independently among distantly related organisms (Keeton & Gould, 1986). Any similarities in traits (i.e., cognitive abilities) can then be attributed to shared environmental selection pressures rather than to characteristics present in a common ancestor (Ridley, 1993). Consequently, the greater the phylogenetic separation between groups, the stronger the case for evolutionary convergence (Papini, 2002).

One example of convergent evolution is the adaptation of active flight among distantly related vertebrate species (Seed, Emery, & Clayton 2009). Birds, bats, and pterosaurs, for example, share the functional ability of flight, but lack structural similarities in their forelimb morphologies (Figure 5.1). Flight in birds evolved through the extension of the bones of the forelimb, whereas bats and pterosaurs support

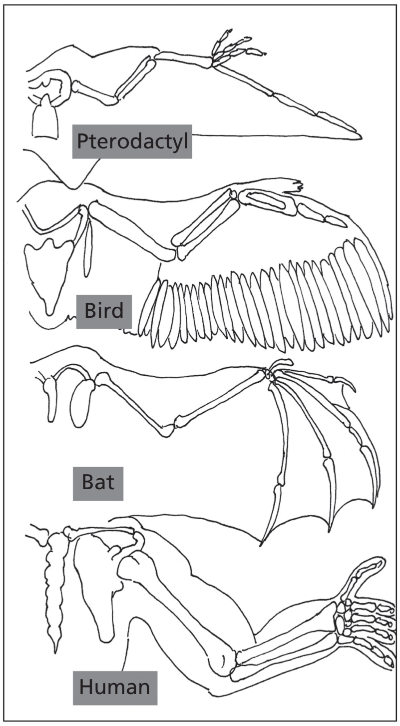

Figure 5.1 Convergent evolution of wing and arm structure in pterodactyls, birds, bats, and humans. Although the structure of the wing is different in pterodactyls, birds and bats, the resultant behavior—flight—is the same. This may represent a parallel to convergent evolution of cognition in corvids and apes, yet with very differently structured brains.

the wing through extended digits: the fifth digit for pterosaurs; and the second, third, fourth, and fifth for bats. Yet, the convergent shape of the wing is the result of environmental selection pressures and the functional constraints imposed by flight.

Cognition has been described as "the mechanisms by which animals acquire, process, store and act upon information from the environment" (Shettleworth, 2010, p. 4). This chapter proposes a model of cognition as a domain-specific adaptive response to specific environmental selection pressures, which can then be generalized and applied to solve novel tasks of functional equivalence. This proposal predicts differences between species based on different levels and types of problem solving in the wild. An alternative hypothesis proposes that there are no qualitative differences in the processes of cognition between species (Bolhuis & Macphail, 2001), even in those that live in different environments. We find no evidence to support this alternative hypothesis.

In addition to such mechanistic controversies is the debate about whether certain behaviors are, in fact, governed by so-called higher-order cognitive processes, or whether intelligent behavior is simply the result of "hardwired" adaptive specializations—conserved associative learning processes (i.e., conditioning). It is, therefore, important that cognitive processes are tested by determining whether certain behaviors can be flexibly expressed across a variety of tasks of general equivalence.

Comparing Intangible Traits & Inferring Tangible Proxies

Unlike wings, which can be easily dissected to reveal any structural differences in morphology, cognition is an intangible trait ascribed to an organism's psychology. Thus, comparisons may be made across species only by identifying measurable proxies that are ecologically relevant to cognitive aptitude, such as measures of relative brain size.

Brain Structure and Function

One useful proxy for intelligence is the size of specific components of an organism's brain relative to its overall body mass (Figure 5.2). Overall brain size has been criticized as a poor measure of cognitive capacity, because (1) brain size correlates with body size, and (2) many brain areas control primary, sensory, and motor functions that are not directly associated with cognition (Jerison, 1973). However, more recent studies have found that overall brain size is a better predictor of general intelligence (at least in primates) than other measures, including relative brain size and neocortex size (Deaner, Isler, Burkart, & van Schaik, 2007). Yet there are certain areas of the brain that are more closely associated with higher-order processing, such as the neocortex in mammals and the forebrain in birds (Striedter, 2005).

Jerison (1973) first proposed an index to rank the cognitive skills of species based on their relative brain size, called encephalization quotient (EQ). Although there are obvious difficulties in making generalized comparisons across taxa that live in different environments, Jerison identified that some species are endowed with an exceptionally high EQ and, hence, a relative brain size that is much larger than would be predicted for their body mass (Jerison, 1973). Of particular interest was the finding that the relative size of the forebrain in corvids (crows, rooks, and jays) and parrots is significantly larger than those of other birds (cf. Emery & Clayton, 2004a). Corvids and parrots, in fact, possess brains that are relatively the same size as those of the great apes, and in both cases they are much

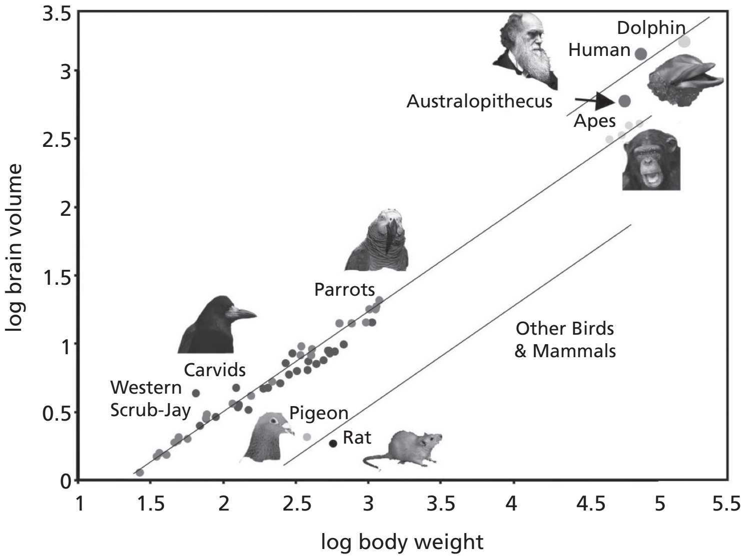

Figure 5.2 Graph of log brain volume against log body weight for a number of birds (corvids, parrots, and pigeons), mammals (rats, primates, cetaceans), *Australopithecus and Homo sapiens*. Data on body size and brain volume were taken from various published sources.

larger than predicted for their body mass (Jerison, 1973). Although the issue of whether brain size reflects cognitive competence remains controversial (Striedter, 2005), it is clear that those avian species that have relatively large brains, such as corvids and parrots, also display cognitive abilities that have hitherto only been demonstrated in large-brained mammals (primates, cetaceans, elephants), especially those with a large prefrontal cortex (Emery & Clayton, 2004b; see later).

The common ancestor of birds and mammals, a stem amniote, lived over 300 million years ago. During the course of such long independent evolutionary trajectories, corvids, parrots, and apes adapted to radically different environmental requirements (arboreal and terrestrial, respectively), but with shared or similar life histories (relatively long developmental period before independence, great longevity, etc.), morphological adaptations (color vision, ability to track moving objects, fine object manipulation, etc.), and socio-ecological traits (omnivory, complex social groups, individualized relationships, etc.).

Evolutionary divergence has resulted in the independent evolution of different neuroanatomical components and structures across species. Mammalian brains, for example, are comprised of different components to those of birds, and they are organized into a laminar arrangement of neurons compared to the nuclear clusters of neurons found in avian brains (Emery, 2006). Yet analogous functions of particular brain components have been identified between these two groups. In the mammalian brain, for example, it is the neocortex that mediates cognitive processes (memory, reasoning, concept formation, and social intelligence). However, birds do not possess a neocortex. Measures of higher cognition, such as foraging innovation and tool use are, instead, identified with certain areas of the avian forebrain (Lefebvre, Nikolakakis, & Boire, 2002), with areas analogous to the mammalian prefrontal cortex, such as the nidopallium and mesopallium (Reineret al., 2004; Rehkamper, Frahm, & Zilles, 1991).

