

7 CANNY CORVIDS AND POLITICAL PRIMATES

A Case for Convergent Evolution in Intelligence

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If men had wings and bore black feathers,
few of them would be clever enough to be crows.

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In the latter half of the nineteenth century, Charles Darwin suggested that mental characteristics are subject to natural selection in much the same way as morphological traits, and, thus, we would expect some characteristics of human intelligence to be present in other descendants of our primate lineage (Darwin 1872). By mental characteristics, we mean more than just the ability to learn and remember. For the purposes of this chapter, intelligence refers to the ability to think, reason, and solve novel problems. Specifically, intelligent beings can think not only about the here-and-now, but they can also reminisce about their past and plan for their future (so-called “mental time travel”). They can also think about what others might be thinking and how this might be different to what

they themselves think (theory of mind). Furthermore, intelligent beings should be capable of devising novel solutions to problems, such as the manufacture of special tools to acquire otherwise unobtainable foods.

Presumably, the development of these mental characteristics confers some reproductive advantage, especially for long-lived animals that require a sophisticated appreciation of their physical and social world in order to survive the trials and tribulations of life. Indeed, a number of hypotheses has been proposed to account for the enhanced intellectual capacities of primates, and these broadly fall into two categories: physical and social. Milton (1981) has argued one physical challenge that primates face is to monitor the availability of fruits and other widely dispersed, ephemeral, high-quality foods; and to do this efficiently, they should remember which foods are where and how ripe they are now, in order to predict when they will be ripe. In addition to spatiotemporal mapping, there may other physical challenges associated with foraging, particularly extractive foraging, which may require tools to be manufactured and used for such purposes (Parker and Gibson 1977, Byrne 1997).

However, Jolly (1966) and Humphrey (1976) independently proposed an alternative hypothesis for the evolution of primate intelligence, namely, that it is the ability to survive the political dynamics of a complex social world that has been the primary driving force shaping primate intelligence. This “social function of intellect” hypothesis states that the complexities of social life have led to an increase in general intelligence, and Dunbar (1992) has further suggested this also leads to a dramatic increase in the relative size of the neocortex during primate evolution. It is certainly plausible to argue that surviving the trials and tribulations of a complex social world makes intellectual demands on many primates. Individuals need to know who is who, they need to keep track of who did what to whom, where and when, and to use this information to predict the actions and intentions of other individuals in their social network, as well as understanding how these relationships change over time (Barrett et al 2003). In short, the need for effective competition and cooperation with conspecifics may have provided the main selective advantage for the evolution of primate intelligence (Byrne and Whiten 1988, Dunbar 1998).

That said, there is no reason to assume that intelligence is restricted to primates or that such abilities have evolved only once. Indeed, we shall

argue that there is good reason to believe that complex mental characteristics have evolved several times and that the existence of intelligence in different, distantly related lineages must have arisen as a result of convergent evolution in species facing similar social and physical problems. By definition, *convergence* refers to similarities between groups that arise as a result of adaptation to similar selection pressures, not because of phylogenetic relatedness, and the more distantly related the two groups, then the stronger the case for convergence. As Conway Morris (2003) has argued, there are many examples of morphological traits that have evolved multiple times in distantly related lineages. One of the best examples of such evolutionary convergence is the development of the camera eye, which has evolved *de novo* three times: namely, in the vertebrates, in some cephalopods (squid and octopus), and also in one group of marine annelid worms (the alciopids).

With regard to the evolution of intelligence, Marino (2002) has made a convincing case for the convergent evolution of intelligence in the cetaceans (dolphins, whales, and porpoises) and the anthropoid primates (monkeys, apes, and humans). There may be other groups of mammals, such as elephants, that also share these mental characteristics. The fact that these abilities are not found in lineages that are more closely related to the primates—for cetaceans and primates diverged at least sixty-five million years ago—suggests that complex cognition has evolved within the mammals more than once. But perhaps the most dramatic case for convergent evolution of cognition comes from comparing primate cognitive abilities with those of crows, given that the common ancestor of mammals and birds lived over 280 million years ago and that not all birds and mammals share the complex mental abilities found in crows and primates. Indeed, “birds as a whole are a rich source of insights into the prevalence of evolutionary convergence, as well as having some striking similarities with other groups” (Conway Morris 2003, 138).