Although there may be fundamental differences in the size and structure of avian and mammalian brains, recent evidence suggests that both groups share advanced cognitive abilities (Emery, 2004). Pepperberg (1999) provides a helpful analogy: "*the structural differences between mammalian and avian brains are like the wiring and processing differences between IBM-PCs and Apple Macs. However, in both cases, the resulting output (i.e. behavior or algorithmic operations) is similar.*" Such similarities in cognitive traits suggest that corvid and ape cognition has undergone a convergent evolution of mental processes (Emery, 2004, Emery & Clayton, 2004b, Seed et al., 2009). In fact, many animals demonstrate intelligent behavior, suggesting that cognition may have evolved independently among several vertebrate groups, including great apes (Tomasello & Call, 1997), corvids (Emery, 2004), cetaceans (Marino, 2002), hyaenas (Holekamp, Sakai, & Lundrigan, 2007) and canids (Miklosi, Topal, & Csanyi, 2004, Hare & Tomasello, 2005), among others (see later).

Is Cognition Similar in Different Species?

Not only do corvids and apes appear to possess analogous neuroanatomical components responsible for cognitive processes, but they may also share similarities in how they form representations of their social and physical worlds. Thus, it is in the recognition of shared socio-ecological challenges that species face in their day-to-day lives that convergent adaptations may be revealed. For example, recent research has revealed evidence that corvids demonstrate similar reasoning abilities as great apes, with regard to how tools work, how social agents can be manipulated, and how events are remembered (cf. Seed et al., 2009).

Recognizing behavioral similarities shared among different species provides a basis for inferring similarities in cognition. For example, using tools to aid in extractive foraging may not only be an adaptive response to acquiring an otherwise inaccessible resource, but proficiency might also be refined over time through social learning. However, it is only by going beyond the broad observations, such as that both apes and corvids are capable of tool manufacture, that information about *how* these species process such information can be revealed. For instance, what range of problems are these animals capable of solving? Do they make or use tools for particular purposes, adapting or modifying them depending on their context of use? Does a species' understanding of how tools work depend on causal reasoning or other psychological processes? Only by conducting experiments using comparative methodology can we explain limits to such similarities and thus establish the convergent processes of cognitive evolution.

Species with dramatically different life histories, morphologies, brain structures, and ecologies may perceive the world quite differently from one another. For this reason, it is important to consider the ecological validity of comparative tests. Attempts to make direct comparisons of psychological processes across phylogenetically distinct species may be marred by species-specific differences in perception, attention, and motivation (Bitterman, 1960, 1965).

An organism's neuroarchitecture is influenced by adaptations to specific environmental selection pressures. For instance, there may be differences in the environmental constraints imposed on brain size among aquatic species compared with aerial species. Moreover, species' life histories may also result in more subtle variations. For example, migratory birds that spend much of their life in flight may be subjected to tighter energetic constraints and, thus, tend to possess significantly smaller brains than those of sedentary or nomadic species (Burish, Kueh, & Wang, 2004). The occurrence of cognitive traits may also be more likely to evolve among certain species. For example, the manufacture and use of tools is more frequently observed in great apes than in birds. This may be because birds possess a multifunctional beak, thus rendering the manufacture of tools unnecessary in many of the foraging challenges that birds encounter.

Prerequsites for Intelligent Behaviour

Cognition is thought to have arisen independently across distantly related species through processes of convergent evolution, driven by the need to solve comparable social and ecological problems (Emery & Clayton, 2004a, 2004b; Marino, 2002; Seed, Emery, & Clayton, 2009). Such environmental challenges often require the ability to respond flexibly by generalizing domain-specific behaviors (i.e., behaviors evolved to solve specific problems), and applying this knowledge to accommodate for more broad and variable interactions that species encounter in their environments. As a result, behavioral flexibility is often attributed as an indicator of intelligence.

Corvids have consistently demonstrated cognitive skills that surpass those described in other birds, and in many cases they rival similar cognitive domains previously thought confined to monkeys and apes (Emery, 2004; Emery & Clayton, 2004a, 2004b, Seed, Emery, & Clayton, 2009). Similarities among species' life history traits may, therefore, provide clues to cognitive aptitude. Corvids and parrots share with the great apes, many of the biological, ecological, behavioral, and psychological attributes thought fundamental to complex cognition. Each of these aspects will be discussed in the following sections outlining any similarities and discrepancies between groups. Both corvids and parrots, for example, possess forebrains that are relatively the same size as apes; experience a long developmental period before becoming independent from their parents; are long-lived, omnivorous extractive foragers; and live in complex social groups—all socio-ecological attributes that have long been suggested as prerequisites for intelligence in primates (Byrne & Whiten, 1988; Humphrey, 1976).

It is likely that each of the socio-ecological attributes described later corresponds with differences in domain-specific cognitive abilities. Chimpanzees, for example, use tools more frequently than their closely related cousins, bonobos, and, hence, possess a more sophisticated understanding of physical causality or "*folk physics*" (Herrmann, Hare, Call, & Tomasello, 2010). Yet, those species with the most advanced cognitive abilities are likely to incorporate a number of these socio-ecological attributes (Emery, 2006), although the question that remains to be answered is to what degree these socio-ecological pressures correlate with cognitive flexibility and how these pressures are reflected in the underlying cognitive systems of animals, which we are still far from knowing.

Biological Similarities

In this section, we highlight a number of shared biological features found in corvids, parrots, and apes, however, we are aware that these are general claims and that some of the traits are shared with other animals. The function of this section is to highlight those features that are shared by these taxonomic groups and may contribute to the similarities in behavior and cognition we will describe in later sections.

PARENTING, DEVELOPMENT, AND LIFESPAN

Ontological differences among species reveal important trends in the evolution of relative brain size, particularly between altricial and precocial species. Altricial species are born into the world blind, helpless, and utterly dependent on parental care. Yet precocial species are immediately capable of surviving independently. Such stark differences in juvenile development may appear at odds with initial survival success, yet they foretell strategic differences in species' life histories.

In birds, altricial hatchlings possess significantly smaller brains relative to their body size than precocial hatchlings (Bennett & Harvey, 1985). However, altricial adult birds possess significantly larger brains relative to their body size than precocial adult birds (Starck, 1993; Starck & Ricklefs, 1998). These findings suggest that the majority of neural development occurs in birds during an extended posthatching period, rather than during incubatory periods. However, prolonged periods of development, whether during the incubatory period or posthatching period, are, in fact, correlated with increases in relative brain size (Iwaniuk & Nelson, 2003). Thus, extended developmental periods and longer durations of parental care correlate positively with relative brain size (Ricklefs, 2004). A similar picture emerges for the great apes. Apes are also an altricial species, displaying a slow rate of development, with substantial increases in brain size in the postnatal period. Indeed, there is also a clear relationship between length of juvenile period (and age at maturation) and relative brain size in primates (Ross, 2004).

Relatively extended periods of juvenile development may serve to accommodate the acquisition of knowledge, either by social learning from adults to offspring or individual learning based on trial-and-error. Although this hypothesis is attractive, there is little data to support such a claim. Indeed, there is no correlation between environmental complexity (social, physical, dietary, ecological, and climatic uncertainty) and brain size in primates when controlling for postnatal growth rates in primates (Ross, 2004), and the developmental period of corvids and parrots is relatively long compared to other birds, but relatively short compared to apes (Iwaniuk & Nelson, 2003). In addition, a species' lifespan may also influence its cognitive capacity because long-lived individuals may accumulate knowledge and experience and use such knowledge to make better decisions and be better prepared to solve and adapt to future problems.

DEXTERITY

Species equipped with grasping or dexterous limbs (primates) or generalized all-purpose beaks (birds) may be better equipped to solve physical tasks than those species that cannot easily manipulate objects. Parrots, for example have particularly dexterous grasping feet, which they effectively use to manipulate food. Similarly, primates possess hands and feet that can be used to manipulate objects. Corvids tend to use their beaks as tools, suitable for prying open, digging, puncturing, and crushing a variety of food sources, as well as a number of fine manipulations. Such a number of flexible movements allow these groups to exploit objects in their environment unavailable to other groups, which in turn require additional levels of neural and cognitive processing power not seen in other species without such dexterity.