Why Study Intelligence in Crows?

If one were looking for avian candidates of intelligence, folklore would point toward two groups, the parrots and the crows. Humans have been

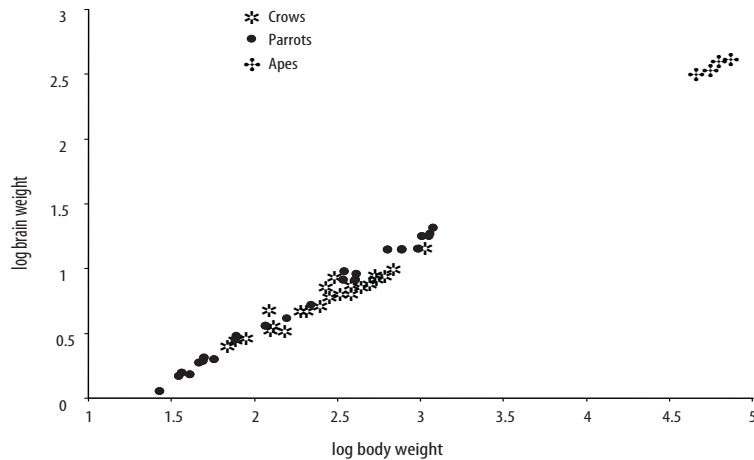
intrigued by the mental abilities of several members of the crow family, which includes jays and ravens, as well crows. Stories of ravens, for example, go back long before the sacred texts of Christianity (Sax 2003). Anecdotes abound, and folklore is rich in examples—from the arms of the Baron von Rindscheit symbolizing the union between the strength of the boar and the wisdom of the crow to the series of Aesop's fables about the canny cleverness of crows. The nature writer David Quammen (1985, 30) claimed that each member of the crow family is "so full of prodigious and quirky behaviour that it cries out for interpretation not by an ornithologist but by a psychiatrist." His theory is that the crows are bored and constantly up to mischief, too clever for their own good, like very bright children!

There are a number of scientific reasons for believing that these animals are very intelligent. Like primates, crows are particularly good at solving laboratory tasks that rely on the ability to abstract a general rule to solve the task and transfer the general rule to new tasks, whereas pigeons show no evidence of abstraction and instead rely on simple rote learning (Wilson et al 1985, Mackintosh 1988). Unfortunately, parrots have not been tested on these tasks, so we do not know whether parrots are also capable of abstraction.

Another similarity is that both the primates and the crows and parrots have very large brains relative to body size (Emery and Clayton 2004a). Although there is some variation in relative brain size between different crow species (Voronov et al. 1994), they all have very large brains relative to all other families of birds (Rehkamper et al 1991). This is also the case for parrots, and some highly social species such as the African grey and various macaws have very large brains relative to body size (Iwaniuk et al 2005; see also Portmann 1947, Burish et al 2004). Figure 1 shows that the relative forebrain size of corvids and parrots is as large as that of the non-human apes.

It is important to note that the structural organization of the brains of birds and mammals is very different and that they evolved from different reptilian ancestors. For example, avian brains have a nuclear structure, whereas mammalian ones have a laminar arrangement (see Emery and Clayton, 2005, for a recent review). In terms of the neural bases for intelligence, one of the key differences is that birds do not have a cortex,

Figure 1. A regression of log brain weight and log body weight for various species of crow, parrot, and ape. The data for birds were obtained from Iwaniuk and Nelson (2003), while the ape data were taken from Rilling and Insel (1999).



whereas mammals do. In both human and nonhuman primates, it is one specific region of the cortex, namely, the prefrontal cortex, that is thought to play a critical role in thinking. Although birds do not have a prefrontal cortex, the nidopallium caudolaterale (formerly, the neostriatum caudolaterale; Reiner et al 2004) appears to be functionally equivalent (Mogensen and Divac 1982, Reiner 1986), and the volume of this brain region correlates with some measures of intelligence such as tool use (Lefebvre et al 2002) and innovation rate as measured by reported frequencies of novel behavior patterns (Lefebvre et al 1997). Furthermore, crows have the largest neostriatum, relative to overall brain and body size, of any group of birds (Emery and Clayton 2004a). This large expansion of the crow neostriatum mirrors the increase in size of the prefrontal cortex in great apes (Semendeferi et al. 2002).