VISUAL ACUITY

Among primates, brain size is positively correlated with visual specialization (Barton, 1998). In fact, the primate neocortex is comprised of about 50 percent of visual areas, allowing for accurate and high-resolution processing (Van Essen, Anderson, & Felleman, 1992). High visual acuity may be particularly beneficial to primates and birds because it may enhance their ability to detect ripe fruits and moving insects, as well as predators. The relatively large brains of frugivorous primates, as opposed to folivorous species (Clutton-Brock & Harvey, 1980), may thus have resulted from selection pressures acting to enhance the detection of edible fruits using specific visual cues such as color. In addition, visual acuity may allow for the detection of social information, such as facial expressions and the gaze direction of conspecifics (Barton, 1996). Thus, it is not surprising that there is a strong relationship between the size of the visual system and socio-ecological variables such as diet and social group size in primates.

Unfortunately, comparable data do not exist for birds. However, birds are highly visual animals (Hodos, 1993), processing color information in a greater frequency range than mammals (including ultraviolet), as well as rapidly processing movement information. The eyes of birds and mammals are quite different, yet the central neural systems are relatively similar (Husband & Shimizu, 2001). We may, therefore, predict a similar relationship between the visual system and socio-ecological variables in birds. Indeed, in the case of prey capture, there is a co-evolutionary relationship between eye size and brain size (Garamszegi, Moller, & Erritzoe, 2002).

BRAIN SIZE

The relative size of corvid, parrot, and ape brains are equivalent in terms of brain size to body size (i.e., are found on the same regression line; Emery and Clayton, 2004b). An enlarged brain is metabolically expensive (Aiello & Wheeler, 1995). Thus, it is generally accepted that there must be correspondingly powerful adaptive benefits from brain enlargement. Understanding the origins of this specialization, therefore, becomes a question of what selective pressure(s) favored enlarged components of the brain during the course of evolution (Isler & Van Schaik, 2009).

As discussed earlier, the relative size of specific components of an organism's brain can be used as a direct proxy to inferring higher cognitive facilities. However, it is important to recognize that any interpretations must be made with caution, because different assumptions and methodological approaches can easily distort species-wide comparisons (see Healy & Rowe, 2007).

Ecological Similarities

UNPREDICTABLE ENVIRONMENTS

The most recently evolved genera of corvids (*Corvus, Pyrrhocorax*) and apes (*Pan*) appeared at roughly the same point in evolutionary time (5–10 million years ago) during the Late Miocene and Pliocene epochs (Emery, 2006; Potts, 2004). This period is characterized by dramatic environmental and climatic variability and instability as a result of numerous ice ages. Such environmental changes would have strongly influenced food availability and consequently species' foraging strategies.

During evolutionary history, the abundance of resources may have fluctuated, becoming less reliable and irregularly distributed through time and space. Food scarcity may have been alleviated by the evolution of foraging techniques to exploit new resources. However, species that are governed by rigid stimulus-response action patterns or hardwired behaviors may not respond as well to such changes as those species that adopt flexible behaviors based on more abstract knowledge (Seed et al., 2009). As such, extracting food hidden within encased substrates or procuring meat as an energy-rich food source may have become incorporated into species' foraging repertoires. Thus, environmental variability may have selected for certain species to adopt innovative, omnivorous, and generalist foraging techniques, powered by increases in relative brain size (Lefebvre, Reader, & Sol, 2004). Such ecological variables have been suggested as important evolutionary drivers of great-ape cognition (Potts, 2004); similar conditions may also be responsible for the evolution of avian (corvid and parrot) cognition (Emery, 2006), as well as other species living in such changeable environments, such as cetaceans (Marino et al., 2007) and elephants (Byrne & Bates, 2009).

One important feature of an unpredictable environment is the source of food. Foods that are ephemeral, that have to be hunted, that appear at certain times of the year, that are distributed in clumps or need to be extracted from casings, will require more cognitive abilities to obtain (e.g., spatial memory, planning, cooperation) than foods that are available all year, located in the same place, and which require little processing, such as foliage.

GENERALIZED DIET

Many corvids, parrots, and primates are omnivorous, generalist foragers. Rooks, in particular, consume over 170 species of plants and animals, including many different parts of plants, insects, worms, seafood, birds' eggs, small vertebrates, and carrion (Cramp & Perrins, 1994). However, rooks acquire the majority of their diet through extractive foraging techniques; digging in the soil for grain, invertebrates, roots, and tubers (Lockie, 1955). Some corvids also use their beaks to hammer and pry open the hard cases of nuts such as walnuts and acorns, and drop mussels, limpets, and bone from the air until their encased contents are released.

Parrots also consume a wide variety of seeds, fruits, and flowers (Juniper & Parr, 2003). Some species, such as the kaka frequently consume insects (Moorhouse, 1997), use their large, down-curved bills to tap sap from trees and excavate grubs from both live and dead wood (Beggs & Wilson, 1987). Another New Zealand parrot, the kea, renowned for its extreme neophilia and advanced intellect (Huber & Gajdon, 2006), is also known to consume a varied diet, including over 40 plant species (Clark, 1970) as well as discarded fat, protein, and carbohydrate-rich foods found in human settlements (Diamond & Bond, 1999; Gajdon, Fijn, & Huber, 2006). The kea is also notable as the only carnivorous parrot known for attacking sheep and eating fat from the back of the animal (Benham, 1906; Diamond & Bond, 1999), as well as excavating sooty shearwater chicks from their underground nest burrows (Cuthbert, 2003). Utilizing such a variety of food sources is a likely response to living in mountainous regions characterized by a harsh and unpredictable climate, resulting in an irregular food supply. It is not yet clear whether the seemingly more complex dietary habits of keas, when compared to other parrots, is reflected in their physical cognition (Liedtke, Werdenich, Gajdon, Huber, & Wanker, 2010).

Seeds are a more common component of parrots' diets, but many seeds have a hard case, requiring dexterous manipulation to extract their contents, preventing most other arboreal foragers access. Yet some parrots, for example, hyacinth macaws (Borsari & Ottoni, 2005) and black palm cockatoos (Wallace, 2000), proficiently open hard-cased seeds by using wedgelike pieces of wood or leaves as tools to better grip nuts with their upper mandible, and, while holding the nut in place with one foot, open the hard casing with their lower mandible.

Primates also demonstrate skillful extractive foraging techniques, the most prominent example being termite fishing by wild chimpanzees (Goodall, 1963; van Lawick-Goodall, 1968). However, chimpanzees (Boesch & Boesch, 1990) and capuchins (Fragaszy, Izar, Visalberghi, Ottoni, & de Oliveira, 2004) also crack hard- cased nuts with hammers and anvils to extract their contents. Although such behaviors are commonly observed, termite fishing and nut cracking require sophisticated manipulation and dexterity to succeed. Chimpanzee infants require years of observation to learn how to make tools (Biro et al., 2003; Lonsdorf, 2006). Similarly, capuchins' success at nut cracking varies considerably between individuals and is likely to require years of practice to attain an efficient technique (Fragaszy et al., 2010).

Extractive foraging may have evolved in response to food scarcity. Species that evolve novel foraging techniques may exploit niches that are not readily available to others, often containing energy-rich foods that are high in nutritive value and available throughout the year. In addition, extracting encased foods often requires a variety of complex sensorimotor skills for locating and manipulating food items. Such processes have been suggested to provide support for the evolution of intelligence in apes (Parker & Gibson, 1977), although other studies on primates found no relationship between extractive foraging and neocortex ratio (Dunbar, 1995).

FORAGING IN SPACE AND TIME

The main foods consumed by corvids, parrots, and primates (fruits, seeds, and invertebrates) are often patchily distributed through space and vary in their temporal availability. Other species may also face similar challenges in locating food items, such as cetaceans' diet of fish, krill, and cephalopods, which may be equally variable in abundance and distribution (Marino, 2002). However, such temporal and spatial patchiness may be predictable; plants remain in the same place and fruits often ripen at predictable intervals. Likewise, regularities in ocean currents or seasonal spawning times may allow cetaceans to predict the location and timing of abundant food supplies.

Yet closely related species can differ substantially in their dietary requirements and hence foraging strategies. Some primates rely on a varied diet of fruits, whereas others predominantly consume leaves. Leaves are, however, considerably more abundant than fruits, and their distribution is regular. Frugivorous primates are, therefore, faced with an additional challenge; locating an ephemeral and patchily distributed resource. However, primates that remember the locations and fruiting patterns of a variety of plant foods might improve their foraging efficiency (Janmaat, Byrne, & Zuberbuhler, 2006). Selection pressures, favoring foraging efficiency, are, therefore, thought to enhance species' cognitive capacities for spatial and temporal memory (Milton, 1981). As such, cerebral expansion is more pronounced in frugivorous primates, rather than folivorous species (Clutton-Brock & Harvey, 1980).

Some animals have evolved specializations for remembering and predicting the location of resources that are irregularly distributed through time and space. The most extensively documented accounts of such behavior come from experiments on spatial memory in food-caching animals (Vander Wall, 1990). When an abundant food supply is available, many animals store food for consumption in later periods of food scarcity. However, to efficiently recover their caches, storers need to process information relating to the location of their cache sites, the type, and perishability of stored food items, and the social context of caching (Clayton & Dickinson, 1999; Clayton, Dally, & Emery, 2007; van Horik & Burns, 2007). Some corvids, such as Clark's nutcrackers, can cache up to 30,000 pine seeds over large areas, recovering a majority of them up to six months later. Such behaviors suggest that these birds possess a proficient long-term spatial memory (Balda & Kamil, 1992). Conversely, other corvids, such as Western scrub jays, cache fewer but a wider variety of food items that differ in their rates of perishability. Consequently, Western scrub jays not only remember where they cached, but also what they cached and when, so that perishable food can be recovered when it is still edible (Clayton & Dickinson, 1998, 1999; Clayton, Yu, & Dickinson, 2001, 2003; de Kort, Dickinson, & Clayton, 2005).

Behavioral Similarities

TOOL USE AND MANUFACTURE

Recently thought to be uniquely human, the first report of tool use outside of humans was in wild chimpanzees (van Lawick-Goodall, 1968). We now know that many species of insects, fish, birds, and mammals use tools in the wild (Beck, 1980; Emery & Clayton, 2009b). However, in the wild, only chimpanzees, orangutans, New Caledonian crows, and woodpecker finches habitually use and manufacture tools during their daily foraging activities (Hunt, 1996; Tebbich, Taborsky, Fessl, & Dvorak, 2002; Tomasello & Call, 1997; van Schaik et al., 2003). Yet the extent to which these animals understand how tools work, that is, their physical properties and the unobservable forces that govern their function—so-called *folk physics*—remains controversial (Emery & Clayton, 2009b; Povinelli, 2000).

Tool use requires "the use of physical objects other than the animal's own body or appendages as a means to extend the physical influence realized by the animal" (Jones & Kamil, 1973, p. 1076). Hence, vultures that crack open eggs by dropping them onto rocks do not demonstrate tool use, whereas vultures that throw stones (as a physical extension of their body) to open eggs fit these criteria. Likewise, the examples of corvids dropping mussels to crack open their hard shells, thrushes that open snail shells by smashing them onto stones (Gibson, 1986), or crows in Japan and California that open hard-shelled walnuts by dropping them from great heights onto hard-surfaced roads (Cristol and Switzer, 1999; Nikei, 1995) do not demonstrate tool use when discussed in terms of the earlier definition. However, manipulating encased food items to extract their contents (extractive foraging) requires certain forms of cognition, particularly when compared with nonextractive forms of foraging.

Although most species of great apes make and use tools, the most proficient primate tool user in the animal kingdom is the chimpanzee (Tomasello & Call, 1997). Yet there have also been numerous reports of tool use in birds, especially corvids (Lefebvre et al., 2002). One of the most striking applications of tool use by any animal can be observed in wild New Caledonian crows. These birds routinely use and transport manufactured tools during daily foraging expeditions, and they use different types of tools depending on their functional requirements: stepped-cut Pandanus leaves are used in a rapid back and forth fashion to search for prey under leaf litter, whereas hooked twigs are used to extract insect larvae from within tree cavities using slow deliberate movements (Hunt, 1996).

Both New Caledonian crows and chimpanzees manufacture tools, either fashioning probing sticks by stripping off smaller twigs and leaves from larger twigs and then inserting them into termite mounds, making hook tools by removing a series of side twigs from a larger twig and then chiseling away at a breakage point to create a hook, or cutting steps into a pandanus leaf to make a pointed and rigid tool for rooting out grubs living under the bark of dead trees (Sanz, Call, & Morgan, 2009; Hunt & Gray, 2004; Hunt, Corballis, & Gray, 2006). In all these cases (and others not described here), the toolmaker starts to create a tool from raw material (twigs, leaves, etc.) by removing or sculpting parts of the raw material that is nonfunctional as a tool, into a functional tool. Although we know little about the psychology of toolmaking, this ability suggests that the toolmaker may have an image of the final tool in mind before it is made.

SOCIALITY

Observations of social interactions among captive chimpanzees first prompted the hypothesis that social living and, thus, the challenges that species face in their social environment play important roles in the evolution of a flexible and intelligent mind (Social Intelligence Hypothesis: Humphry, 1976). This hypothesis was later recognized as a key component of primate cognition, attributing social intelligence to the recognition and subsequent manipulation, coordination, and deception of individuals within a social group (Machiavellian Intelligence Hypothesis: Byrne & Whiten, 1988). Further support for these theories was later found in positive correlations between social-group size and neocortex size in primates (Social Brain Hypothesis: Dunbar, 1998, chapter 6 of this volume), and cetaceans (Marino, 1996). The rationale behind these theories is that selection favors those animals that proficiently keep track of the identities and interactions of numerous individuals within large social groups. Over evolutionary time, this process resulted in the refinement of social cognition as an adaptive specialization.

Although there appears to be a clear indication that group size has played a significant role in the evolution of brain size in primates, similar relationships are not shared among birds (Emery, Seed, von Bayern, & Clayton, 2007). Such differences may, therefore, be attributed to the structure of social groups. For example, primates form polygynous social groups, whereas birds are often monogamous, forming life-long pair bonds. Moreover, group size in primates may be relatively stable, yet there can be considerable seasonal variation in birds' flock size. Similar correlations between relative brain size and certain aspects of sociality have, however, been identified in some avian species such as corvids (Emery, Clayton, & Frith, 2007). Social intelligence in birds may have thus evolved in response to the requirements of maintaining relationships and coordinating cooperative behavior within monogamous pairs, rather than having been driven by the need to manage competitive interactions imposed by group living as in primates. In other words, it may be the quality rather than the quantity of relationships that are important for birds (Emery, Seed, et al., 2007). In socially monogamous birds, an increase in the quality of parental care may lead to increasing payoffs; more experienced pairs (those that have paired for more than one breeding season) may raise more chicks. As such, comparisons between brain size and mating system in birds have revealed that the largest relative brain sizes are found among long-term monogamous species and cooperative breeders (Emery, Clayton, et al., 2007).

Species that live within fission-fusion societies are presented with the additional cognitive challenge of adjusting to dynamic social changes, resulting from the movement of numerous individuals into and out of groups at various times (Aureli et al., 2008). Rooks, for example, congregate in large colonies during the breeding season; then, after they have raised their offspring, each breeding pair will disperse to form smaller foraging groups. Similar social structures are exhibited across a number of distantly related species that demonstrate high levels of sociality and social complexity such as chimpanzees (Goodall, 1986), cetaceans (Connor, Mann, Tyack, & Whitehead, 1998; Marino, 2002; Smolker, Richards, Connor, & Pepper,1992), and possibly some corvids (Emery, 2004).