Another feature crows have in common with primates is that they are long lived, with an extensive developmental period in which they are dependent on their parents, which allows them ample opportunities to learn various essential skills for later life (Iwaniuk and Nelson 2003, Clayton and Emery, 2007). Many species of the crow family also live in com-

plex social groups. For example, in the cooperatively breeding Florida scrub-jay, several closely related family members share the responsibility of raising the young with the parents. Furthermore, rooks congregate in large colonies, where juveniles associate with many nonrelatives as well as kin. In both cases, however, this long developmental period provides increased opportunities for learning from many different group members (Emery et al 2007).

For all these reasons, Emery and Clayton (2004b) have argued that the social complexity of some crows is comparable to that of chimpanzees and that these two very distantly related families face similar challenges. Following Emery and Clayton (2004b), we shall argue that some members of the crow family possess intellectual abilities that are not only similar to some primates but are on a par with the great apes.

Evidence for Convergent Evolution of Intelligence in Crows and Primates

One feature of human intelligence is the ability to reminisce about the past (episodic memory) and plan for the future. Suddendorf and Corballis (1997, in press) have argued that such mental time travel is unique to humans, and, thus, animals are incapable of mentally travelling backwards in time to recollect specific past events about what happened where and when or forward to anticipate future needs. However, recent experiments in crows question this assumption by showing that one species of crow, the Western scrub-jay, can recall previous caching episodes. By *caching*, we mean that these birds hide food for future consumption and rely on memory to recover their hidden caches of food at a later date. In a series of experiments, we have shown that these birds form integrated memories of what they cached and where and when they hid it (Clayton and Dickinson 1998, Clayton, Yu, and Dickinson 2003) and that they can also keep track of who was watching when they hid particular caches and return to protect those caches appropriately at a later date (Dally et al 2006). The jays are also capable of prospective cognition, adjusting their caching behavior in anticipation of future needs as opposed to current ones (Clayton, Yu, and Dickinson 2003; Clayton et al 2005; Correia et al 2007; de Kort et al, 2007; Raby et al 2007). The ability to remember the “what-

where-and-when” of a particular episode has not yet been demonstrated in nonhuman primates. The “when” component of these personal past experiences is critical. Although multiple events can occur at the same time, you can experience only one at any given moment in time. In short, you may recall two episodes that share the same “where” or “what,” but they will not share the same “when” (Clayton, Bussey, and Dickinson 2003).

A second feature of intelligence is the ability to understand and reason about the minds of other individuals and, thus, to think about what others might be thinking (theory of mind). There has been much debate about the question of whether any animal has theory of mind, in part because humans rely on language to assess these sorts of abilities. In humans, it has been suggested that the most unequivocal evidence for theory of mind lies in demonstrating that the subject can understand that another individual may have different beliefs about the world. An individual that had theory of mind could practice *tactical deception*, the intentional manipulation of another’s beliefs leading to him or her to think something contrary to the truth (Byrne and Whiten 1988). The trouble with any apparent demonstration is that it is difficult to establish that the deceiver is not simply attempting to manipulate another individual’s behaviour rather than his or her beliefs. A second property of theory of mind is *experience projection*, the ability to use your own experience to predict another individual’s future behavior, in relation to your own. This ability has been tested only once in animals so far: in scrub-jays, not apes.