RELATIONSHIPS

Many animals not only recognize individuals within a group but also understand intragroup relationships, such as kinship and the social status of individuals relative to other group members (e.g., dominance rank). Such interactions become particularly clear during disputes over food or mates. During disputes, animals may recruit support from bystanders or relatives to form alliances; however, supporting a loser may prove costly. Therefore, it pays to recruit and support high-ranking individuals as well as consider the strength of preexisting intragroup alliances. Making such decisions relies on the possession of a detailed understanding of third-party relationships (Schino, Tiddi, & Di Sorrentino, 2006; Silk, 1999), however, heuristics such as "always recruit the most dominant animal" may also explain behavior consistent with that of third-party recognition (Range & Noe, 2005).

Until recently, third-party relationships were considered a unique attribute of primate cognition (Tomasello & Call, 1997). However, many mammals, such as elephants, whales, dolphins, and hyenas, form long-lasting groups that are comprised of similar kin and dominance networks to those of primates (Connor, 2007; de Waal & Tyack, 2003; Holekamp et al., 2007). Like primates, hyenas support conspecifics engaged in agonistic interactions. Engh and colleagues (Engh, Siebert, Greenberg, & Holekamp, 2005) observed that in most disputes, the aggressor was the more dominant individual. As such, support from conspecifics was usually directed toward the more dominant individual, possibly confirming a "join the aggressor" rule of thumb, rather than specific knowledge of an individual's relative rank. However, in a minority of cases, when a subordinate attacked the dominant, joiners also supported the dominant, suggesting knowledge of the relative rank of each individual (Engh et al., 2005).

After disputes, hyenas (Engh et al., 2005) and primates (Tomasello & Call, 1997) are more likely to redirect their aggression toward relatives of a former opponent rather than other low-ranking individuals. This suggests a knowledge of kinship, dominance, and third-party relationships. However, these findings may be biased because of close proximity of relatives and hence increased interactions. To further test this, Holekamp and colleagues (2007) played back distress calls of hyena pups and found that both mothers and nearby relatives of the calling cubs were more likely to elicit a response than unrelated individuals. Moreover, the dominance rank of the mother also influenced the looking of others. Together, these results provide support for kin, dominance, and third-party recognition in hyenas.

Captive rooks and jackdaws also form long-term alliances with other group members, sometimes irrespective of sex or kinship (Emery, Seed, et al., 2007). Relationships in young rooks and jackdaws are thought to be initiated by food sharing, demonstrated by the unsolicited transfer of food from one individual to another (active giving; de Kort, Emery, & Clayton, 2003), which is considered an essential component of pair formation (von Bayern, de Kort, Clayton, & Emery, 2007). Alliances in corvids and apes are maintained through the use of affiliative behaviors, such as allopreening and grooming, respectively (de Waal & Lutrell, 1988; Emery, Seed, et al., 2007; Seyfarth & Cheney, 1984).

Rooks that form pairs enhance their individual dominance rank compared to those that remain single (Emery, Seed, et al., 2007). Enhanced dominance in turn provides associated benefits such as increased food acquisition. Emery, Seed, and colleagues (2007) also report that rooks are sensitive to third-party relationships, as they redirect aggression to the partner of an individual that they have received aggression from. Furthermore, rooks engage in third-party affiliation with their partner (i.e., bill twining) after conflicts with other group members, however, unlike primates, they do not reconcile with former opponents (Seed, Clayton, & Emery, 2007).

Cooperative coalitions are often observed in many social species. Female primates and cetaceans for instance, demonstrate alloparental care—"babysitting" or staying within close proximity to unrelated juveniles (Marino, 2002; Nicolson, 1986). Chimpanzees (Uehara, 1997), bonobos (Hohmann & Fruth, 2008), whales (Hain, Carter, Kraus, Mayo, & Winn, 1982; Jurasz & Jurasz, 1979), and dolphins (Leatherwood, 1975; Wursig & Wursig, 1980) all exhibit cooperative feeding strategies that require coordinated efforts of individuals within a group to capture prey. Male chimpanzees (Watts, 1998; Wrangham, 1999) and bottlenose dolphins (Connor, Smolker, & Richards, 1992) also form cooperative alliances or coalitions for the purposes of intergroup aggression ("warfare") and mate guarding. Recently, brown-necked ravens have been shown to also use cooperative hunting, with individuals taking different roles when hunting large lizards (Yosef & Yosef, 2009).

INNOVATIONS

To accommodate rapid changes in their environment, some animals may behave flexibly by adopting innovative techniques to solve novel problems. Overcoming such challenges may require species to possess advanced cognitive mechanisms to process and manipulate environmental information, resulting in enlarged components of the brain (Dunbar, 1992). Comparing relative brain size with measures of behavioral complexity across species has revealed some of the most compelling evidence linking the evolution of brain and cognition (Lefebvre, Whittle, Lascaris, & Finkelstein, 1997; Lefebvre et al., 2004).

Ethologists have long observed the complex and flexible behaviors performed by animals in the wild, documenting the emergence of novel behaviors and publishing anecdotal reports as short notes in scientific journals. Reports of such innovations have been collated across numerous species and used to produce measures of species' behavioral plasticity (Lefebvre et al., 1997, 2004). Accounts of innovations, in terms of their relative frequencies of occurrence (innovation rates), have been compared across species and found to correlate positively with relative brain size in birds and primates (Lefebvre et al., 1997, 2004), with corvids, parrots, and apes at the forefront of innovative groups (Seed et al., 2009). Similar relationships between the observed frequency of tool use in birds and relative brain size have also been identified (using the same method of collating anecdotes; Lefebvre et al., 2002). Likewise, the relative size of the "executive brain" (neocortex and striatum) in primates has been found to correlate positively with the number of reports of innovation and tool use in primates (Reader & Laland, 2002).

Psychological Similarities

SOCIAL REASONING

Sociality is thought to have played an important role in the evolution of intelligence (Byrne & Whiten, 1988; Dunbar, 1998; Humphrey, 1976; Jolly, 1966). As such, individuals within a group may gain a competitive advantage (and fitness benefits) through the use of social cognition (Humphry, 1976). It has, thus, been proposed that the recognition of other group members as intentional agents, which possess individual beliefs and desires, independent of one's own, provide the basis for complex social interactions (Tomasello & Call, 1997).

Terms such as "chimpanzee politics" have been used to describe the sophisticated social interactions of primates (de Waal, 1982), especially involving cooperation, alliance formation, social maneuvering, manipulation, and deception. However, such complex "political" interactions may not be restricted to primates, because similar behaviors have also been observed in numerous species such as corvids (Emery, Seed, et al., 2007), cetaceans (Marino, 2002), and hyenas (Holekamp et al., 2007). Evidence from such a wide variety of distantly related species further supports the theory of an evolutionary convergence of social cognition.

One of the consequences of social living is that individuals within a group are likely to forage in the same areas for the same resources, thus resulting in direct competition. For instance, chimpanzees naturally compete over food (Tomasello & Call, 1997), although in certain circumstances food sharing does occur: from mother to infant, or when close associates share prey that cannot be monopolized by any one individual, such as a monkey killed during a cooperative hunt (Uehara, 1997).

Often resources may be irregularly distributed and found in aggregated patches. Hence, when foraging in a group, it may be advantageous for individuals to be vigilant of where other group members are successfully locating food. Likewise, competition may pose risks of food theft or displacement from abundant food supplies by more dominant individuals. Thus, animals that know what conspecifics can and cannot see may benefit by using this knowledge in food competition situations.

Hare and colleagues (Hare, Call, Agnetta, & Tomasello, 2000) tested this theory by presenting chimpanzees with two pieces of food placed in an arena; the subordinate chimp could see both pieces of food, whereas the dominant chimp could see only one. Because dominant chimpanzees monopolize resources, the only way for the subordinate to gain any of the food was to obtain the food that the dominant could not see. When released into the arena, subordinates typically adopted this strategy, however, there are some discrepancies in the interpretation of these results (see Karin-D'Arcy & Povinelli, 2002).