In a series of experiments, we tested whether the birds could adjust their caching strategies to minimize potential stealing by other birds, for example, by moving the food to new hiding places when other birds were not watching (Emery and Clayton 2001). Scrub jays that had prior experience of stealing another bird’s caches did move the food to new hiding places, but only if they had been observed by another bird at the time of caching and were then given the opportunity to recover and recache their food in private. If they had hidden their caches in private, however, they did not recache the food in new places when given the chance to recover them in private. One important point is that recaching is not dependent on the presence of the potential thief because the birds are always alone (in private) at the time of recovery. In order to know whether to recache, the bird must remember whether another bird was present at the time of

caching. The dramatic finding was that this behavior depended on prior experience of being a thief. Jays without this experience of stealing another bird's caches did not move the caches to new places, even though they had watched other jays caching food. These results suggest that the ability to move the caches and rehide them in new sites unbeknown to the observer depends upon the previous experience of having stolen food cached by other jays, as well as on remembering whether another bird was watching them cache the food in the first place. The inference is that scrub-jays can remember not only the social context of caching (presence or absence of another bird) but can also relate information about their previous experience as a thief to the possibility of future stealing by another bird to modify their caching strategy accordingly. Other experiments on the cache protection tactics of both the scrub-jays and another fellow corvid, the raven, suggest that these birds have a complex understanding of social cognition (e.g., Bugnyar and Kotrschal 2002, Bugnyar and Heinrich 2005, Dally et al 2004, 2005, 2006).

Another classic feature of intelligence is problem solving. Indeed, we argued that intelligent beings should be capable of devising novel solutions to problems and that one of the most dramatic examples of this is the manufacture of special tools to acquire otherwise unobtainable foods. By tool use, we mean "the external deployment of an unattached environmental object to alter more efficiently the form, position or condition of another object" (Beck 1980, 10), and this is differentiated from tool manufacture, which refers to "any modification of an object by the user or conspecific so that the object serves more effectively as a tool" (Beck 1980, 11).

The New Caledonian crow is extraordinarily skilled at making and using tools. These birds make different types of tool that have different functions (Hunt 1996). Some tools are made from Pandanus leaves, and these stepped-cut tools are used for probing for prey under leaf detritus. They also make hooked twig tools for poking insect larvae out of tree holes. The same tool may be used in different ways for different jobs; for example, when using the stepped-cut tools, crows make rapid back-and-forth movements for prey under soil, yet they use slow deliberate movements to spear the prey onto sharpened barbs of the leaf when the prey is in a hole (Hunt 2002). Furthermore, crows from different geographical

areas have different designs of tool (Hunt and Gray 2003). The only other animals that display this diversity and flexibility in tool use and manufacture are the great apes. Thus, chimpanzees have been observed to manufacture a range of different tools that are used for specific purposes (Beck 1980), and different geographical populations of chimpanzees use different tools for different uses, suggesting that there may be cultural variations in tool use (Whiten et al 1999). Does this ability imply some understanding of appropriate physical reasoning in these great apes and corvids?

Povinelli (2000) tested chimpanzees' understanding of how tools work, how using tools causes particular outcomes, and how certain objects are connected. He examined whether chimps understood that specific tools could only be used for specific jobs and that some tools were useless due to their physical properties. Surprisingly, his chimps were poor at almost all of the tasks they were presented, even when they were analogues of tool use in the wild. These experiments suggest that, although chimpanzees use tools, they may not understand the physical properties of the tools they are using. Povinelli (2000, 7) concluded that "chimpanzees do not represent abstract causal variables as explanations for why objects interact in the ways that they do."

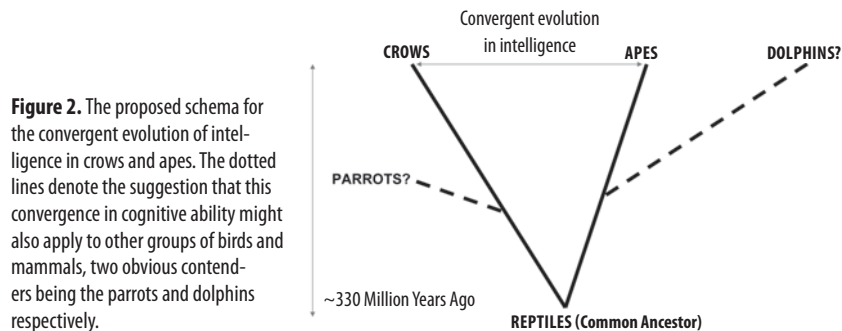
These failures to demonstrate insight into the physical properties of tools are particularly intriguing in the light of some recent laboratory studies with the New Caledonian crows. When presented with a variety of sticks of different lengths and food positioned in a tube such that a stick was required in order to reach the food, the birds correctly chose the appropriate length of stick to push out the piece of food (Chappell and Kacelnik 2002). In a subsequent task, the crows were able to select the right diameter of tool (Chappell and Kacelnik 2004), suggesting that these birds have an advanced level of folk physics. Even more intriguingly, Weir and colleagues (2002) have shown that these tool-using crows can manipulate novel man-made objects to solve a problem. Two crows, Betty and Able, were presented with the problem of reaching food in a bucket that was only accessible by using a hook to pull the bucket up. Unfortunately, Able stole the bent wire and then dropped it somewhere out of Betty's reach. Betty found a piece of straight wire that was lying on the floor, bent this wire into a hook, and used it to lift up the bucket and reach the food! Betty proceeded to do this successfully on nine out of the ten test trials.

Evidence of tool use and manufacture suggests that animals can sometimes combine past experiences to produce novel solutions to problems. However, careful experimentation is required to establish whether the animal can flexibly exploit the tool in a way that suggests it can understand and reason about the causal relations between them. To date, there is no convincing evidence that animals do understand the physics of tools, but the most promising tool-using candidate, the New Caledonian crow, has yet to be tested. There is also recent evidence that one of the non-tool-using species of corvid, the rook, has some understanding of cause-and-effect relations in a modified tool task (Seed et al 2006).

Conclusions and Implications

Much of the research on the evolution of mental characteristics has focused on the large-brained social primates because of their close evolutionary relationship to humans. The common assumption is that intelligence has evolved once within the primate lineage and that the complexities of social life led to an increase in mental abilities and to an expansion of the prefrontal cortex. However, intelligence may have evolved in other lineages of large-brained social animals such as cetaceans. In this chapter, we argue that crows are large-brained social birds with mental abilities that are similar to great apes. As the last common ancestor to corvids and apes lived over 300 million years ago, we suggest that these similarities in intelligence must have developed through a process of convergence, rather than common ancestry (homology), as a result of adaptation to similar selective pressures. Furthermore, we suggest that this process of convergent evolution was driven by the requirement to solve comparable social and ecological problems.

The most recently evolved genera of the crow family (*Corvus*, *Aphelecoma*) and apes (*Pan*) appeared at approximately the same geological time (five-to-ten million years ago). The late Miocene to Pliocene was a period of great environmental and climatic variability. This variability will have influenced food availability. As such, extant crows and apes may have had to adapt strategies for locating food dispersed in time and space, extracting food hidden in cased substrates, and, thus, becoming innovative omniv-



orous generalist foragers. Such conditions will have had an effect on the organization of social groups. These ecological variables have been suggested to have played an important role in the evolution of ape cognition (Potts 2004), and we propose a similar scenario for the evolution of crow cognition. Interestingly, Lefebvre and colleagues found that flexibility in behavior, as measured by innovation rate, correlated with relative brain size in both birds and mammals. Furthermore, the crows and apes displayed similar ratios of innovation rate to relative brain size, with members of the crow family having the highest values for birds and chimpanzees having the highest values for mammals (Lefebvre et al 2004).

Marino (2002, 30) has argued that

Cetacean brains and primate brains represent alternative ways brains can increase in size and complexity and arrive at similar cognitive or even computational capacities. Therefore, this example implies that there may be general principles or “rules” that underlie the evolution of intelligence and that the specific way that a species arrives at a functional solution is not perhaps the only level at which to understand intelligence.

The case for crows (and possibly also for parrots) is even more striking because the anatomical organization of the brain of birds and mammals is so different (Figure 2). Unlike the highly intelligent mammals, birds do not have a prefrontal cortex. We conclude that intelligence in both crows and primates has evolved through a process of divergent brain evolution yet convergent mental evolution (see also Emery and Clayton 2004b).

These findings have important implications for understanding the evolution of intelligence because they suggest that intelligence can evolve in the absence of a prefrontal cortex. Perhaps it only a matter of time until the galaxy of the crows transcends the planet of the apes!

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