A series of controls that allowed subordinates a head start in retrieving the food further revealed that subordinates were not responding to the approach behavior or gaze direction of the dominants (Hare et al., 2000). This suggests that the subordinate's decision about which piece of food to obtain was dictated by their understanding of what the dominant could or could not see. However, an alternative explanation is that the subordinates based their decision of where to forage on their memory of where the dominant was looking before the barrier was raised (i.e., where the dominant was looking before they made an approach movement; Povinelli & Vonk, 2004).

In subsequent experiments, Hare and colleagues (Hare, Call, & Tomasello, 2001) further investigated what chimpanzees know about what others know (i.e., what others have and have not seen in the immediate past), by manipulating (1) whether a dominant individual could see where the food was hidden, (2) misinforming the dominant's knowledge, and (3) replacing informed dominants with uninformed dominants. The findings of this study suggest that chimpanzees can recall what another conspecific had and had not seen in the immediate past, and attribute specific knowledge of events to particular individuals (Hare et al., 2001). Although widely cited, this study is not without its critics who suggest that the chimpanzees' behavior does not have to be the result of mental attribution; rather, it only needs to be based on sophisticated behavior-reading (Emery & Clayton, 2009a; Karin-D'Arcy & Povinelli, 2002; Povinelli & Vonk, 2004).

Other examples of conspecific perspective taking and knowledge attribution are illustrated in experiments on food-caching corvids. Many birds and mammals hide food for future consumption (Vander Wall, 1990). However, storing food poses the risk of theft, especially if the storer cannot defend their caches. In species that forage in social groups, theft from conspecifics may be particularly accentuated. Corvids, for example, have an excellent observational spatial memory and observe one a nother's caching behavior to accurately locate others' stores and pilfer their contents at a later time (Bednekoff & Balda, 1996a, 1996b; Bugnyar & Kotrschal, 2002; Clayton et al., 2001), even if caches were made from a completely different perspective (Watanabe & Clayton, 2007). As such, corvids have evolved numerous strategies to reduce the probability of their caches being stolen by others (Dally, Clayton, & Emery, 2006). Corvids readily cache in lab aviaries, basing their caching decisions on the presence or absence of conspecifics (Emery & Clayton, 2001). Under solitary conditions, birds do not apply cache-protection strategies. However, when conspecifics are present, birds attempt to reduce the amount of information available to observers by caching in places that are either difficult for the observer to see (i.e., further away or behind barriers; Dally, Emery, & Clayton, 2005) or where the information of cache location is visually degraded (i.e., in dark places; Dally, Emery, & Clayton, 2004). Storers also move their caches from locations observed by potential thieves to places unbeknown to thieves, and they appreciate that different individuals have seen different events. Whether these differences are based on different knowledge states (i.e., knowledgeable or ignorant) is debatable (Emery & Clayton, 2008). Similar studies have also revealed that ravens can discriminate between human and conspecific competitors based on differences in the information they have been given access to (Bugnyar & Heinrich, 2005). Although studies on cache-protection strategies in corvids reveal similar findings to studies on food competition in chimpanzees, both groups, for example, appear to appreciate the perspectives of others, and it remains unclear whether such findings are based on reading the behavior of others or reading their mental states.

The strongest cue representing what others see and where others are looking is the direction of their eye gaze. Perceiving such a cue may be particularly valuable for social species with immediate adaptive benefits, such as locating food sources, predators, and mating partners. Although primatologists in the field have long suspected that primates respond to the presence of gaze cues in conspecifics (Emery, 2000), Emery and colleagues (Emery, Lorincz, Perrett, Oram, & Baker, 1997) were the first to experimentally test this behavior in the context of gaze following. They found that captive rhesus monkeys reliably followed the gaze direction of conspecifics toward target objects, ignoring distractors of the same object. The extent to which nonhuman species utilize gaze cues to locate food or infer mental states, rather than following gaze, is controversial (Emery & Clayton, 2009a). It is clear that both corvids and apes follow the gazes of a human experimenter, but they also reposition themselves to follow the experimenter's gaze around a visual barrier (Brauer, Call, & Tomasello, 2005; Bugnyar, Stowe, & Heinrich, 2004; Schloegl, Kotrschal, & Bugnyar, 2007).

Another common paradigm to test whether animals understand that gaze cues can refer to objects outside of view is the object-choice task. In this test, animals have to use experimenter-given social cues, such as pointing and gaze, to locate food hidden under one of two containers. Success varies across species; apes often perform inconsistently (Call, Hare, & Tomasello, 1998; Call, Agnetta, & Tomasello, 2000), African grey parrots rapidly learn to attend to some experimenter cues, but in most cases they did not do so spontaneously (Giret, Miklosi, Kreutzer, & Bovet, 2009), whereas jackdaws use cues that serve a communicative function in humans (von Bayern & Emery, 2009). Perhaps surprisingly, domesticated species, such as goats and dogs, have had more success than primates (Hare, Brown, Williamson, & Tomasello, 2002; Kaminski, Riedel, Call, & Tomasello, 2005, but see Emery and Clayton, 2009a, Miklosi and Soproni, 2006).

TACTICAL DECEPTION

Species that forage in social groups share direct competition over access to resources. Selection is, thus, thought to favor individuals that can mitigate these costs by using social knowledge as a means to employ socially manipulative tactics. Hence, the *social intelligence*, *social brain,* and *Machiavellian intelligence hypotheses,* link the cognitive demands of social living with the evolution of enhanced social skills and increases in brain size (Byrne and Whiten, 1988; Dunbar, 1998, 1992; Humphrey, 1976).

Tactical deception (TD) has been used to describe how individuals psychologically manipulate the behavior of others within a social group (Byrne & Whiten, 1985). Behaviors suggested to represent such psychological manipulations have been reported for numerous primate species, but they are anecdotal in nature and not replicable, so their utility as a source of information on social cognition is questionable (Whiten & Byrne, 1988). Interestingly, however, the number of records of tactical deception correlates significantly with neocortex size in primates (Byrne & Corp, 2004). This relationship remains when group size is accounted for, eliminating concerns that larger groups present more opportunities for deception. Furthermore, this relationship is also consistent with the idea that cognitive problem solving is constrained by neocortex size, supporting the link between the evolution of the neocortex and increased complexity of social living (Byrne and Whiten, 1988; Dunbar, 1998; Humphrey, 1976). However, it is not clear whether such behaviors, if they exist, are unique to primates; comparable studies on other species have not focused on their intelligence in the wild. Studies on birds, for example, far exceed those on primates (certainly in terms of the number of observation hours recorded and the number of species studied), but no field study has yet, to the best of our knowledge, focused on questions of cognition (social or physical). It is, therefore, less likely that such reports of novel social behavior would be reported for nonprimate species.

This does not mean that we have no comparable data on tactical deception in birds. One potential example is the cache-protection behavior of food-storing corvids. Strategies such as making false caches (stones, small objects; Clayton, Griffiths, & Bennett, 1996; Heinrich, 1999), as well as going through the actions of caching but without depositing any items (Heinrich, 1999) could be classified as examples of tactical deception as defined by Byrne and Whiten (1988). It has been suggested that corvids cache inedible objects in view of conspecifics, to learn about others' pilfering intentions or pilfering techniques. To test this, Bugnyar and colleagues (Bugnyar, Schwab, Schloegl, Kotrschal, & Heinrich, 2007) allowed ravens to cache plastic objects in front of either a pilfering (P) bird or an onlooker (O) human. After caching, P always stole the ravens' caches, whereas O inspected the objects but never stole them. The ravens were then allowed to cache food; again in front of P or O. Ravens that had experienced the P condition cached food more quickly, hid food behind obstructions, and made more of an effort to conceal their stores than those in the O condition. However, this pattern was not repeated with objects, suggesting that the caching of inedible objects might be used as a deceptive tool to learn about an individual's propensity to steal food (Bugnyar et al., 2007).

Another potential example of tactical deception is moving caches between cache sites in front of an observer (Emery & Clayton, 2008). If jays had cached items in specific locations in front of a specific observer and then retrieved these caches in front of the same or a different observer, they recovered only those items that the observer had seen being cached and left the other unknown caches alone. The caches that were recovered tended to be moved around multiple times and were not necessarily left in the last cache site that the jay made a bill probe into (Dally, Emery, & Clayton, 2006). This suggests that the caching jays may have been deceiving the observers about the final location of the cache.

PHYSICAL REASONING

It is a long-held assumption that species that employ the use of tools to aid in procuring food from inaccessible areas have greater intelligence, especially in terms of physical cognition, than those species that do not use tools (Emery & Clayton, 2009b). Although chimpanzees use a variety of tools in the wild, there is little evidence that they necessarily understand how the tools that they use work (Povinelli, 2000). Indeed, there is also good evidence that chimpanzees perform better on physical tasks when they do not have to use a tool, compared to versions of the same task requiring tool use (Seed, Call, et al., 2009). There is also substantial evidence that the physical cognition of non-tool-using animals is not fundamentally different to that of tool-using animals (Emery & Clayton, 2009b).

Although there does not appear to be a striking cognitive difference between tool users and nontool users, there are differences between species. Studies on corvids and apes have found a shared aptitude for folk physics or understanding the functional properties of tools. Using similar test paradigms, corvids and apes both demonstrate the ability to select, modify, and manufacture tools according to the specific demands of a given problem. New Caledonian crows (NCC) and rooks spontaneously select tools of a certain size or length to access concealed food items (crows, Chappell and Kacelnik, 2002, 2004; rooks, Bird and Emery, 2009a) as well as manufacture tools with respect to the functional requirements of retrieval tasks (crows, Weir, Chappell, & Kacelnik, 2002; rooks, Bird and Emery, 2009a). Similarly, gorillas and orangutans are capable of selecting tools with properties relevant to specific tasks (Mulcahy, Call, & Dunbar, 2005).

New Caledonian crows (Taylor, Hunt, Holzhaider, & Gray, 2007; Taylor, Elliffe, Hunt, & Gray, 2010), rooks (Bird & Emery, 2009a), gorillas, and orangutans (Mulcahy et al., 2005) are also capable of sequential tool use (i.e., using a small tool to acquire a larger tool suitable for accessing food). Such tasks are thought to present additional cognitive challenges to that of regular tool use, because they require hierarchical forethought. Accordingly, the related metatool use or use of one tool to shape another into a better tool (e.g., stone-knapping) represents an important breakthrough in hominid evolution (St Amant & Horton, 2008). Although corvids and great apes rapidly accomplish sequential tool tasks, monkeys have had limited success, often persistently attempting to retrieve a food reward directly with an inadequate tool (Hihara, Obayashi, Tanaka, & Iriki, 2003, Santos, Rosati, Sproul, Spaulding, & Hauser, 2005). Corvids and apes, however, demonstrate an advanced ability to manage their primary inhibitions and organize their behaviors in a hierarchical fashion (Taylor et al., 2007).

Corvids and apes also demonstrate the ability to change the form of one object to manufacture a tool (such as break side twigs off a branch to make a straight stick) or shape and manipulate materials to make them into better tools (such as sculpting the end of a broken-off branch into a hook tool). One apparent difference between corvids and apes is the ability of both NCC and rooks to manipulate a seemingly nonfunctional (in the context of the experiment) novel material (metal wire) into a new functional tool (a hook), which could then be used to pull up a bucket containing food located in a vertical tube (Bird & Emery, 2009a; Weir et al., 2002). Such behaviors suggest that these two species of corvids understood that, to retrieve the food, they had to (1) pull the bucket upward to remove the food from the well, (2) recognize the inadequacies of the available tool (straight wire instead of a hook), and (3) identify the malleable properties of the wire (which could be fashioned into a hook; Emery, 2006). What is perhaps most striking is that rooks do not use tools in the wild, so they must have formed a mental image of a successful hook tool (which they had used in a previous study and which was completely different in shape and structure to the available materials in the latter task) and modified the novel material into a hook based on this mental image. Rooks (Bird & Emery, 2009b) and orangutans (Mendes, Hanus, & Call, 2007) have also demonstrated innovative flexibility when faced with a similar problem based on an Aesop's fable in which food was located inside a vertical tube without a bucket. Both species spontaneously solved the problem. In the case of the rooks, some water was contained inside the tube, so the rooks dropped stones into the tube to raise the level of the water and thus bring the food into reach. In the case of the orangutans, the tube contained no water, so the apes spat water into the tube, so that the food could float to within reach.

Extractive foraging and tool-using behavior have thus been considered important mechanisms for driving the evolution of primate intelligence (Byrne, 1996, 2004; van Schaik, Deaner, & Merrill, 1999). Further support is also found in the relationship between relative brain size and the amount of reported tool use in primates (Reader & Laland, 2002) and birds (Lefebvre et al., 2002). However, the sophisticated understanding of the physical properties of tools demonstrated by non-tool-using species, such as rooks (Bird & Emery, 2009a, 2009b), suggests the possibility of a domain-general cognitive toolkit, rather than domain-specific adaptive specializations that have evolved to solve specific tool-related problems (Bird & Emery, 2009a, Emery & Clayton, 2009b). Such findings question previous accounts that correlate physical intelligence specifically with tool use.

MENTAL TIME TRAVEL

Mental time travel (MTT) is the ability to recall subjective experiences and project oneself into the past or future to re-experience or pre-experience specific events. However, the unique component of such an episodic form of cognition, be it episodic memory or future thinking, in contrast to semantic knowledge, is that its utility invokes individual perspectives that are detached from current mental states (Clayton & Russell 2009; Raby & Clayton, chapter 12 of this volume).

Although MTT is a feature of human cognition (Suddendorf & Corballis, 2008), recent work has challenged the view that it is uniquely human (Raby & Clayton, chapter 12 of this volume). To do so, one must develop criteria that tap the behavioral elements of episodic cognition, given that it is impossible to test the phenomenological aspects of re- and pre-experience in the absence of any agreed behavioral markers of consciousness in nonlinguistic animals. Clayton and Dickinson (1998), therefore, suggested that one could test whether an animal could remember the what, where, and when of a specific event, and termed this "episodic-like" memory. Hence descriptions of MTT in nonverbal animals are often referred to as *episodic-like* or *what-where-when* (WWW) memory.

A number of studies have subsequently shown that this form of MTT, or WWW memory, is present in a variety of nonhuman animals, including corvids (Clayton & Dickinson, 1998; Zinkivskay, Nazir, & Smulders, 2009), chickadees (Feeney, Roberts, & Sherry, 2009), apes (Martin-Ordas, Haun, & Call, 2010) and rats (Babb & Crystal, 2006a, 2006b). Subsequently, it has also been found that animals can take action now for the future, suggesting that they also have the prospective component of MTT (for example, Correia, Dickinson, & Clayton, 2007; Mulcahy & Call, 2006; Osvath, 2009; Osvath & Osvath, 2008; Raby, Alexis, Dickinson, & Clayton, 2007).

Possibly the most convincing evidence for MTT in nonhuman animals has been documented for corvids and apes. Capitalizing on their natural propensity to cache food, detailed experiments on Western scrub jays have revealed that they understand what items of food they stored, where they stored them, and when these items were stored (Clayton & Dickinson, 1998). Clayton and Dickinson (1998) presented jays with the opportunity to cache perishable wax worms and nonperishable peanuts. Following caching, the jays were subjected to two experimental conditions of either a short delay prior to retrieval (4 hrs) or a long delay (124 hrs). After a short delay, jays preferentially searched for wax worms, which were favored over peanuts. However, after experiencing a long delay, in which the worms had decayed and become inedible, jays avoided searching for the worms and instead recovered peanuts. The preferential recovery of particular food items, depending on when they were cached, suggests that the jays used an episodic-like memory to recall past experiences about the degradation rates of different food types, as well as where and when each item of food was stored.

Further experiments have revealed that jays' caching decisions are constructed from anticipating their future needs, irrespective of their current motivational states (Correia et al., 2007; Raby et al., 2007). Raby and colleagues (2007) housed jays in one of two separate rooms over six alternative days. In one room, they were always given breakfast and in the other they were not. After this training period, the jays were unexpectedly given food to eat and cache in the evening. Raby and colleagues (2007) found that the jays stored more food in the nonbreakfast room, where they could expect to be hungry the following morning, compared to the room where breakfast was provided. In a second "breakfast-choice" experiment, Raby and colleagues (2007) controlled for any conditioning that may have influenced caching in places associated with hunger by always providing breakfast in each room. However, in this experiment, each room was associated with a particular type of food (i.e., dog kibble or peanuts). If the jays based their caching decisions on a conditioned response, formed from associating a particular room with a particular food, they would be predicted to cache dog kibble in the room previously associated with dog kibble and vice versa. However, jays in this experiment cached more of the different food rather than the same food in each room, suggesting that they preferred a choice of food at breakfast and were capable of forward planning (Raby et al., 2007).

Using a similar methodology to Clayton and Dickinson (1998), but with preferred perishable (because it was frozen and could melt) juice and less preferred, but nonperishable grapes, Martin-Ordas and colleagues (2010) recently found that chimpanzees, orangutans and bonobos were capable of distinguishing between different events in which the same food items were hidden in different places at different times, suggesting that the apes also remembered in an integrated fashion what, where and when certain events occurred (Martin-Ordas et al., 2010).

Likewise, Mulcahy and Call (2006), found that apes are capable of selecting, transporting, and saving a suitable tool, not because they currently needed it, but because they would need it in the future. Apes learned to use a tool to obtain a reward from an apparatus. In a separate testing room with no apparatus, the apes were then provided with a choice of one out of two suitable and six unsuitable tools. The subjects then experienced either a 1- or 14-hour delay after which they were allowed to return to the test room, with their selected tool, to access the apparatus. The apes succeeded in selecting and retaining appropriate tools for future use (Mulcahy & Call, 2006). Similar results were also found in studies that increased the cognitive load of subjects by disassociating the locations of the tool and apparatus as well as increasing the delay period and housing subjects socially instead of individually (Osvath & Osvath, 2008).

Welcome to the Clever Club

Although we have primarily restricted our arguments to corvids and apes, we have included examples from other animals where appropriate. Indeed, there is

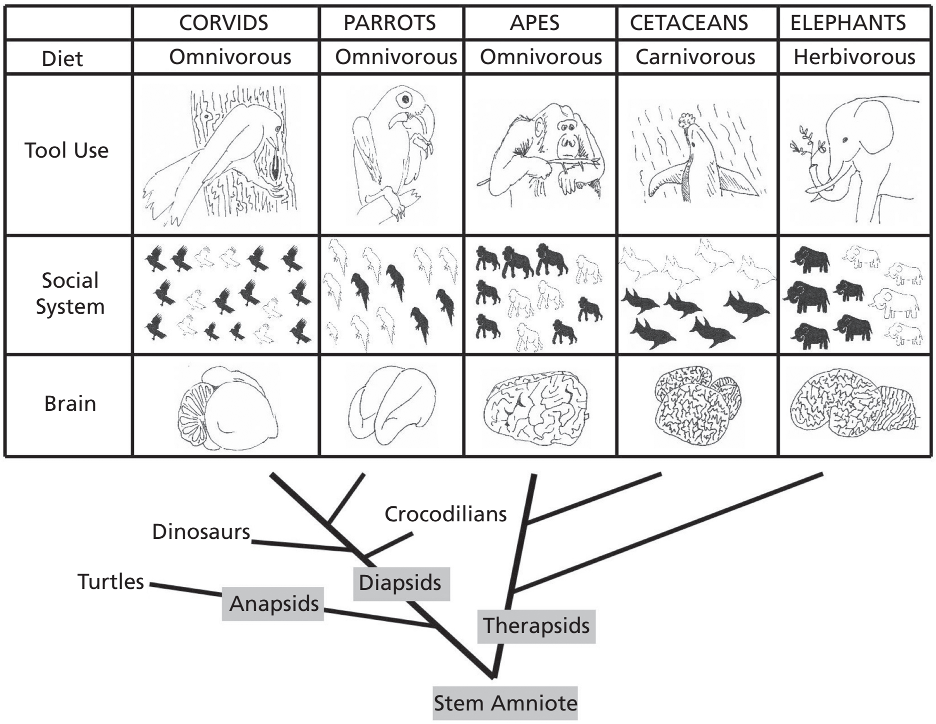

Figure 5.3 *Upper*. Diagram displaying various biological (brain structure), ecological (diet), and behavioral (tool use [stick use by New Caledonian crows, wood- tool aid to opening palm nuts in hyacinth macaws, termite fishing in chimpanzees, sponge-tool use by dolphins, fly switching by elephants]), and social-system (black and white figures represent different individuals within a social group and so the variety of individuals suggest social complexity) traits in corvids, parrots, apes, cetaceans, and elephants. Despite very different brain structures, such as the lack of cortical folding in birds but extensive folding in apes, cetaceans, and elephants, there are striking similarities in the diet, use of tools, and social system, in these distantly related animal groups. *Lower*. Basic evolutionary tree displaying the relationships between these main animal groups.

good evidence that cetaceans (whales and dolphins) also demonstrate convergent evolution of cognition with apes (Marino, 2002). We could extend the invitation to parrots; possibly other groups of birds with relatively large brains, behavioral flexibility, and a complex diet, such as hornbills and some birds of prey; elephants; and pack-hunting carnivores, such as hyenas (see Emery, 2006). We would not extend the invitation to domestic dogs because their cognitive abilities, impressive as they are (Miklosi, 2007) cannot be an example of convergence, because their cognitive evolution is likely the result of domestication by humans, rather than a response to socio-ecological selection pressures in their adaptive environment. Domestication thus seems to be the most appropriate hypothesis to explain dogs' intelligence, especially in the social realm (but see Miklosi & Topal, chapter 11 of this volume).

If our hypothesis is correct, that shared cognitive traits have arisen in distantly related groups such as corvids and apes because they have solved similar environmental problems, then we should expect groups that have faced similar problems to have evolved similar solutions to these problems. This could be in the form of complex behavioral strategies or cognitive processes. Based on a simple analysis of such problems and similar life-history traits, Emery (2006) found that many animal groups displayed similar traits at the biological, ecological, behavioral and psychological levels (Figure 5.3). Underlying all of these similarities is behavioral flexibility as applied to the solution of problems faced by living in an unpredictable environment (Sterleny, 2003). As such, those species with a varied, ephemeral, and even unpredictable diet, that lived in a complex (but not necessarily large) society, that had a relatively large brain, went through a long developmental period, lived a long life, and lived in a fluctuating habitat, could all be considered candidates for convergent evolution.

Conclusion

It is likely that there is no one particular mechanism that is responsible for driving the evolution of cognition across all species. Cognition is, instead, likely to have evolved as a result of the many challenges animals face in their environments. Group living may have provided a foundation for social cognition and, hence, social cooperation and manipulation, but qualitative relationships in the form of monogamous pair bonds or the arms race between cachers and pilferers may have also been important. Similarly, methods for manipulating the environment, such as building a nest or extractive foraging (with or without tool use) may have provided the foundation for physical cognition. Although still not clear, it seems probable that neither the social or physical realm alone drove the evolution of intelligence. Rather, the ability to adapt to a changing environment, as encountered by the species under consideration here, is perhaps the best explanation we have for why some animals display the cognitive abilities they do and why such abilities have evolved convergently in very distantly related groups.

Future Directions

1. Are the behavioral similarities of corvids and apes (and other animals) based on a similar cognitive architecture? How can this be investigated empirically?
2. What features of the social and physical environment may have driven cognitive convergence in corvids, apes, and other animal groups, such as parrots, cetaceans, and elephants?
3. How do convergences in cognition occur with divergences in neural structures?

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